

Performance of native tree species planted under nurse trees for dry forest restoration in Puerto Rico

By

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Abstract

Tropical dry forests are the most threatened tropical terrestrial ecosystem. Most of the original dry forest has been converted to agriculture or pastureland. The need to restore these forests is critical, but a lack of specific restoration techniques hinders its progress. This project explored the use of nurse trees to restore dry forests in Puerto Rico. Three plots with 400 native saplings in total were planted under 100 *Leucaena leucocephala* nurse trees at four different planting distances and directions. The planting directions (north, south, east and west) and planting distances (from close to the trunk in the first planting distance to full sun in the fourth distance) were tested for growth, mortality, light environment (assessed as leaf area index) and the variation in leaf morphology of ten native tree species. Leaf area index decreased moving away from the nurse tree, indicating the presence of a light gradient under the nurse trees. However, there was no relationship between leaf area index and growth in either in the planted saplings or the reference plot in a mature forest, indicating that factors other than light are affecting growth. Overall mortality, 37.5%, was low compared to other dry forest and nurse tree restoration projects. Mortality at the Cabo Rojo National Wildlife Refuge was 17.5% greater at full sun in the fourth planting distance, reflecting greater solar radiation and possibly more water soil evaporation, heat loading or photoinhibition. Otherwise, trends in mortality by distance or direction from the nurse tree were species specific. *Erythroxylum areolatum* had a better performance moving away from the nurse tree with 23% lower mortality in the third and fourth planting distances. *Pisonia albida* had only one dead individual at the first planting distance, suggesting improved attainment closer to the nurse tree. *Stahlia monosperma* mortality responded to planting direction, with no dead individuals at the north planting direction. *Bourreria succulenta*, *Stahlia monopserma* and *Trichilia hirta* had no mortality under nurse trees at the Cabo Rojo National Wildlife Refuge. Growth varied by species, with *Erythroxylum areolatum*, *Pisonia albida* and *Trichilia hirta* having 0.13 m or less of growth and *Bursera simaruba*, *Citharexylum fruticosum* and *Tabebuia heterophylla* having an average of 0.28 m of growth or greater. Overall, planting closer to the nurse tree at the first and second planting distances increased growth by 0.10 m, indicating a facilitative effect. However, since leaf area index was not related to growth, then other factors like water availability could be affecting growth. Also, no relationship was found between leaf area index and survivorship with the variation in specific leaf mass or leaf density. For the planted saplings, growth increased as leaf density increased. Greater variation in specific leaf mass and leaf density in dry forest species does not indicate increased growth or survivorship, as has been shown in wetter forest types. The results of this study suggests that using *Leucaena leucocephala* as a nurse tree can be a promising tool for dry forest restoration since they can lower mortality depending on the species and generally increases growth of native saplings when planted closer to the trunk of the nurse tree.

Resumen

Los bosques secos tropicales son los ecosistemas tropicales terrestres más amenazados. La mayor parte del bosque seco original en Puerto Rico se ha convertido a la agricultura o pastoreo. La necesidad de restaurar estos bosques es crítica, pero la falta de técnicas de restauración específicas obstaculiza su progreso. Este proyecto explora el uso de árboles nodrizas o “nurse trees” para restaurar los bosques secos de Puerto Rico. Tres parcelas con 400 árboles nativos fueron sembrados bajo 100 *Leucaena leucocephala* “nurse trees” a cuatro diferentes distancias y direcciones. El crecimiento, mortalidad, índice de área foliar y la variación en la morfología de las hojas de diez especies nativas de árboles fueron estudiadas según la dirección de siembra (norte, sur, este y oeste) y distancia (según el radio de la copa de cada “nurse tree”, desde cerca del tronco en la primera distancia hasta pleno sol en la cuarta distancia). El índice de área foliar disminuyó alejándose del “nurse tree”, indicando la presencia de un gradiente lumínico bajo “nurse trees”. Sin embargo, no se encontró una relación entre el índice de área foliar y el crecimiento de los árboles sembrados o la parcela de referencia en un bosque maduro, lo que indica que otros factores abióticos en lugar de luz deben estar afectando su crecimiento. La mortalidad total, 37.5%, fue baja comparada con otros proyectos de restauración de bosques secos y proyectos con “nurse trees”. La mortalidad en el Refugio Nacional de Vida Silvestre de Cabo Rojo fue 17.5% mayor a pleno sol en la cuarta distancia de siembra, lo que refleja mayor radiación solar y posiblemente mayor evaporación de agua del suelo, mayor carga de calor o fotoinhibición. De otra manera, las tendencias de mortalidad por distancia o dirección desde el “nurse tree” variaron por especies. *Erythroxylum areolatum* mostró 23% menor mortalidad alejándose del “nurse tree” en la tercera y cuarta distancia de siembra, mientras que *Pisonia albida* sólo tuvo un individuo muerto en la primera distancia de siembra. La mortalidad de *Stahlia monosperma* respondió a la dirección de siembra, con ningún individuo muerto en la dirección de siembra norte. La mortalidad de *Bursera simaruba* en el Bosque de Guánica fue 40% mayor en la dirección de siembra oeste. *Bourreria succulenta*, *Stahlia monosperma* y *Trichilia hirta* no tuvieron mortalidad bajo el “nurse tree” en el Refugio Nacional de Vida Silvestre de Cabo Rojo. El crecimiento varió según las especies, con *Erythroxylum areolatum*, *Pisonia albida* y *Trichilia hirta* tuvieron en promedio 0.13 m o menos de crecimiento mientras *Bursera simaruba*, *Citharexylum fruticosum* y *Tabebuia heterophylla* tuvieron un promedio de 0.28 m o mayor de crecimiento. La siembra de árboles nativos en las primeras dos distancias bajo “nurse trees” se obtuvo un mayor crecimiento de 0.10 m, indicando un efecto de facilitación. Sin embargo, como el ambiente lumínico no estaba relacionado con el crecimiento, otros factores, como la disponibilidad de agua podría estar afectando el crecimiento. No se encontró relación entre la variación de masa foliar específica y la densidad de hojas con el índice de área foliar o la supervivencia. En los árboles sembrados, se encontró un mayor crecimiento cuando la densidad de las hojas aumentó. Los resultados de este estudio sugiere que el uso de *Leucaena leucocephala* como un “nurse tree” puede ser una herramienta prometedora para la restauración de bosques secos, ya que pueden reducir la mortalidad según la especie y en general aumentan el crecimiento de especies arbóreas nativas cuando se siembra el árbol más cercano al “nurse tree”. La variación de la masa foliar

específica y la densidad de hojas en las especies del bosque seco no indica un aumento en el crecimiento o la supervivencia, como se ha encontrado en bosques mas húmedos.

Dedication

- To my parents Ana and Antonio for their unconditional love and support.
- To all my family and friends who have been there always.
- To Life. Thank you for everybody and everything in my life; thank you for this wonderful opportunity.
- To myself, because this is the result of my hard work and persistence to never quit.

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CHAPTER 1

INTRODUCTION

Global deforestation has been occurring at the alarming rate of an estimated 130,000 km² per year from 2000-2005 (FAO 2006). Of all forest types, tropical and subtropical dry forests are the most threatened tropical terrestrial ecosystem in the world (Janzen 1988). These forests once occupied 42% of the terrestrial tropics and were the dominant forest ecosystem of the Eastern Caribbean and half of Central America (Murphy and Lugo 1986a). In Puerto Rico, approximately 17.6% of the land area would be covered by subtropical dry forest (Murphy *et al.* 1995), but today dry forests only cover about 4% or 35,407 ha of Puerto Rico's total land area (Gould *et al.* 2008). Most of the original dry forests in the tropics have been eliminated due to the conversion of this ecosystem to agricultural land (Janzen 1988). In Puerto Rico, subsistence farming, logging, grazing by domestic animals, selective logging for charcoal production and fence posts along with industrial development and urbanization, have contributed to the elimination of dry forests (Carvajal 2001, Molina-Colón and Lugo 2006).

Today, the need to restore these forests is critical in light of development pressures. However, the cost of managing planted trees can be very high and large-scale reforestation projects can be very expensive (Lamb *et al.* 2005). Therefore, tree planting for reforestation must be seriously evaluated by land managers before initiation, since monetary and human resources are key elements to consider in establishing a reforestation project. Reforestation projects should only be implemented when natural regeneration has failed and no natural forests exist, or when management goals require different plant species composition. Currently, natural regeneration worldwide restores more forest cover in areas that have been deforested than tree plantations do. From 2000-2005, tree plantations have established an estimated area of 28,000 km² per year, whereas natural regeneration has established an estimated area of 45,000 km² per year, although these figures vary across regions (FAO 2006).

If reforestation is the preferred method over natural regeneration because of a requirement for a particular species composition either for timber, wildlife or restoration purposes, effective techniques are needed to ensure the establishment of the planted trees. Nurse tree reforestation is a type of enrichment planting that can be used as a forest restoration technique where tree saplings can be planted under mature trees that can facilitate establishment by providing shade, nutrient or water to the saplings (Cavieres *et al.* 2006). This technique could be useful in dry forests, which are characterized by having high solar radiation, high temperatures and high evaporation. The discontinuous canopies of dry forests create heterogeneous forest-floor light microenvironments that are susceptible to fluctuations in light intensity during dry periods due to leaf drop (Brown and Ray 1993) which may exacerbate water stress.

Selecting species for planting under nurse trees is a critical step in determining the success of any reforestation project since selecting inadequate species for a particular habitat may result in total mortality of the individuals planted plus losing time, effort and the financial investment. A strategy for this problem can be to relate an ecological performance trait such as growth and survivorship to a plant morphological characteristic and use it as a criterion for species selection in reforestation projects. Variability in leaf mass and leaf density can be used as one of those indicator characters because it can be related to the species ability to adjust to the heterogeneous light environment that saplings will experience during forest succession. In rainforest restoration projects, variability in these leaf traits has resulted in higher growth and survival of the planted saplings (Martínez-Garza *et al.* 2005); however it is not known how these traits relate to growth and survival in dry forests.

The goal of this project is to evaluate the effectiveness of nurse tree reforestation as a restoration tool for tropical dry forests and to assess morphological traits related to reforestation success. The general objective of this research was to develop planting and management techniques that increase the performance of native trees planted under nurse trees for dry forest restoration. Specific objectives include:

- To study the initial growth and mortality of saplings of ten native tree species planted at different distances and directions under the nurse tree *Leucaena leucocephala*.
- To study the relationship between light environment and tree growth and mortality.
- To study the relationship between variability in leaf mass and leaf density on tree growth and mortality to determine if the leaf traits are good indicators of establishment success in dry forest tree species.

Thesis layout

This thesis is divided into two main chapters. Each chapter described a project with separate hypothesis and data that is intended to be submitted for publication in a peer-review journal. Chapter 2 describes the response of growth, mortality and leaf area index of ten native tree species to four planting distances and directions from the nurse tree *Leucaena leucocephala*. Chapter 3 describes the relationship between variability in leaf mass and leaf density on tree growth and mortality of the planted saplings and a mature forest plot. A concluding chapter summarizes the major results of the entire project and includes recommendations for dry forest management and future research.

Chapter 2. Performance of native trees planted under nurse trees for dry forest restoration

Literature Review

Introduction

Most of the original dry forests in the tropics have been eliminated due to the conversions of these ecosystems to agricultural land (Janzen 1988). By 1938, less than 5% of the forest cover of Puerto Rico remained intact (Aide *et al.* 1995). Dry forests were intensively used for wood, charcoal and agriculture and today only 4% or 35, 407 ha of Puerto Rico's total land area remains as dry forest (Gould *et al.* 2008) of the original 17.6% of the total area of Puerto Rico (Murphy *et al.* 1995). Thus, the need to restore these forests is critical and urgent because of the rapid disappearance of this ecosystem.

However, large-scale reforestation projects for restoration can be very costly and the cost of managing planted trees can be very high (Lamb *et al.* 2005). Therefore, tree planting for reforestation must be seriously evaluated by land managers before initiation, since monetary and human resources are key elements for establishing a reforestation project. Reforestation projects should only be implemented when natural regeneration has failed and no natural forests exist, or when management goals require different plant species composition. Currently, natural regeneration worldwide restores more forest cover in areas that have been deforested than tree plantations do. From 2000-2005, tree plantations have established an estimated area of 28,000 km² per year, whereas natural regeneration has established an estimated area of 45,000 km² per year, although these figures vary across regions (FAO 2006).

Challenges for dry forest restoration

The scarcity of viable seeds in the soil presents a major barrier for forest regeneration and restoration. Ray (1993) concluded that the seed bank in St. John, U.S. Virgin Islands might be insufficient for recovery for this reason. In Guánica Commonwealth Forest, most of the canopy species seem to have been recruited from stochastic establishment of seedlings (Castilleja 1991). Therefore, native seed banks will rarely lead to forest regeneration of deforested dry tropical areas (Janzen 2002). However, dry tropical forests are considered more resilient to disturbances and recover more quickly in terms of structure than wet forests mainly because of their relatively small and simple structure and because of the predominance of coppicing as the primary regeneration mechanism in dry forests that have been cut, with stumps and roots remaining in place (Murphy and Lugo 1986b). As a result, dry forests in the early stages of succession have a very patchy development followed by a long-lived stage of a large density of small and multi-stemmed trees (Murphy and Lugo 1986b). The relative

resilience of dry forests should not divert attention from the fact that the recovered forest might not be the same in species composition even after many years of abandonment. Forests will usually recover from even the most intense land-use, but the species composition of these emerging forests will be different from undisturbed forest (Lugo 1997). In Puerto Rican dry forest, altered species composition and alien species invasion are the most significant long-term effects of human land-use and landscape modification. These alien species persist in the mature forests even after 100 years of abandonment and forest composition does not return to that of the original forest (Molina-Colón and Lugo 2006). This pattern of dry forest regeneration presents a challenge to land managers who want to restore the species composition of these forests.

Environmental conditions also present challenges to dry forest restoration. Typical dry forest sites are characterized by having high solar radiation, high temperatures and high evaporation. Highly variable precipitation and frequent dry spells are common, with several months of severe or total drought (Murphy *et al.* 1995). Also, it is possible that solar radiation and the light environment created under the forest canopy, along with soil moisture, regulate seed germination, seedling establishment and growth (Lugo *et al.* 1978). Precipitation patterns and the spatial and temporal variation in canopy thickness will regulate light availability under the canopy which in turn regulates soil moisture content (Castilleja 1991). The patchy canopies typical of early-successional dry forest communities will create heterogeneous forest-floor light microenvironments that are susceptible to fluctuations in light intensity during rainy periods, and generally high exposure to solar radiation during dry periods due to leaf drop (Brown and Ray 1993). However, it is not well known what the relationship is between the light environment under the forest canopy and tree growth and survival. For example, treefall gaps, which are focal regeneration sites in moister tropical forests, can decrease seedling survival in dry forests because of the intense solar radiation, high temperatures and low humidity (Viera and Scariot 2006). Previous greenhouse (Carvajal 2001) and field experiments (Ray 1993, Ray and Brown 1995) have shown that partial shading significantly increased seedling survival for dry forest species in Puerto Rico and St. John, respectively. These results suggest that native species of early secondary dry forest communities may be restored by underplanting within the existing vegetation (Ray and Brown 1995).

Nurse tree reforestation

If reforestation is the preferred method over natural regeneration because of a particular species composition requirement, effective techniques are needed to ensure the establishment of the planted trees. One way to approach this problem is by reforestation using nurse trees. Nurse tree reforestation is a type of enrichment planting that consists of planting saplings under a mature or established tree. The positive interactions sometimes created between the nurse trees and the planted saplings are the result of the facilitative mechanisms that cause the modification of the understory into a more favorable microhabitat compared to the surrounding areas with no vegetation cover. These effects can be lowering air and soil temperature, reducing soil

water evaporation, protecting against herbivory, increasing nutrient and water availability, decreasing the effects of wildfires, decreasing vapor pressure deficit, heat loading or photoinhibition of the planted saplings (Badano *et al.* 2009, Cavieres *et al.* 2006, Padilla and Pugnaire 2006). When compared to open site reforestation, nurse trees have been successfully used to establish saplings by increasing growth and survivorship in the Sierra Nevada mountains in Spain (Gómez-Aparicio *et al.* 2004), Mexican oak forests (Badano *et al.* 2009), subarctic barren sites in Russia (Eränen and Kozlov 2007), degraded rainforests in Vietnam (McNamara *et al.* 2006) and dry forests in Puerto Rico (Santiago-García *et al.* 2008).

The spatial proximity among plants is an important interaction to consider when planting saplings close to mature trees. Plant interactions can affect the spatial distribution, establishment and performance of plant communities (Eränen and Kozlov 2007). These interactions can be either negative (competition) or positive (facilitation) and could determine spatial distributions in plant communities. Competition between plants is a consequence of having to share limited resources such as nutrients, water, light or space or by inhibiting the growth of other species by the release of chemicals in the soil (allelopathy). On the contrary, facilitation is the process in which at least one nearby species benefits from the interaction by enhanced growth, establishment or survival. However, their relative importance and intensities depend and change along environmental gradients and can even occur simultaneously, resulting in complex effects (Schulze *et al.* 2005). The net result between facilitation and competition indicates the magnitude and sign (negative or positive) of the interaction and may also vary over time (Padilla and Pugnaire 2006). The role of facilitation may increase with increasing abiotic stress on plants, appearing to be more evident in harsh environments such as arid lands (Flores and Jurado 2003). Facilitation often increases with intensified stress, as has been reported in south-facing slopes vs. west-facing slopes in rocky plant communities, in dry vs. mesic adjacent sites or in high vs. low altitudes in alpine and semi-arid environments. Interspecific interactions can also vary at the same site between years depending on climatic conditions, although the relationship between climatic variability and the net result of the interaction is still unclear (Gómez-Aparicio *et al.* 2004). All forest restoration projects should consider plant interactions and other factors such as scale of the project and site conditions. It is important to consider nurse trees for reforestation since they can emulate both positive and negative natural plant interactions such as facilitation and competition.

Restoration projects will probably be more successful if they are small scale and are in favorable site conditions (Carvajal 2001); however these key requirements are rarely available to land managers. Brown and Ray (1993) proposed a reforestation model using the non-native *Leucaena leucocephala* as a nurse tree to improve soil nitrogen content. Planting under the existing vegetation takes advantage of the present canopy which can provide shade, facilitating the establishment of saplings, instead of clearing the land to reforest. Under this plan, introduction of later successional (more shade tolerant) species can be more successful in dry

pasturelands (Ray 1993). This restoration technique can be implemented by forest and land managers to help speed up the process of restoring plant and wildlife biodiversity.

***Leucaena leucocephala* ecology and use as a nurse tree**

Leucaena leucocephala (Lam.) de Wit is a shade-intolerant, nitrogen fixing legume with seeds that are mainly wind-dispersed. This semi-deciduous, naturalized tree grows on abandoned pasturelands, along roadsides and in early secondary dry forests in the arid zones of Puerto Rico. Its natural distribution ranges from Southern Mexico to Guatemala, Belize, El Salvador and Honduras. *Leucaena* is one of the most extensively cultivated leguminous trees in the world and is either cultivated or naturalized worldwide between the latitudes of 25° N and 25°S (Parrotta 2000). *Leucaena* is sometimes considered a weed due to its ability to colonize disturbed sites and form dense thickets. However, this aggressive colonizing ability makes them suitable for reforestation in steep, denuded slopes and open, degraded pastures (Parrotta 2000). *Leucaena* was planted for erosion control in Saipan, the Northern Marianas and Guam after World War II. On these islands, seeds were aerially broadcast in the fields heavily damaged by bombing. Fifty years later, some parts of the island were completely dominated by *Leucaena*, but with no natural regeneration under its canopy (D'Antonio *et al.* 2001). Although *Leucaena* can be an aggressive colonizer, in some locations it has been found to promote native species establishment. In exotic dry forest patches in southern Puerto Rico, where *Leucaena* dominated the canopy, Pérez-Martínez (2007) found that seedling and sapling regeneration was dominated by *Leucaena* with 29.9 and 17.9 of importance value respectively. However, natural regeneration of native tree species was present mainly with native pioneer species like *Amyris elemifera*, *Croton humilis* and *Eugenia foetida*. Wolfe (2009) found that open grasslands in Puerto Rico had almost no seed rain from native species; while *Leucaena* dominated forests had higher native seed rain than open grass areas. In many regions of the tropics, *Leucaena* is used as part of agroforestry systems, mainly as a shade tree and for their ability to fix nitrogen and improve soil conditions. It has been used in coffee, cacao, tea, vanilla, corn and teak plantations (Parrotta 2000). Santiago-García *et al.* (2008) found in southwestern Puerto Rico, that in case of a wildfire, *Leucaena* nurse trees reduced mortality and increased growth of native tree species compared to open-site reforestation by limiting grass growth and reducing fuel loads.

In order to understand the patterns of growth and mortality of native species when planted under the nurse tree *Leucaena leucocephala* and how the sub canopy light environment relate to these two traits, I planted native dry forest saplings at four different distances from the nurse trees. With these data, I tested the following hypotheses:

1. Native saplings will have higher growth and lower mortality under the nurse tree than in open areas.
2. Growth will decrease and mortality will increase with increasing light levels under the nurse tree.

Materials and Methods

Description of Tropical and Subtropical Dry Forests

Tropical and subtropical dry forests are frost-free areas characterized by having a mean annual bio-temperature above 17°C, mean annual rainfall from 500 to 1500 mm and an annual ratio of potential evapotranspiration to precipitation that exceeds one (Holdridge 1967). In Puerto Rico, the subtropical dry zone covers mostly the southern part of the island, extending from Cabo Rojo in the west towards Guayama in the east. It also occurs in the east coast between Fajardo and Ceiba and the islands of Mona, Vieques and Culebra. Annual rainfall is distributed bimodally into two seasons with a strong dry period from December to April and a lesser one from June to August (Murphy and Lugo 1986a).

Site descriptions

Three plots were established in the municipalities of Cabo Rojo and Guánica, Puerto Rico to test growth and survivorship of ten native tree species planted at different distances under the nurse tree *Leucaena leucocephala*. Planting was performed in Cabo Rojo at a private property in the Sierra Bermeja hills and at the U.S. Fish and Wildlife Cabo Rojo National Wildlife Refuge and in Guánica at Guánica Commonwealth Forest.

Sierra Bermeja, Cabo Rojo: This site was located on a 16.5 ha property owned by Dr. Philip Sollins of Oregon State University. Mean annual rainfall from 2002-2007 was 829 mm (P. Sollins pers. com.). The site was divided into two plots: a north-facing slope and the top of a flat hill. The land was previously used for grazing. The site experienced two recent fires, one in February 2006 and another in March 2007. *Leucaena leucocephala* dominated the upper part of the hill while downhill *Leucaena* was present along with *Bucida buceras* L., *Bursera simaruba* (L.) Sarg. and *Bourreria succulenta* Jacq. The moderate-to-well drained, shallow cobbly sandy loam soils are Aridisols derived from ultrabasic rock (serpentinite) from the Casabe-Cerro Mariquita-Llanos Costa-Maguayo association (<http://www.mo15.nrcs.usda.gov/>). Soils were high in % N, % S, Fe and Mn and low in Ca and Al compared to the other sites (Table 1).

Cabo Rojo National Wildlife Refuge, Cabo Rojo: This site was located in the 751 ha Cabo Rojo National Wildlife Refuge (CRNWR), part of the Caribbean Islands National Wildlife Refuge Complex. Mean annual rainfall averaged 840 mm from 1991 through 2000. Past land uses included almost two hundred years of sugar cane production and cattle ranching. It is also prone to fire and has burned in the past. The property was transferred to the U.S. Fish and Wildlife Service in 1974 where cattle ranching continued until 1978 when the first CRNWR manager arrived (Weaver and Schwagerl 2008).

The CRNWR was dominated by exotic grasses like *Urochloa maxima* and *Pennisetum ciliare* and trees like *Leucaena leucocephala*, *Prosopis pallida* and *Melicoccus bijugatus*. The well drained to excessively drained, level to sloping sandy soils are Vertisols from the Americo-Guayabo-Sosa association. Soils were high in %LOI, Ca, Mg and Mn and low in P compared to the other sites (Table 1). (<http://www.mo15.nrcs.usda.gov/>).

Guánica Commonwealth Forest, Pitirre sector: This sites is located within the 4,400 ha Guánica Commonwealth Forest. Annual rainfall has averaged 860 mm over the last 70 years and it is distributed bimodally into two seasons, a strong dry period from December to April and a lesser one from June to August (Murphy and Lugo 1986a). This plot is a patch of coastal forest located at sea level and had been previously used for agriculture until the 1970's. It was a *Leucaena leucocephala* dominated stand with some *Croton* spp. in the understory along with exotic grasses like *Pennisetum ciliare* and *Urochloa maxima*. Growth data of experimental plantings were compared to saplings found in a mature forest stand which has no evidence of cutting for charcoal since the 1930's. This plot was established by Murphy and Lugo in 1986 but saplings growth was measured by Dr. Skip Van Bloem beginning in 1998. The moderately well drained to poorly drained, nearly level to sloping and calcareous alluvial soils are Mollisols from the Fraternidad-Aguirre-Cartagena association (<http://www.mo15.nrcs.usda.gov/>). Soils were high in %C, Al, K, and Ca and low in Mg and Mn compared to the other sites (Table 1).

Table 1. Total soil nutrients of each planting site as determined from 5 subsamples randomly placed throughout the site. The top 20 cm of soil was sampled. Soil organic carbon (%C) was analyzed by automated carbon-nitrogen-sulfur (CNS) analysis. Loss of ignition (%LOI) method was employed to analyze soil organic matter. Soil P was analyzed by the Olsen method and the other standard elements were analyzed following the Montana Soil-NIST 2711 soil research methods. Analyses provided by the Soil Analysis Laboratory of the U.S. Forest Service-International Institute of Tropical Forestry.

Site	%C Average	% N Average	% S Average	% LOI Average	Al (mg/g)	Ca (mg/g)	Fe (mg/g)	K (mg/g)	Mg (mg/g)	Mn (mg/g)	Na (mg/g)	P (mg/g)
Guánica Forest, Pitirre	9.84	0.29	0.06	16.08	24.11	177.64	24.20	2.55	3.72	0.55	0.19	1.06
Cabo Rojo National Wildlife Refuge	6.57	0.27	0.05	21.34	19.62	110.84	24.68	2.10	4.10	0.67	0.14	0.47
Top hill, Sierra Bermeja	5.07	0.39	0.07	10.49	6.93	21.24	76.29	0.79	1.26	0.27	0.15	1.74
North facing slope, Sierra Bermeja	3.39	0.33	0.08	10.91	17.38	4.86	38.98	2.51	18.35	1.344	0.08	0.59
Avg. Sierra Bermeja	4.23	0.36	0.07	10.70	12.15	13.05	57.63	1.65	9.81	0.81	0.11	1.16

Experimental Design

Leucaena leucocephala was chosen as the nurse tree species. This species is present at each site and none were planted. *Leucaena* trees were selected based on a diameter at breast height (DBH) ≥ 2.5 cm and a minimum tree height of 2 m. Forty *Leucaena* were chosen in the Guánica and CRNWR plots. Due to the lack of availability of *Leucaena* that matched the criteria, Sierra Bermeja only had twenty *Leucaena*. Each *Leucaena*'s height, DBH, canopy diameter and number of stems were measured. Eight native tree species were chosen for planting at Guánica and the CRNWR based on that they naturally occur in the vicinity of both sites. Six species are common between them and two species only planted at each site. Only four species were planted at Sierra Bermeja, these were also planted in Guánica and at the CRNWR (Table 2). Five species were present in the Mature Forest Plot with a total of 239 individuals (Table 3).

Table 2. List of species and their planting sites. Aspects of their leaf habit and type of seed dispersal are also mentioned following Little, Wadsworth and Marrero (2001).

<u>Species</u>	<u>Planting Site</u>			<u>Leaf Habit</u>		<u>Seed Dispersal Mechanism</u>	
	<u>Guánica Commonwealth Forest</u>	<u>Cabo Rojo National Wildlife Refuge</u>	<u>Sierra Bermeja</u>	<u>Deciduous</u>	<u>Evergreen</u>	<u>Animal</u>	<u>Wind</u>
<i>Bourreria succulenta</i> Jacq.	X	X			X	X	
<i>Bucida buceras</i> L.	X	X	X	X			X
<i>Bursera simaruba</i> (L.) Sarg.	X	X		X		X	
<i>Citharexylum fruticosum</i> L.	X	X	X		X	X	
<i>Coccoloba uvifera</i> (L.) L.	X				X	X	
<i>Erythroxyllum areolatum</i> L.	X	X	X	X		X	
<i>Pisonia albida</i> (Heimerl) Britton	X			X		X	
<i>Stahlia monosperma</i> (Tul.) Urban		X			X	X	
<i>Tabebuia heterophylla</i> (DC.) Britton	X	X	X	X			X
<i>Trichilia hirta</i> L.		X		X		X	

To test the relationship between growth, mortality and the distance from the nurse tree, four trees from different species selected for each site were planted under each nurse tree at the cardinal positions (north, east, south and west). Planting distance was chosen according to the canopy radius of the nurse tree. The first planting distance, regardless of the direction, was one third of the crown radius for that particular nurse tree. The second distance was two thirds the crown radius, the third distance was at the crown edge and the fourth distance was at full sun using the same length of one third of the radius (Fig. 1). The first cardinal direction was selected at random and the next three saplings followed clockwise from the first direction. Figure 2 shows an example of the planting arrangement at the Cabo Rojo National Wildlife Refuge. The same arrangement was used at the other sites but with a different combination of species.

Figure 1. Top view of the crown of a nurse tree showing the position of the planting distances according to the crown radius.

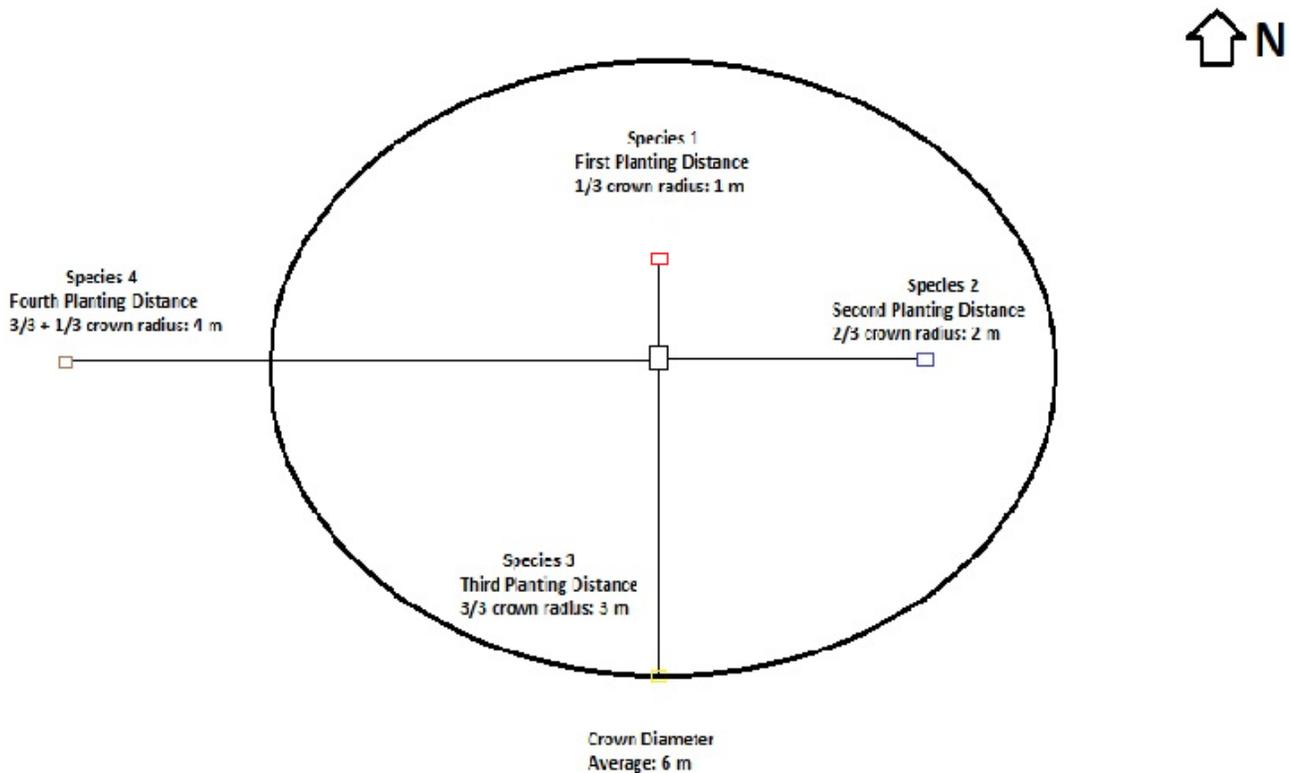
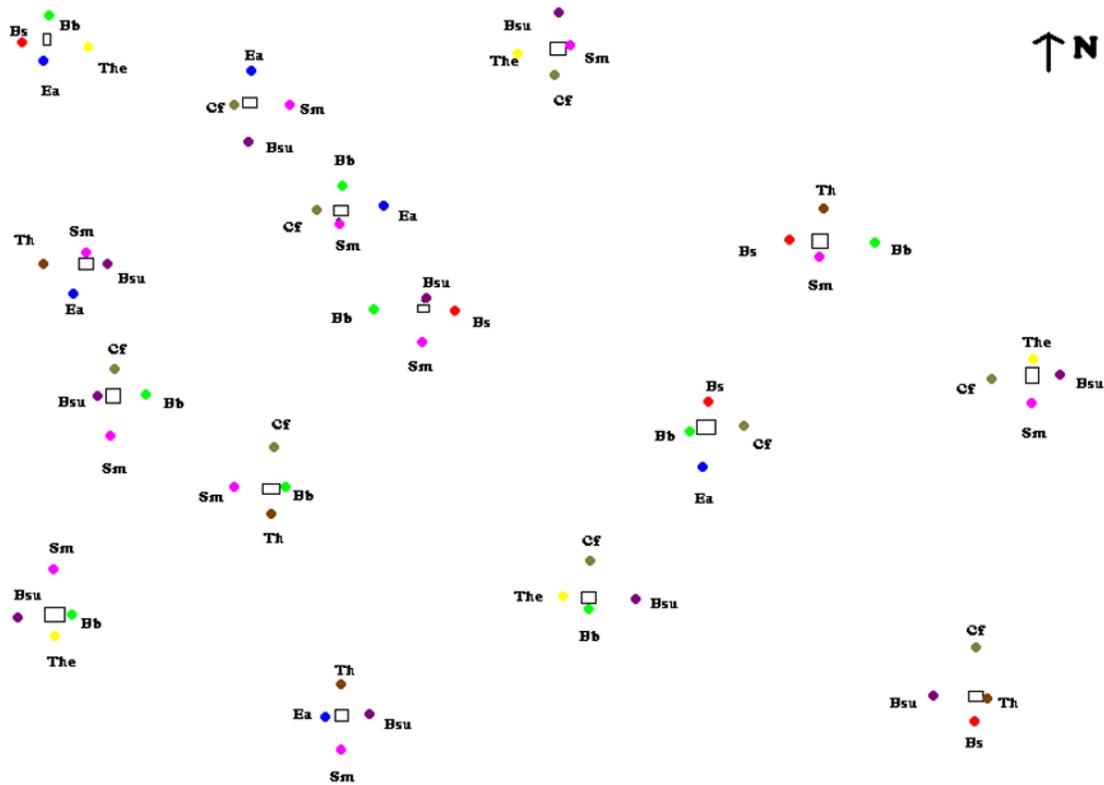


Figure 2. Planting arrangement at the Cabo Rojo National Wildlife Refuge. The same arrangement was used at the other sites but with a different combination of species. The central square represents a *Leucaena leucocephala* nurse tree. The dots around it are the different species planted starting from the first planting position closest to the nurse tree to the fourth planting position in full sun. The species are: *Bourreria succulenta*- Bs, *Bucida buceras*-Bb, *Bursera simaruba*-Bs, *Citharexylum fruticosum*-Cf, *Erythroxylum aereolatum*- Ea, *Stahlia monosperma*- Sm, *Tabebuia heterophylla*- The and *Trichilia hirta*- Th



For each of the four planting distances, five individuals per species were planted in each plot for a total of twenty individuals per species. In the Guánica and CRNWR plots, each with eight species, 160 trees were planted in each plot and in Sierra Bermeja with four species, 80 saplings were planted for a total of 400 trees. Planting at the CRNWR was performed between the end of August and mid-September 2007, in Guánica in October 2007 and in Sierra Bermeja in February 2008. Weeding was performed primarily by hand and weedwacking around each *Leucaena* prior to planting. This was done to minimize competition with the planted trees and to act as a fire break. Irrigation was performed for the first three weeks in the CRNWR and in Sierra Bermeja watering was done weekly in the initial three weeks and then every two weeks until March 2008. Watering was not done in Guánica because the distance between the closest water source to the planted trees was too great and only the trees closest to the road would have been practical to water, so I decided not to water any of the trees. Trees were obtained from local nurseries, the CRNWR nursery, Departamento de Recursos Naturales y Ambientales and Fideicomiso de Conservación de Puerto Rico. Species selected for this project were based mainly on availability from the nurseries. Initial tree sapling sizes ranged from 0.2 to 2.2 m

Initial height was measured for each sapling at the time of planting. Growth and mortality were measured in all plots in January, May and September 2008 and January and May, 2009. Light environment was recorded with a LICOR LAI 2000 as the leaf area indices (LAI) and measured at the point where each sapling was planted, one reading above the crown of the nurse tree and one below the crown just above each planted sapling. Measurements were taken in November 2009. These were taken early in the morning (7:30-10:30) and in the afternoon (3:30-5:30). Also, LAI measurements were taken on the Mature Forest Plot to compare with the LAI and growth of the saplings planted. The coefficient for light diffusion and standard error for the LAI's were calculated by the LAI-2000 data logger.

Statistical Analysis

Data were analyzed with the software Infostat/Professional. A Shapiro-Wilks test was used to verify the normality of the variables. Distribution was tested using a Levene Test ($p= 0.05$). The sapling growth data were log transformed. An Analysis of Covariance (ANCOVA) was used to test growth in a nested design, where species were nested within the site. Initial tree size and nurse tree crown diameter were the covariates. Differences between treatments were determined using post-hoc multiple comparisons (LSD Fischer test). The treatments, all fixed effects, were distance from nurse tree, cardinal position and site and were analyzed for each species separately. Chi-square was used to analyze mortality. An alpha value of 0.1 was used because rejecting the null hypothesis (nurse trees do not have an effect on growth and mortality) falsely will not have negative long term effects on restoration projects, but failure to identify important planting techniques because of low sample size would be more serious.

Leaf area index and survivorship were analyzed using nonlinear regressions. 75% survivorship was chosen as the threshold for an acceptable range of successful establishment for dry forest species. This range is reported as the mean LAI value on the 75% threshold along with a minimum and a maximum value represented by the 95% confidence intervals.

Results

Leaf area index and light environment

Average leaf area index (LAI) for all planting sites was 1.16, with a maximum of 3.16 and a minimum of 0.00 (Table 3). Initial height ($df= 1$, $F=0.03$, $p=0.8727$) and crown radius ($df= 1$, $F=3.29$, $p=0.0706$) of nurse trees did not significantly influence LAI. Mean LAI did not vary across sites ($df= 2$, $F=0.80$, $p=0.4523$). LAI increased by 1.95 at the first planting distance closest to the nurse tree as opposed to the full sun position, reflecting greater foliage density directly under the nurse tree ($df= 3$, $F=1612.38$, $p=0.0001$). Regardless of the planting site, leaf area index decreased moving away from the nurse tree, with mean LAI being highest at the first planting distance at the CRNWR with 2.30 and the lowest LAI also being at the CRNWR with 0.20 at full sun ($df= 6$, $F=4.04$, $p=0.0006$). Differences in leaf area indices across the planting distances indicate a light gradient from the base of the nurse tree extending outwards towards full sun. Since LAI not only measures foliage but all light-blocking objects like the trunk and branches, less light will be available to saplings closer to the nurse tree at the first planting distance compared to full sun exposure at the fourth planting distance.

Table 3. Descriptive statistics for Leaf Area Index (LAI) for all saplings planted by site, planting distance and site by distance interaction. Different letters indicate significant differences in LAI ($p<0.1$)

		n	Mean	S.E.	Minimum	Maximum	Median	
All Saplings		400	1.16	0.04	0.00	3.16	1.08	
Site								
	Guánica	160	1.15	0.06	0.00	3.16	1.03	A
	CRNWR	160	1.15	0.06	0.04	2.78	1.08	A
	Sierra Bermeja	80	1.19	0.08	0.00	2.51	1.22	A
Distance								
	1.00	100	2.21	0.03	1.49	3.16	2.18	A
	2.00	100	1.47	0.02	0.97	1.92	1.46	B
	3.00	100	0.70	0.02	0.00	1.09	0.72	C
	4.00	100	0.26	0.01	0.00	0.59	0.23	D
Site	Distance							
CRNWR	4.00	40	0.20	0.02	0.04	0.53	0.17	A
Sierra Bermeja	4.00	20	0.28	0.03	0.00	0.54	0.25	A
Guánica	4.00	40	0.31	0.02	0.00	0.59	0.29	A
CRNWR	3.00	40	0.66	0.03	0.26	1.09	0.66	B
Guánica	3.00	40	0.71	0.03	0.00	1.06	0.75	B
Sierra Bermeja	3.00	20	0.76	0.03	0.33	1.09	0.76	B
CRNWR	2.00	40	1.43	0.03	0.99	1.92	1.40	C
Guánica	2.00	40	1.47	0.04	0.97	1.88	1.48	C
Sierra Bermeja	2.00	20	1.54	0.03	1.35	1.79	1.52	C
Guánica	1.00	40	2.13	0.04	1.49	3.16	2.14	D
Sierra Bermeja	1.00	20	2.20	0.04	1.77	2.51	2.22	D
CRNWR	1.00	40	2.30	0.04	1.52	2.78	2.26	E

Leaf area index and survivorship

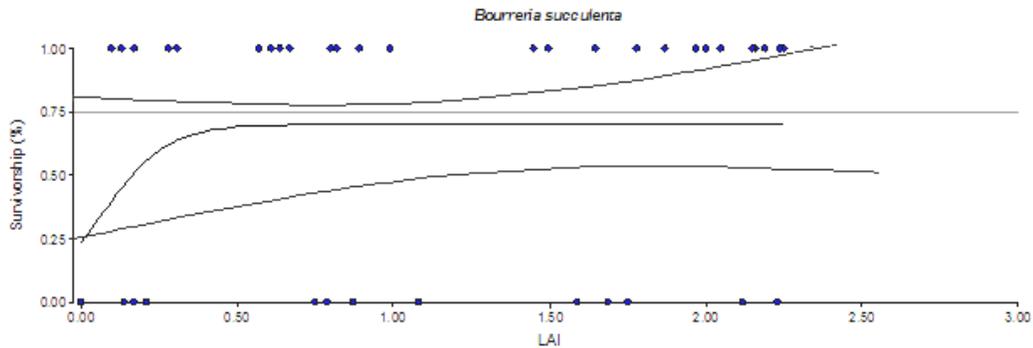
Low survivorship excluded *Coccoloba uvifera* from this analysis which only had two survivors. *Trichilia hirta*, with only one dead individual and *Bursera simaruba* with two dead individuals, were also excluded from the analysis. Figure 3 shows the relationship between LAI and survivorship for the remaining seven species. *Bourreria succulenta*, *Bucida buceras*, *Citharexylum fruticosum* and *Tabebuia heterophylla* presented no trends of survivorship and LAI. *Erythroxylum areolatum* (Fig. 3D) had a threshold of 75% survivorship in a range of leaf area index between 0 and 1.25, indicating a preference for open sites moving away from the nurse tree. *Pisonia albida* (Fig. 3E) attained 75% survivorship at LAI of approximately 2.0 and increasing as leaf area index increases. This pattern indicates a preference for *Pisonia* for shady sites. *Stahlia monosperma* (Fig. 3F) also presented a similar pattern, attaining 75% survivorship at an LAI of 0.9 and then leveling off with increasing LAI, indicating that *Stahlia* performs better in shady sites. These data clearly show that not all species survivorship respond to leaf area index and the ones that do require a different range of LAI in order to obtain 75% survivorship under the nurse trees.

Leaf area index and growth

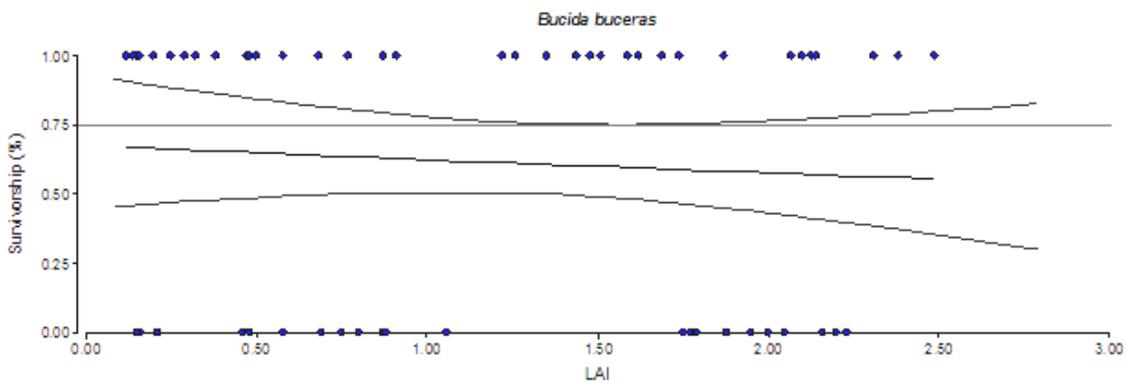
No relationship was found between leaf area index and growth ($p=0.0014$, $r^2=0.04$) for all species and sites together (Fig.4). When analyzed by species, only *Stahlia monosperma* presented a positive trend between leaf area index and growth (Fig. 5). For *Stahlia*, growth tended to increase as leaf area index increased ($r^2=0.46$, $p=0.0147$), indicating a preference for shady sites.

Figure 3. Relationship between leaf area index and survivorship of (A) *Bourreria succulenta* (B) *Bucida buceras* (C) *Citharexylum fruticosum* (D) *Erythroxyton aerolatum* (E) *Pisonia albida* (F) *Stahlia monosperma* and (G) *Tabebuia heterophylla*. Values of 0 represent dead individuals and values of 1 are surviving individuals. The center line is the main regression line along with the 95% confidence intervals. A reference line at 75% survivorship is shown as the threshold for survivorship.

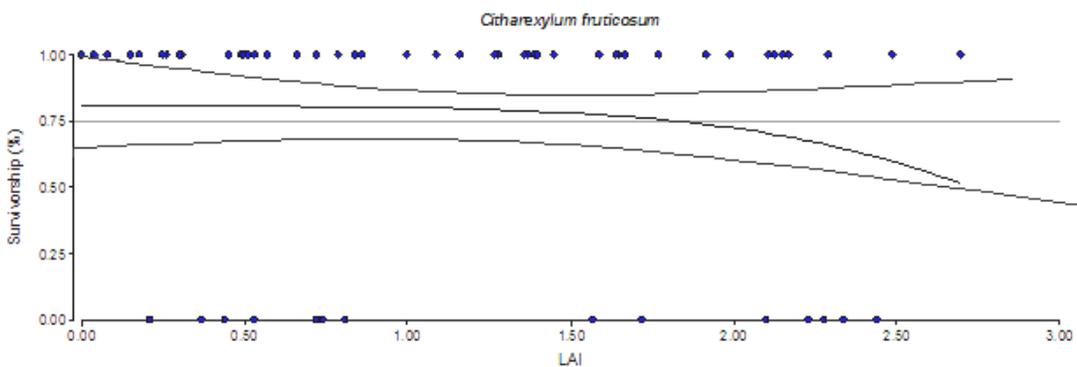
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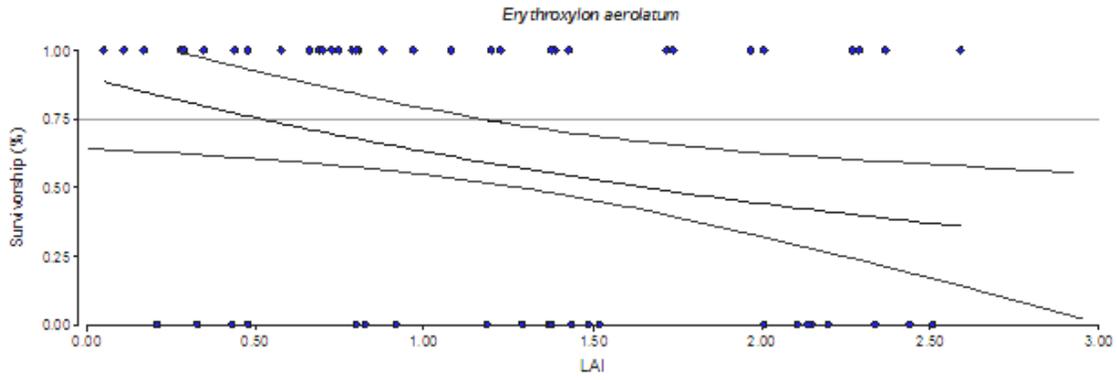
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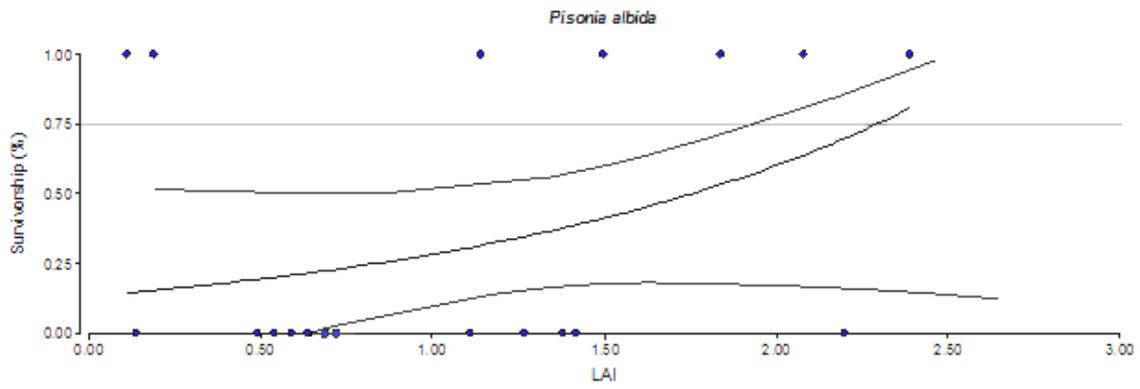
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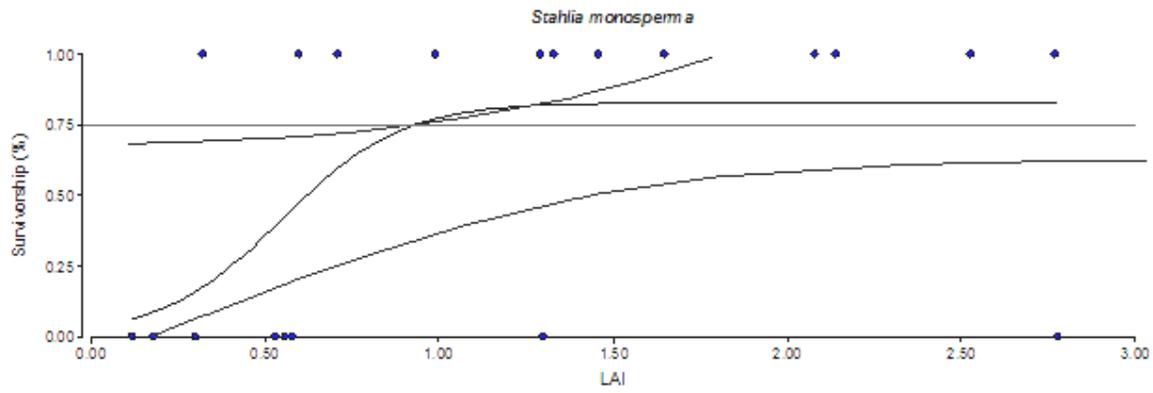
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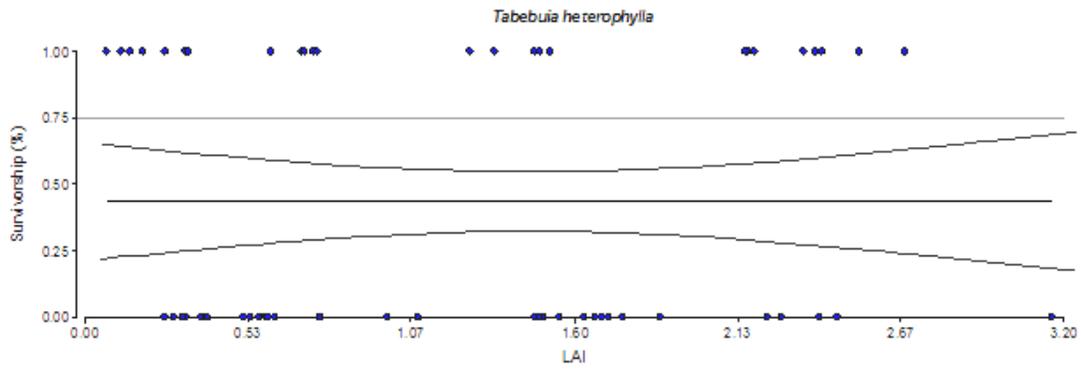
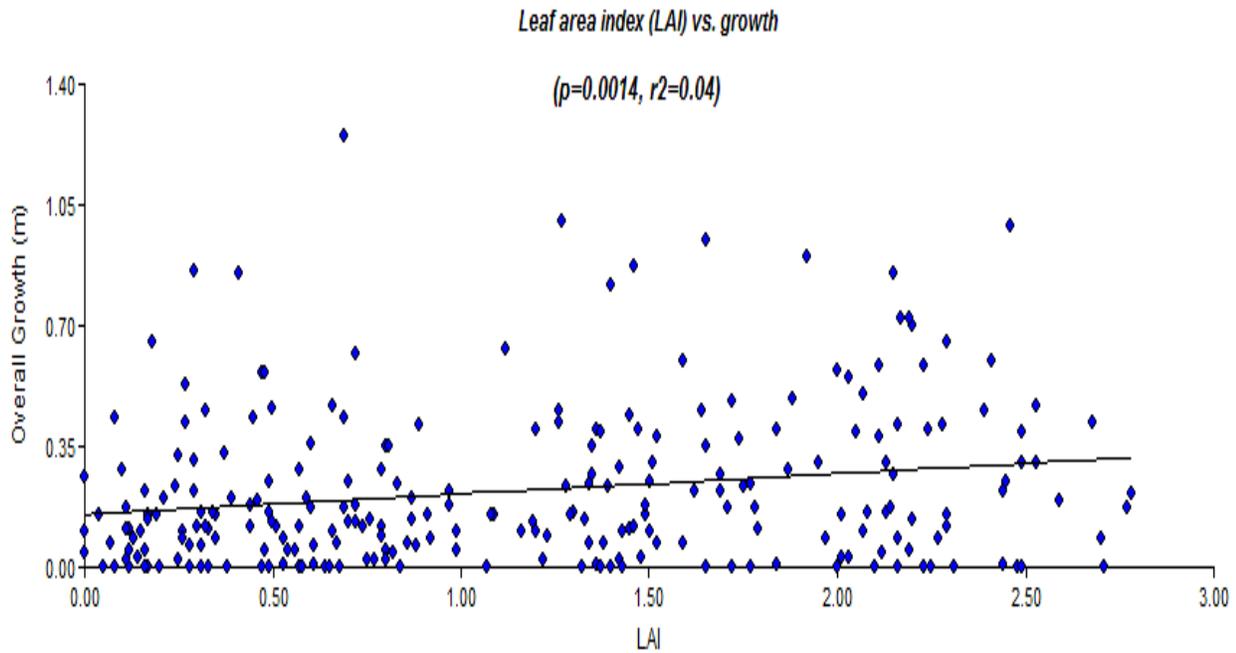
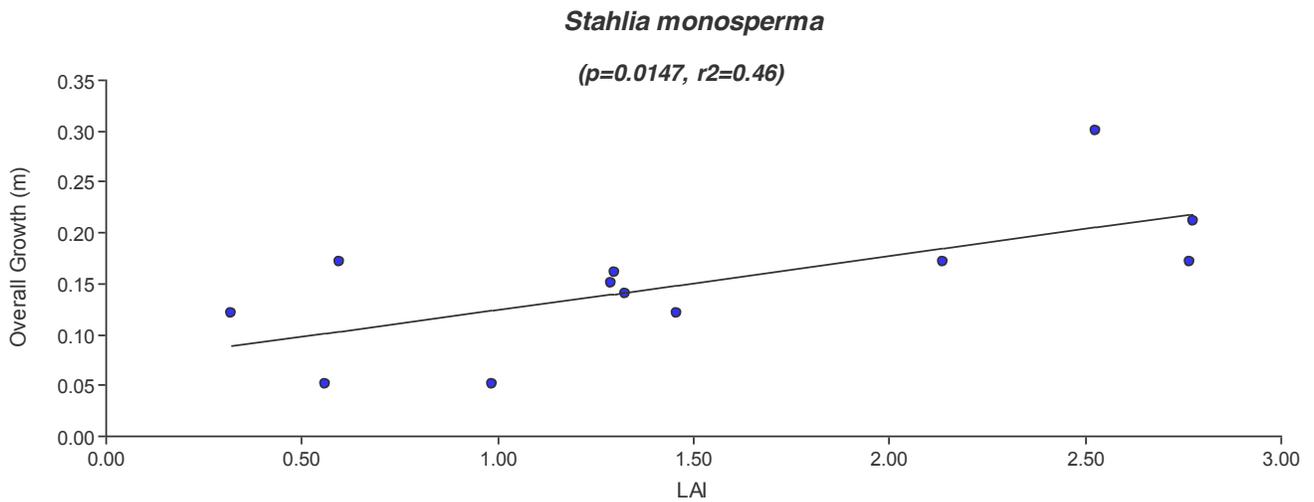


Figure 4. Regression for leaf area index and growth for the 250 surviving saplings from all 10 species combined.

Figure 5. Regression for leaf area index and growth for *Stahlia monosperma*.

Mortality

In May 2009, 1.25-1.75 years after planting, overall mortality across all three plots was 37.5%, representing 150 dead trees of the 400 originally planted. Mortality reflected different water treatments and time of planting and therefore the CRNWR only had 8.1% mortality compared to 53% mortality at Guánica and 65% mortality at Sierra Bermeja ($\chi^2=101.39$, 2 df, $P < 0.0001$). Mortality varied by species, with *Coccoloba uvifera*, *Pisonia albida* and *Tabebuia heterophylla* having 55% or greater mortality and *Bursera simaruba*, *Trichilia hirta* and *Citharexylum fruticosum* having 25% or lower mortality ($\chi^2=71.75$, 9 df, $P < 0.0001$). The number of dead individuals of each species by site in each planting distance and direction are shown in Tables 4 and Table 5 respectively.

Mortality by planting distance and planting direction were only significant for certain species. Of the 10 species planted, only *Erythroxylum areolatum* and *Pisonia albida* showed significant differences in mortality by distance from the nurse tree. In Guánica, *Erythroxylum* had 90% lower mortality moving away from the nurse tree ($\chi^2=7.43$, 3 df, $P < 0.0593$). *Pisonia* had only 20% mortality at the first planting distance compared to 80% moving away from the nurse tree ($\chi^2=7.69$, 3 df, $P < 0.0528$). Within sites, only two species' mortality responded to direction. In *Bursera simaruba* at Guánica, mortality was 40% greater at the west planting direction with two dead individuals ($\chi^2=6.27$, 3 df, $P < 0.0833$). In the CRNWR, *Stahlia monosperma* mortality responded to cardinal direction with no dead individuals in the north planting direction and four dead individuals at the east ($\chi^2=8.33$, 3 df, $P < 0.0396$).

When the performance of all species were pooled together, mortality at the CRNWR was 17.5% greater at full sun in the fourth planting distance ($\chi^2=6.95$, 3 df, $P < 0.0735$). Mortality throughout the four planting distances was not significant in Guánica ($\chi^2=2.69$, 3 df, $P < 0.4427$) or Sierra Bermeja ($\chi^2=2.64$, 3 df, $P < 0.4510$). In Guánica the north planting direction had 35% lower mortality than the other directions ($\chi^2=7.50$, 3 df, $P < 0.0574$). Mortality was not affected by planting direction at Sierra Bermeja ($\chi^2=3.08$, 3 df, $P < 0.3799$) or the CRNWR ($\chi^2=5.61$, 3 df, $P < 0.1322$).

Mortality of species under the nurse tree vs. full sun

To compare mortality under the nurse trees against full sun, the first, second and third planting distances were pooled together and compared to mortality in the fourth planting distance at full sun. *Bourreria succulenta* had no mortality under the nurse trees at the CRNWR ($\chi^2=3.16$, 1 df, $P < 0.0756$). *Erythroxylum areolatum* had

80% greater mortality under the nurse tree than in full sun at Sierra Bermeja ($\chi^2=2.86$, 1 df, $P < 0.0910$). *Stahlia monopserma* had 27% less mortality under the nurse tree than in full sun ($\chi^2=4.44$, 1 df, $P < 0.0350$). *Trichilia hirta* had no mortality under the nurse tree ($\chi^2=3.16$, 1 df, $P < 0.0756$). Also, the third and fourth planting distances were pooled together and compared to the first and second planting distances. *Erythroxylum areolatum* had 60% higher mortality under the first two planting distances in Guánica ($\chi^2=5.49$, 1 df, $P < 0.0191$) and 90% higher in Sierra Bermeja ($\chi^2=3.81$, 1 df, $P < 0.0510$). *Stahlia monopserma* was 20% lower mortality under the first two planting distances ($\chi^2=3.33$, 1 df, $P < 0.0679$).

Table 4. Mortality of species by planting distance in each site by February 2009. Numbers indicate the amount of dead individuals. Five individuals per species were planted in each distance for a total of twenty individuals per species. Numbers with ^x represent individuals that were accidentally mowed in May 2008.

Site/Species	Planting Distance				Total
	1	2	3	4	
Guánica Commonwealth Forest					
<i>Bouyeria succulenta</i> Jacq.	2	4	3	4	13
<i>Bucida buceras</i> L.	2	2	4	2	10
<i>Bursera simaruba</i> (L.) Sarg.	0	1	0	1	2
<i>Citharexylum fruticosum</i> L.	3	1	1	2	7
<i>Coccoloba uvifera</i> (L.) L.	4	4	5	5	18
<i>Erythroxylum areolatum</i> L.	3	3	0	1	7
<i>Pisonia albida</i> (Heimerl) Britton	1	4	5	3	13
<i>Tabebuia heterophylla</i> (DC.) Britton	2	5	4	4	15
Guánica Total	17	24	22	22	85/160
Cabo Rojo National Wildlife Refuge					
<i>Bouyeria succulenta</i> Jacq.	0	0	0	1 ^x	1
<i>Bucida buceras</i> L.	1	0	0	0	1
<i>Bursera simaruba</i> (L.) Sarg.	0	0	0	0	0
<i>Citharexylum fruticosum</i> L.	0	0	0	0	0
<i>Erythroxylum areolatum</i> L.	1	0	0	1	2
<i>Stahlia monosperma</i> (Tul.) Urban	1	1 ^x	2	4	8
<i>Tabebuia heterophylla</i> (DC.) Britton	0	0	0	0	0
<i>Trichilia hirta</i> L.	0	0	0	1	1
Cabo Rojo Total	3	0	2	6	13/160
Sierra Bermeja					
<i>Bucida buceras</i> L.	4	2	3	3	12
<i>Citharexylum fruticosum</i> L.	2	1	2	2	7
<i>Erythroxylum areolatum</i> L.	5	4	3	2	14
<i>Tabebuia heterophylla</i> (DC.) Britton	5	5	4	5	19
Sierra Bermeja Total	16	12	12	12	52/80
Grand Total	36	36	36	40	

Table 5. Mortality of species by cardinal direction in each site by February 2009. Numbers indicate the amount of dead individuals. Five individuals per species were planted in each direction for a total of twenty individuals per species. Numbers with ^x represent individuals that were accidentally mowed in May 2008.

Site/Species	Planting Direction				Total
	N	S	E	W	
Guánica Commonwealth Forest					
<i>Bouyeria succulenta</i> Jacq.	2	5	3	3	13
<i>Bucida buceras</i> L.	3	1	3	3	10
<i>Bursera simaruba</i> (L.) Sarg.	0	0	0	2	2
<i>Citharexylum fruticosum</i> L.	0	2	2	3	7
<i>Coccoloba uvifera</i> (L.) L.	4	4	5	5	18
<i>Erythroxylum areolatum</i> L.	1	2	2	2	7
<i>Pisonia albida</i> (Heimerl) Britton	2	4	5	2	13
<i>Tabebuia heterophylla</i> (DC.) Britton	2	5	4	4	15
Guánica Total	14	23	24	24	85/160
Cabo Rojo National Wildlife Refuge					
<i>Bouyeria succulenta</i> Jacq.	0	1 ^x	0	0	1
<i>Bucida buceras</i> L.	0	0	0	1	1
<i>Bursera simaruba</i> (L.) Sarg.	0	0	0	0	0
<i>Citharexylum fruticosum</i> L.	0	0	0	0	0
<i>Erythroxylum areolatum</i> L.	0	0	1	1	2
<i>Stahlia monosperma</i> (Tul.) Urban	0	1	4	3	8
<i>Tabebuia heterophylla</i> (DC.) Britton	0	0	0	0	0
<i>Trichilia hirta</i> L.	0	1	0	0	1
Cabo Rojo Total	0	3	5	5	13/160
Sierra Bermeja					
<i>Bucida buceras</i> L.	3	3	2	4	12
<i>Citharexylum fruticosum</i> L.	3	2	2	0	7
<i>Erythroxylum areolatum</i> L.	5	3	3	3	14
<i>Tabebuia heterophylla</i> (DC.) Britton	5	5	4	5	19
Sierra Bermeja Total	16	13	11	12	52/80
Grand Total	30	38	41	41	

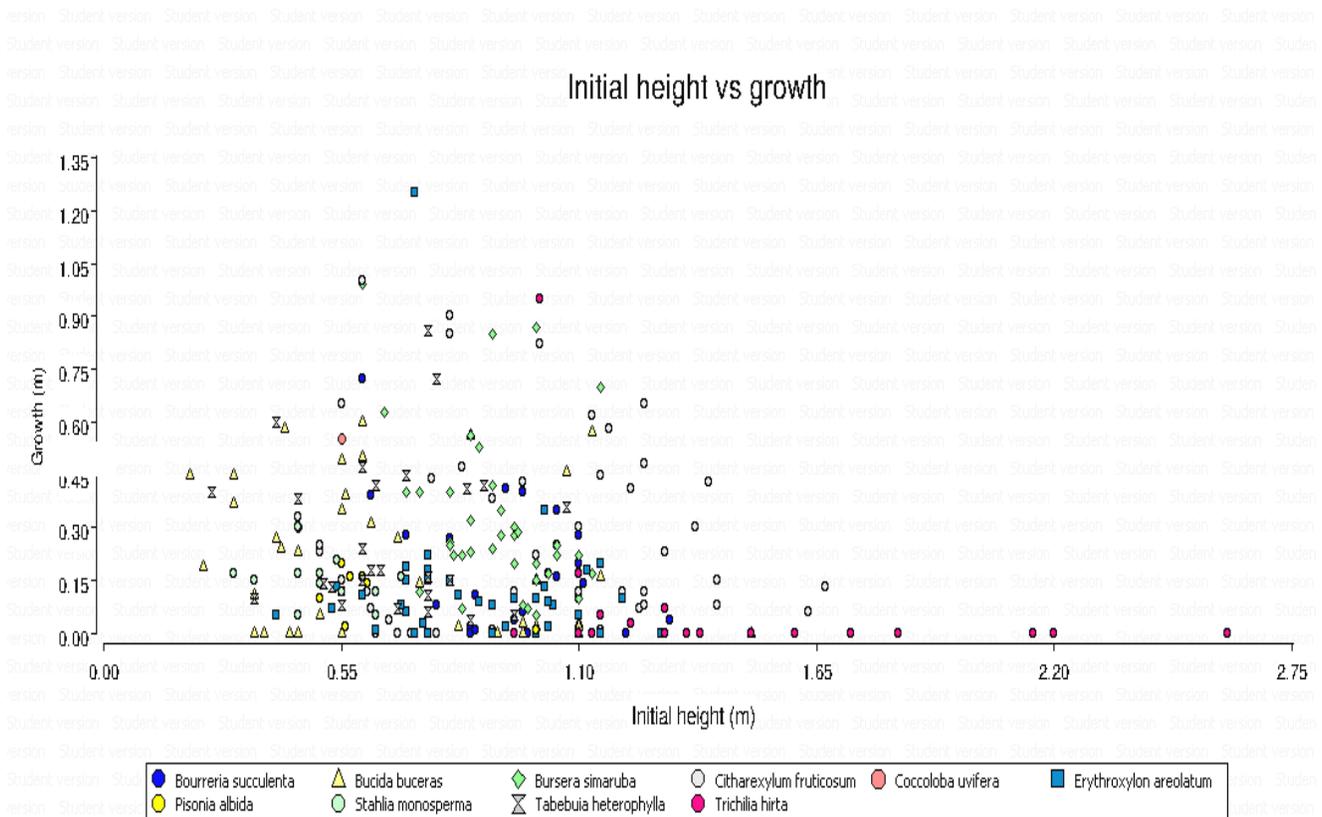
General growth

Overall mean growth was $0.22 \text{ m} \pm 0.23$ across all three sites for the period of September 2007 to May 2009 (Table 6). Initial height ($df= 1$, $F=0.29$, $p=0.595$) and crown radius ($df= 1$, $F=0.18$, $p=0.671$) did not influence growth (Figure 6). Growth varied by species, with *Erythroxylon areolatum*, *Pisonia albida* and *Trichilia hirta* having 0.13 m or less of average growth and *Bursera simaruba*, *Citharexylum fruticosum* and *Tabebuia heterophylla* having an average of 0.28 m of growth or greater. The species nested in site factor was significant, with *Bucida buceras* in Guánica and Sierra Bermeja having higher average growth (0.22 m) and *Pisonia albida* and *Bourreria succulenta* in Guánica having lower average growth of 0.11 m ($df= 19$, $F=2.07$, $p=0.027$). Planting distance was significant, with the first and second planting distances closer to the nurse tree having an average of 0.10 m of higher growth than the third and fourth planting distances ($df= 3$, $F=2.28$, $p=0.094$). Growth did not vary with planting direction ($df= 3$, $F=0.04$, $p=0.989$) (Table 7).

Table 6. Growth of saplings planted in this experiment. Descriptive statistics for growth by site, species, planting distance and direction. All units presented are in meters (m). Different letters indicate significant differences in growth ($p < 0.1$)

	n	Mean	S.E.	Minimum	Maximum	Median	
All Saplings	250	0.22	0.01	0.00	1.25	0.15	
<u>Site</u>							
Guánica	75	0.28	0.03	0.01	1.25	0.20	
CRNWR	147	0.21	0.02	0.00	1.00	0.14	
Sierra Bermeja	28	0.12	0.03	0.02	0.47	0.06	
<u>Species</u>							
<i>Bourreria succulenta</i>	26	0.18	0.03	0.02	0.72	0.13	
<i>Bucida buceras</i>	37	0.22	0.03	0.02	0.60	0.16	
<i>Bursera simaruba</i>	38	0.32	0.04	0.05	0.99	0.25	
<i>Citharexylum fruticosum</i>	46	0.28	0.04	0.01	1.00	0.19	
<i>Coccoloba uvifera</i>	02	0.43	0.13	0.30	0.55	0.43	
<i>Erythroxylon areolatum</i>	37	0.13	0.03	0.01	1.25	0.09	
<i>Pisonia albida</i>	07	0.11	0.03	0.01	0.20	0.14	
<i>Stahlia monosperma</i>	12	0.15	0.02	0.05	0.30	0.16	
<i>Tabebuia heterophylla</i>	26	0.28	0.04	0.04	0.86	0.18	
<i>Trichilia hirta</i>	19	0.07	0.05	0.00	0.95	0.17	
<u>Distance</u>							
1.00	64	0.26	0.03	0.01	0.99	0.18	A
2.00	63	0.26	0.03	0.02	1.00	0.20	A
3.00	64	0.19	0.03	0.02	1.25	0.13	B
4.00	59	0.16	0.02	0.00	0.86	0.11	B
<u>Direction</u>							
E	60	0.18	0.03	0.02	1.25	0.12	A
N	70	0.25	0.03	0.01	0.95	0.18	A
S	64	0.24	0.03	0.02	0.99	0.20	A
W	56	0.18	0.03	0.00	1.00	0.12	A

Figure 6. Initial height of all saplings vs. growth (m) for all sites combined.



Discussion

Leaf area index and light environment

Leaf area index (LAI) decreased moving away from the nurse tree, indicating the presence of a light gradient under the nurse trees. One possible explanation could be due to the *Leucaena leucocephala*'s crown that consists of small compound leaves that are composed of many small leaflets. The small leaflets, combined with *Leucaena*'s semi-deciduousness, make it an irregular and patchy crown because it drops its leaves depending on the availability of water and varies greatly among individuals. These two factors may influence the presence of the light gradient under the nurse trees. The LAI values for the nurse trees, which ranged from 0.0–3.16 with a mean of 1.16, agree with LAI values of 1.3–3.5 in coastal scrub forests and 2.1–4.0 in semi-deciduous forests at

Guánica Commonwealth Forest (Lugo *et al.* 1978, Murphy and Lugo 1986b). Lugo *et al.* (1978) found that LAI values fluctuate among forest types, with lower values found in open shrublands and higher values found in semi-deciduous forests with deeper soils at Guánica Commonwealth Forest. My results also agree with the LAI of approximately 2 found in Guánica Forest by Dugger (1980). However, these LAI values are low compared to other dry forests in India and Thailand which have mean LAI's of 8 and 6.6, respectively (Murphy and Lugo 1990). Thailand's dry forest receives higher rainfall (1,200 mm/y) than Guánica (860 mm/y) which may explain the higher LAI. In India, however, dry forests receive approximately 800 mm/y of rainfall, lower than Guánica. This difference in higher LAI might be due to India's dry forest having larger forest structure (canopy height and aboveground biomass) (Murphy and Lugo 1990).

Leaf area index and survivorship

All species survivorship responded differently to leaf area index, which indicated different threshold requirements for the light environment under the nurse trees. The two species for which mortality responded to planting distance, agreed with the range found for LAI and survivorship. For example, *Erythroxylon areolatum* had 23% lower mortality moving away from the nurse tree in the third and fourth planting distances. A 75% survivorship was found in a range of LAI between 0.0-1.25 which agreed with the mean LAI found under all nurse trees of 0.23 in the fourth planting distance and 0.78 in the third planting distance. This indicated a preference for *Erythroxylon* for more open environments rather than shady sites under the nurse tree. *Pisonia albida* had only one dead individual in the first planting distance and a threshold of 75% survivorship at 2.0 LAI. These values are similar to the LAI found under all nurse trees in the first planting distance of 2.21 and the second planting distance with 1.47, indicating a preference for more shade under the nurse tree. *Stahlia monosperma* survivorship trend to increase as LAI increased also indicated the species preference for shaded sites. This is an important factor to consider when planting, especially considering that *Stahlia* is an endangered species and needs specific planting techniques in order to assure its survival. This result is particularly of interest to agencies in charge of endangered species, such as the U.S. Fish and Wildlife Service and the Departamento de Recursos Naturales y Ambientales de Puerto Rico which can protect better this species now applying these results to their management plans.

Light environment and growth

Since there was no relationship between leaf area index and growth in either the planted saplings or the Mature Forest Plot, other environmental factors appear to regulate growth. Murphy and Lugo (1986b) have shown that in Guánica Commonwealth Forest, structure and function are closely tied to the availability of water. For example, soil moisture is a major determinant of biomass in tropical forest and in Guánica Forest, almost

50% of the forest biomass is concentrated in its root system, most of it found in the first 90 cm. of soil (Murphy and Lugo 1986b). This not only reflects the overall smaller structure of dry forests in relation to its biomass when compared to wet forests, but also shows how the root distribution increases the efficiency of capturing rainfall. Net primary productivity correlates with annual rainfall and duration of the wet seasons. Peaks of leaf litter production occur during the two dry seasons when the fall of leaves and fine litter is maximum. The ratio of leaf fall to live leaf biomass decreases exponentially with increasing soil moisture reflecting the sensitivity of leaf turnover to changes in water availability. Periods of wet season growth may alternate with periods of dry season shrinkage, clearly indicating the effects of water availability on the two growing seasons (Murphy and Lugo 1986b). Water availability is not the only environmental factor affecting growth in Guánica Forest, Van Bloem *et al.* (2006) found that soil nutrient supply and the effects of hurricane winds also limit growth of dry forest species.

However, light should not be discarded as an environmental factor that could affect growth in indirect ways. The reduced light intensities found under the canopy of nurse trees in the Sierra Nevada Mountains of Spain caused lower radiation and temperatures which produced higher soil humidity. This facilitative mechanism is necessary for successful woody plant establishment and growth (Gómez *et al.* 2001). In open areas of dry forests in India, seedlings encounter high light intensities which resulted in reduced growth from competition from herbs and grasses (Khurana and Singh 2001). Santiago-García *et al.* (2008) found that in Sierra Bermeja in Puerto Rico, native saplings attained greater height in a nurse tree plot compared to an open plot. Canopy closure was approximately 100% in the nurse tree plot which resulted in lower grass accumulation in the understory, reflected by the lower fuel load. Although both plots had a decrease in sapling height after wildfires, saplings in the nurse tree plot were taller than in the open plots, reflecting the effect of high light intensities that produce higher density of grasses which compete and reduce growth of native saplings. Seedlings from dry forests in Mexico achieved higher growth rates under high light treatments (light available under medium-sized gaps) than at low under low light intensities (light under the canopy during the rainy season) (Rincón and Huante 1993). However, Ray and Brown (1995) found that for the 10 species they planted in dry forests in St. John, shade plots had no effects on growth compared to unshaded plots.

Stahlia monosperma was the only species that growth responded to leaf area index. Although there is little information about the shading requirements for this species, *Stahlia's* growth trend to increase as LAI increased agrees with the mortality patterns found in this project for this species, which follow the same trends. These results further suggest *Stahlia's* preference for shaded sites.

Mortality

Overall general mortality was comparable to other nurse tree and dry forest restoration projects. In the only other nurse tree project in Puerto Rico, with *Leucaena leucocephala* also as its nurse tree, overall mortality was 62% of 165 trees after 6 years of planting (Santiago-García *et al.* 2008) compared to 53-65% mortality of 240 trees after 2 years of planting at Guánica and Sierra Bermeja. Even though having the same nurse tree species and sharing a common planting site (Sierra Bermeja), it is worth noting that this research only measured data for two years compared to six years in Santiago-García *et al.* (2008). Also, both had different causes of mortality, with most of the mortality in the Santiago-García project caused by two wildfires and the mortality in this project can be attributed to different water treatments and time of planting. This site received an annual 829 mm of rainfall for the period of 2002-2007 (Santiago-García *et al.* 2008), similar to the annual rainfall for Guánica (860 mm). Ray and Brown (1995) had 48% mortality of 800 seedlings after 9 months of planting in a dry forest restoration project evaluating propagation techniques on the island of St. John. Their experimental sites received an annual rainfall of 880 mm for the period of 1990-1992, also similar to the sites of this project. In a nurse tree experiment in Russia, Eränen and Kozloz (2007) had 95% mortality of 100 trees after two years of planting in one of their study sites and 50% mortality after 5 years in their second site. Other reforestation projects have resulted in lower mortalities. Since 1980, for example, in Puerto Rico the U.S. Fish and Wildlife Service has planted nearly 17,500 trees of 80 species in the whole Caribbean Islands National Wildlife Refuge complex, mainly in the Laguna Cartagena and the Wildlife Refuge areas of which approximately 80% of the species have survived. These two sites receive an annual rainfall of 940 mm (Weaver and Schwagerl 2008).

Difference in mortality between sites can be attributed to different water treatments and time of planting. Low mortality (8.1%) at the CRNWR was most likely because planting was performed during the rainy season (September 2007) and I was able to water the trees for approximately three months after planting. Although planted in October in the rainy season, the high mortality (53%) at Guánica Commonwealth Forest can be attributed to the fact that I was not able to water after planting and the saplings only received rainwater. The high overall mortality of 65% in Sierra Bermeja can be attributed to time of planting. This plot was planted during the dry season (February 2008) however; the trees were watered weekly for at least two months after planting. These results suggests that the combination of planting during the rainy season and watering for at least three months after planting, along with planting under nurse trees as shown by the low mortality at the CRNWR compared to full sun planting, will result in lower mortality than planting during the dry season with no watering at full sun.

Patterns of mortality within sites

Higher mortality at full sun at the CRNWR clearly shows that even with planting during the rainy season and with supplemental watering, planting under nurse trees resulted in lower mortality. As shown by the low mean value of leaf area index of 0.26, the high light environment of the fourth planting distance may result in decreasing vapor pressure deficit and photoinhibition, which may cause reduced photosynthetic performance of the saplings (Badano *et al.* 2009). Light environment could potentially be a more regulating factor for establishment for seedlings rather than saplings for dry forest species, since it is likely that solar radiation and soil moisture together regulate seed germination, seedling establishment and survival (Ray and Brown 1995). However, many dry forest restoration studies have not used saplings in their trials. In India, dry forest seedlings that emerge during the rainy season experience reduced intensities of light under relatively closed canopies while those in open areas encounter high light intensities and face competition from fast growing dense populations of grasses and shrubs (Khurana and Singh 2001). In the island of St. John, Ray and Brown (1995) found that in greenhouses, shading significantly increased survivorship of germinated seedlings from six species, with 47.3% survivorship in shaded plots and 38.9% survivorship in unshaded plots. Also in the same experiment, survivorship of seedlings planted in the field from ten species was 22.5% higher in shaded than in unshaded plots (Ray and Brown 1995). Greenhouse experiments with 16 native tree species from Puerto Rico have shown that in general, germination and seedling survival increased with an augment in shading and soil moisture levels (Carvajal 2001). However, since mortality did not respond to planting distance from the nurse tree at any other site, suggests that other environmental stress factors rather than light environment may be affecting mortality. These other factors can include competition, time of planting (wet vs. dry season) and watering treatments. Ray and Brown (1995) found that seedling survivorship was generally related to the timing and quantity of rainfall, with most species having greater mortality during drought periods in the dry season. Badano *et al.* (2009) concluded that, for dry forest restoration in Mexico, higher survival of oak seedlings required the presence of nurse trees and additional watering during some months of the dry season. My results agree with this finding, that the combination of planting during the rainy season and watering for at least three months after planting, along with planting under nurse trees reduces mortality of native dry forest species.

Differences in mortality among species

Erythroxylum areolatum and *Pisonia albida* showed significant differences in mortality by distance from the nurse tree. *Pisonia* had only one dead individual at the first planting distance while *Erythroxylum* showed lower mortality moving away from the nurse tree in the third and fourth planting distance indicating a preference for more open sites, possible due to competition for water or nutrients from the nurse tree (Padilla and Pugnaire 2006). In one of their study sites, Eränen and Kozloz (2007) found that pine seedlings planted closest to the

nurse tree had the highest mortality rate during the first year of planting, however seedling survival was not affected by planting distance in their second site.

Stahlia monosperma showed significant differences in mortality in cardinal direction with no dead individuals in the north planting direction. The north planting direction had less mortality at Guánica and at the CRNWR, which could indicate a preferable planting direction for future reforestations, although the actual mechanisms for which this operates is not known. For *Bursera simaruba* at Guánica, mortality was 40% greater at the west planting direction with two dead individuals. Although there is little information about the effect of planting direction on planted trees under nurse trees, Castro *et al.* (2004) found in the Sierra Nevada mountains of Spain that when thorny shrubs are used as nurse plants, establishment of plants varied by the north and south directions. The north planting direction was similar under the nurse plant on which there was higher growth and survivorship than the south side which was similar to open sites. They attribute the facilitation mechanism to the modification of the understory microclimate due to the improved water status of the seedlings through reduction of radiation, lowering soil temperature, and conserving soil moisture. They supported their conclusion by the fact that survival on the south side of the nurse shrubs, where microclimatic conditions were close to those in open microhabitats was similar to the survival in the open microhabitat in contrast to the higher values for the north side of the nurse shrubs, supporting a direct effect of shading (Castro *et al.* 2004).

Bourreria succulenta, *Stahlia monosperma* and *Trichilia hirta* had low or no mortality under the nurse trees. In a dry forest restoration project, Ray and Brown (1995) found that seedling survivorship was significantly higher in artificially shaded plots than in unshaded plots. Gómez-Aparicio *et al.* (2004) found that shrubs acting as nurse plants significantly increased planted seedling survival in a restoration project in the Sierra Nevada mountains in Spain. After the first year of planting, establishment was more than double under the shrubs than in open areas but the outcome varied depending the nurse plant target species and year after planting. Seedling mortality of the giant cardon cactus was high until the first year of planting, then varied differentially according to the leguminous nurse tree species (Suzan-Azpiri and Sosa 2006). The high mortality in *Coccoloba uvifera* and *Pisonia albida* needs to be noted since they have low replications and only planted in one site. Further research with these two species is needed to confirm these results.

Growth

The generally low growth of all species can be the result of a range of factors. Since dry forests species generally have a large proportion of their biomass concentrated in their root system (approximately 50% in Guánica Forest, Murphy and Lugo 1986a), it is possible that the saplings were rooting to become established and would later concentrate growth on the aerial part of the plant. This root:shoot ratio biomass is high compared to

other moist and wet forests, where the root biomass comprises 30% of the total biomass (Brown and Lugo 1982). This slow growth, with a general mean growth between all species of 0.22 m, is higher than a set of saplings from 5 species, including *Bursera simaruba*, in the Mature Forest Plot in Guánica Commonwealth Forest, which averaged 0.07 m (Van Bloem, unpublished data). The higher mean growth in my plots could be explained by the fact that the saplings in the Mature Forest Plot are older than the saplings planted in this project, with the Mature Forest Plot saplings being measured since 1998. Most of these saplings have already grown to become young trees, which they may already have reached their maximum mean growth rates. Also, early successional species like *Bourreria succulenta* and *Tabebuia heterophylla* sometimes tend to grow faster than late successional species which would also lead to higher overall growth (Murphy and Lugo 1986a).

Overall average growth increased by 0.10 m closer to the nurse tree, indicating facilitative effect of the nurse trees on the planted saplings. My growth results match other nurse tree experiments in that planting distance affected growth. Eränen and Kozloz (2007) found in one of their sites that planting distance had a marginally significant effect on seedling height but in their second site planting distance had no effect on growth. Santiago-García *et al.* (2008) found higher median height of saplings planted under *Leucaena* nurse trees than in an open plot. In the Sierra Nevada Mountains of Spain, Gómez-Aparicio *et al.* (2004) found that 76% of their planted seedlings had higher growth under the shrub nurse plants than in open sites.

Dry forest management

In general, this study suggests that *Leucaena leucocephala* nurse trees at the CRNWR can decrease mortality compared to full sun planting and increase growth, indicating that nurse trees are not competing with the planted saplings. On a species level, *Bourreria succulenta*, *Pisonia albida*, *Stahlia monosperma* and *Trichilia hirta* had lower mortality or no mortality under the nurse tree, indicating that these species respond positively to being planted under nurse trees. Conversely, *Erythroxylum areolatum* mortality was significantly higher under nurse trees, highlighting that not all species are appropriate for nurse tree reforestation. Overall growth was 0.10 m higher closer to the nurse tree in the first two planting distances, which indicates that nurse trees can be a promising tool for establishing native dry forest species for restoration. There are other benefits of having nurse trees besides increasing growth and lowering mortality, like reducing the risk of a wildfire. Santiago-García *et al.* (2008) found that in southwestern Puerto Rico planting under *Leucaena leucocephala* limited grass growth, reduced fuel loads, and resulted in greater postfire stem survival. Also, nurse trees can provide perches for birds to rest, feed and disperse seeds (Wolfe 2009), help control erosion, enrich the soil by leaf litter and sediment accumulation, higher mineralization rates and larger microorganism populations (Padilla and Pugnaire 2006).

Chapter 3. Using specific leaf mass and leaf density as criteria for species selection in dry forest restoration

Literature Review

Introduction

Specific leaf area, leaf mass and leaf density are important plant traits that are related to resource use and acquisition. Specific leaf area is the ratio of projected leaf area to leaf weight (Awal *et al.* 2004) while specific leaf mass (SLM) is dry leaf weight by unit area (Martínez-Garza *et al.* 2005). Leaf density, measured in this study, is the amount of cytoplasm in a leaf (Martínez-Garza *et al.* 2005). These traits are related to ecological processes such as light interception, leaf growth, structure, net photosynthesis and transpiration. Specific leaf area can be used to estimate total leaf area at various stages of growth and, in conjunction with leaf area and leaf mass, it is used to for growth estimates and nutrient balance calculations (Awal *et al.* 2004).

Environmental factors, especially light, can have substantial developmental effects on the area and thickness of leaves. Generally, plants growing in high light intensities, like dry forest species, have smaller leaf area, higher leaf density, water content and SLM than species growing in lower light intensities like rain forests (Raven *et al.* 2003, Martínez-Garza *et al.* 2005). The increased thickness of these high light species is due mainly to a greater development of the palisade parenchyma. Also, their vascular system is more extensive and the walls of epidermal cells are more extensive than rain forest species growing in low light intensities. The ratio of the internal surface area of the mesophyll to the area of the leaf blade is much bigger in high light species. Although both types of species have similar photosynthetic rates at low light intensities, dry forest species are adapted to high light intensities and consequently have considerably higher maximum photosynthetic rates under these conditions (Raven *et al.* 2003). In tropical rain forests, quantitative changes in these leaf traits are in part responsible for increased growth rates under high light levels (Martínez-Garza and Howe 2005).

These morphological and physiological traits are in response to tolerance in favorable and unfavorable environmental conditions. Species with smaller leaf area per dry weight and higher leaf density, like dry forest tree species, are able to tolerate drought stress to a greater degree because they possess lower rates of CO₂ assimilation and are still able to photosynthesize during periods of low precipitation (Schulze *et al.* 2005). As stomata close during water stress, water-use efficiency may increase by taking up more CO₂ per unit of water transpired because stomatal closure inhibits transpiration more than it decreases intercellular CO₂ concentrations (Taiz and Zeiger 2002). In general, species with low specific leaf area, high leaf density and high SLM show a lower metabolic activity than species with higher specific leaf area and lower SLM. It is likely that these traits maximize resource use in leaves by maximizing photosynthesis and minimizing water loss (Martínez-Garza *et*

al. 2005, Schulze *et al.* 2005). Specific leaf mass has been positively correlated with leaf water use efficiency in some crops like alfalfa, in which the leaves are cooler under a given radiation load due to higher stomatal conductance and lower water vapor pressure deficit (Awal *et al.* 2004).

Small leaf area, high leaf density and high SLM are adaptations for high light conditions that are present in early-successional habitats and tropical dry forests. The high light conditions are created by the high turnover of fast growing pioneer species and their patchy canopies, previous land use or disturbance that are typical of early-successional habitats in dry forest communities. These will create heterogeneous forest-floor light microenvironments that are susceptible to fluctuations in light intensity during dry periods due to leaf drop (Brown and Ray 1993). Precipitation patterns and the spatial and temporal variation in the canopy thickness will regulate light availability under the canopy which in turn regulates soil moisture content (Castilleja 1991). Also, some species will have to adjust to a change in specific leaf area if they have to drop their leaves due to water stress. Such a leaf area adjustment is an important long-term adaptation that improves the plant's fitness in a water-limited environment like dry forests. Leaf abscission during water stress results largely from enhanced synthesis of and responsiveness to the plant hormone ethylene (Taiz and Zeiger 2002). Plant species that are able to adjust these morphological traits either have a phenotypic response to immediate environmental conditions or have strategic responses to environmental conditions through developmental change (Martínez-Garza and Howe 2005). Through either mechanism, these species already have the morphological adaptations to survive in these highly variable light conditions, then a measure of variability of leaf area, leaf density and leaf mass known to change in response to light and water availability may reflect the species capacity to adjust leaf morphology to different light or water microhabitats.

These morphological traits could be used as an advantage when it comes to restoring early-successional dry forest communities. Planting a mix of early-successional pioneer species along with later-successional mature species may be an alternate reforestation method that can catalyze succession by reestablishing forest structure and composition quickly and promote native plant-animal interactions. Empirical evidence suggests that late-successional species can grow and survive in early-successional habitats if they get there (Martínez-Garza *et al.* 2005). In any restoration project, selecting adequate species is a critical step that can determine the success of a restoration project since selecting inadequate species can result in total mortality of the individuals planted. This is also true when planting later-successional species in early-successional habitats; however, it is unknown what species are better able to tolerate the variable and sometimes severely xeric abiotic conditions of early-successional dry forest communities. This is an important aspect to consider when restoring dry forest, since altered species composition and alien species invasion are the most significant long-term effects of human land-use and landscape modification that result in these early-successional communities. These alien species persist in mature forests even after 100 years of abandonment and forest composition does not return to that of

the original forest (Molina-Colón and Lugo 2006). This pattern of dry forest regeneration presents an opportunity to enrich the species composition of early-successional plant communities.

In order to plant these species, one must decide what species would be suitable and what characteristics provide adaptability to harsh early-successional habitats. One approach is to determine a plant trait that relates to growth and survival. Since saplings will be growing in a heterogeneous light environment due to the high turnover of fast growing pioneer species and their patchy canopies, variability in specific leaf mass and density may reflect the capacity of saplings to adjust to the changing light environment, as has been demonstrated in tropical forests (Martínez-Garza *et al.* 2005). Variability in specific leaf mass and leaf density can therefore be expected to be positively related to growth and survivorship.

Materials and Methods

Study site

This study was conducted in the municipalities of Cabo Rojo and Guánica in southwestern Puerto Rico. This area is classified as subtropical dry forest (Holdridge 1967). Annual rainfall averages 860 mm at Guánica Commonwealth Forest and it is distributed bimodally into two seasons. There is a strong dry period from December to April and a lesser one from June to August (Murphy and Lugo 1986a).

Samples were taken from three established reforestation plots at a private property in the Sierra Bermeja hills, at the U.S. Fish and Wildlife Cabo Rojo National Wildlife CRNWR and in Guánica Commonwealth Forest. Samples were also taken at a mature forest plot in Guánica (Murphy and Lugo 1986a) to compare variability in leaf mass and density with species in a reforestation project.

Sierra Bermeja, Cabo Rojo: This site was located on a 16.5 ha property. Mean annual rainfall from 2002-2007 was 829 mm. The site was previously used for grazing. The site experienced two recent fires, one in February 2006 and another in March 2007. *Leucaena leucocephala* dominated the upper part of hill while downhill *Leucaena* was present along with *Bucida buceras* L, *Bursera simaruba* (L.) Sarg. and *Bourreria succulenta* Jacq. The moderate to well drained, shallow sandy loam soils are Aridisols derived from ultrabasic rock (serpentinite) from the Casabe-Cerro Mariquita-Llanos Costa- Maguayo association.

Cabo Rojo National Wildlife CRNWR, Cabo Rojo: This site was located in the 751 ha Cabo Rojo National Wildlife CRNWR, part of the Caribbean Islands National Wildlife CRNWR Complex. Annual rainfall has averaged 840 mm from 1991-2000. Past land uses included almost two hundred years of sugar cane production and cattle ranching. It is also prone to fire and has burned in the past. The property was transferred to

the U.S. Fish and Wildlife Service in 1974 where cattle ranching continued until 1978 when the first CRNWR manager arrived. The CRNWR was dominated by exotic grasses like *Urochloa maxima* and *Pennisetum ciliare* and trees like *Leucaena leucocephala*, *Prosopis pallida* and *Melicoccus bijugatus*. The well drained to excessively drained, level to sloping sandy soils are Vertisols from the Americo-Guayabo-Sosa association.

Guánica Commonwealth Forest, Pitirre sector and Mature Forest Plot: These sites were located within the 4,400 ha that comprises the Guánica Commonwealth Forest. Annual rainfall has averaged 860 mm. over the last 70 years. The Pitirre sector is patch of coastal forest that lie at sea level and had been previously used for agriculture until the 1970's. It was a *Leucaena leucocephala* dominated stand with some *Croton* in the understory along with exotic grasses like *Pennisetum ciliare* and *Urochloa maxima*. The Mature Forest Plot is a mature stand that lies between 125-150 m above sea level. It has been a closed forest since at least 1938 and there is no evidence of logging since the 1930's (Murphy and Lugo 1986a). The moderately well drained to poorly drained, nearly level to sloping and calcareous alluvial soils are Mollisols from the Fraternidad-Aguirre-Cartagena association.

Sample collection

400 saplings from 10 native species (Table 7) were planted between September 2007 and January 2008. From these saplings, the 250 surviving individuals were sampled in April 2009. These saplings were planted under nurse trees of *Leucaena leucocephala* from a previous experiment (Chapter 2). *Coccoloba uvifera* was excluded from the analyses because it only had two surviving individuals. Initial tree sapling sizes ranged from 0.2 to 2.2 m at the time of planting. Growth (m) and survivorship were measured for the period of 2007-2009. Sampling was also performed on 229 individuals from five species in the Mature Forest Plot (Table 8). For these species, growth and survivorship was used from data for the period of 1998-2006. To determine variability in specific leaf mass (SLM) and density (LD), one mature, fully expanded leaf per individual was collected and stored in individual plastic bags. For species with compound leaves, one mature, fully expanded leaflet was collected. Fresh weight (g) was measured within 2-3 hours of collection and then pressed and air dried for one week to obtain dry weight. Leaves were scanned using ImageJ program to measure leaf area. With these data, leaf mass per unit area [SLM = (dry weight/leaf size)] and leaf density [LD = fresh weight/dry weight] were calculated. Variability in SLM and leaf density is reported as the coefficient of variation for each trait.

Leaf area indices (LAI) were measured at the point where each sapling was planted and recorded with a LICOR LAI 2000. Measurements were taken in November 2009. These were taken early in the morning (7:30-10:30) and in the afternoon (3:30-5:30), one above the crown of the nurse tree and one below the crown just

above each sapling. Also, LAI measurements were taken on the Mature Forest Plot to compare with the LAI of the saplings planted. The coefficient for light diffusion and standard error for the LAI's were calculated by the LAI-2000 data logger.

Statistical Analysis

Data were analyzed with Infostat/Professional. Descriptive statistics were performed by species to determine mean and the coefficient of variation for each leaf trait. Relationships between specific leaf mass and density and growth, mortality and leaf area indices were analyzed with linear regressions. A alpha value of 0.1 was used because rejecting the null hypothesis (variability in leaf mass and density do not have an effect on growth and mortality) falsely will not have negative long term effects on restoration projects, but failure to identify important planting techniques because of low sample size would be more serious.

Table 7. List of species and their planting sites. Aspects of their leaf habit and type of seed dispersal is also mentioned following Little, Wadsworth and Marrero (2001).

<u>Species</u>	<u>Planting Site</u>			<u>Leaf Habit</u>		<u>Seed Dispersal Mechanism</u>	
	<u>Guánica Commonwealth Forest</u>	<u>Cabo Rojo National Wildlife CRNWR</u>	<u>Sierra Bermeja</u>	<u>Deciduous</u>	<u>Evergreen</u>	<u>Animal</u>	<u>Wind</u>
<i>Bourreria succulenta</i> Jacq.	X	X			X	X	
<i>Bucida buceras</i> L.	X	X	X	X			X
<i>Bursera simaruba</i> (L.) Sarg.	X	X		X		X	
<i>Citharexylum fruticosum</i> L.	X	X	X		X	X	
<i>Coccoloba uvifera</i> (L.) L.	X				X	X	
<i>Erythroxylum areolatum</i> L.	X	X	X	X		X	
<i>Pisonia albida</i> (Heimerl) Britton	X			X		X	
<i>Stahlia monosperma</i> (Tul.) Urban		X			X	X	
<i>Tabebuia heterophylla</i> (DC.) Britton	X	X	X	X			X
<i>Trichilia hirta</i> L.		X		X		X	

Table 8. List of sapling species measured at the Mature Forest Plot in the Guánica Commonwealth Forest (Van Bloem, unpublished data).

<u>Species</u>	<u>Leaf Habit</u>		<u>Seed Dispersal Mechanism</u>	
	<u>Deciduous</u>	<u>Evergreen</u>	<u>Animal</u>	<u>Wind</u>
<i>Amyris elemifera</i> L.		X	X	
<i>Bursera simaruba</i> (L.) Sarg.	X		X	
<i>Eugenia foetida</i> Pers.		X	X	
<i>Exostema caribaeum</i> (Jacq.) Roem. & Schult	X			X
<i>Gymnanthes lucida</i> Sw.		X	X	

Results

Average and Coefficient of Variation of Specific Leaf Mass

The average specific leaf mass (SLM) and their respective coefficient of variations (CV) of all surviving individuals by April 2009 are shown in Table 9. Average SLM for all planted saplings was 12.43 mg/cm². For the planted saplings, *Citharexylum fruticosum* was the species with the highest mean SLM with 19.2 mg/cm² and *Trichilia hirta* was the species with the lowest mean SLM with 2.28 mg/cm². *Pisonia albida* was the species with the highest CV of SLM with 84.8 and *Bourreria succulenta* was the species with the lowest CV of SLM with 9.2. In the mature forest plot, the average SLM was 8.6 mg/cm². *Amyris elemifera* had the highest mean SLM with 13.3 mg/cm² and *Eugenia foetida* had the lowest mean SLM with 1.4 mg/cm². *Bursera simaruba* was the species with the highest CV of SLM with 61.4 and *Gymnanthes lucida* was the species with the lowest CV of SLM with 15.8.

Table 9. Distribution of the specific leaf mass (mg/cm^2) by species. Species in bold were sampled in the mature forest plot at Guánica Commonwealth Forest.

Species	n	Mean	S.E.	CV	Minimum	Maximum	Median
<i>Amyris elemifera</i>	53	13.3	2.2	54.3	5.4	23.5	12.2
<i>Bourreria succulenta</i>	26	14.2	0.7	9.2	12.8	15.4	14.3
<i>Bucida buceras</i>	37	15.1	2.4	31.3	9.3	20.8	15.0
<i>Bursera simaruba</i>	15	12.1	1.8	61.4	8.1	14.6	11.2
<i>Bursera simaruba</i>	38	11.5	1.3	23.0	7.9	13.9	12.0
<i>Citharexylum fruticosum</i>	46	19.2	1.3	13.4	16.7	22.7	18.7
<i>Erythoxylon aerolatum</i>	37	11.3	1.1	18.6	9.2	13.3	11.4
<i>Eugenia foetida</i>	60	1.4	1.4	27.2	1.1	3.9	2.4
<i>Exostema caribaeum</i>	41	3.7	2.0	33.2	1.5	4.9	3.6
<i>Gymnanthes lucida</i>	60	12.5	1.1	15.8	10.2	14.2	12.9
<i>Pisonia albida</i>	7	11.3	4.8	84.8	2.8	21.9	11.7
<i>Stahlia monosperma</i>	12	12.2	3.1	51.3	4.9	19.5	12.2
<i>Tabebuia heterophylla</i>	26	2.3	0.3	28.3	1.6	3.2	2.2
<i>Trichilia hirta</i>	19	2.3	1.1	33.3	1.2	3.4	2.3

Average and Coefficient of Variation of Leaf Density

The coefficients of variations (CV) for leaf density of all surviving individuals by April 2009 are shown in Table 10. *Coccoloba uvifera* was excluded from the analyses because it only had two surviving individuals. For the planted saplings, *Bursera simaruba* had the highest mean leaf density with 3.8 and *Stahlia monosperma* had the lowest mean leaf density with 1.2. *Pisonia albida* was the species with the highest CV of leaf density with 12.5 and *Tabebuia heterophylla* was the species with the lowest mean CV with 2.0. In the mature forest plot, *Eugenia foetida* had the highest mean leaf density with 2.7 and *Exostema caribaeum* had the lowest mean leaf density with 1.2. *Bursera simaruba* had the highest CV with 5.3 and *Exostema caribaeum* had the lowest CV with 2.3.

Table 10. Distribution of leaf density by species. Species in bold are present in a mature forest plot at Guánica Commonwealth Forest.

Species	n	Mean	S.E.	CV	Minimum	Maximum	Median
<i>Amyris elemifera</i>	53	1.3	0.03	3.5	1.2	2.1	1.7
<i>Bourreria succulenta</i>	26	1.5	0.02	2.9	1.5	1.6	1.5
<i>Bucida buceras</i>	37	1.4	0.03	4.6	1.3	1.5	1.4
<i>Bursera simaruba</i>	15	3.3	0.14	5.3	3.2	4.5	3.8
<i>Bursera simaruba</i>	38	3.8	0.1	5.8	3.6	4.2	3.8
<i>Citharexylum fruticosum</i>	46	3.2	0.08	5.4	3.0	3.5	3.2
<i>Erythoxylon aerolatum</i>	37	1.6	0.04	4.6	1.5	1.9	1.7
<i>Eugenia foetida</i>	60	2.7	0.07	4.2	1.4	2.8	1.9
<i>Exostema caribaeum</i>	41	1.2	0.03	2.3	1.1	1.8	1.2
<i>Gymnanthes lucida</i>	60	1.5	0.07	3.7	1.2	2.0	1.5
<i>Pisonia albida</i>	7	2.2	0.12	12.5	1.7	2.4	2.2
<i>Stahlia monosperma</i>	12	1.2	0.04	7.1	1.2	1.4	1.2
<i>Tabebuia heterophylla</i>	26	1.5	0.01	2.0	1.5	1.5	1.5
<i>Trichilia hirta</i>	19	1.5	0.02	2.7	1.5	1.6	1.6

Leaf Area Indices and Specific Leaf Mass

There was not a relationship between the specific leaf mass and leaf area index ($r^2=0.003$, $p=0.3582$) or the coefficient of variation of specific leaf mass and leaf area index ($r^2=0.01$, $p=0.1243$). In the mature forest plot, no relationship was found between specific leaf mass and leaf area index ($r^2=0.0009$, $p=0.6413$) or the coefficient of variation of specific leaf mass and leaf area index ($r^2=0.04$, $p=0.2040$).

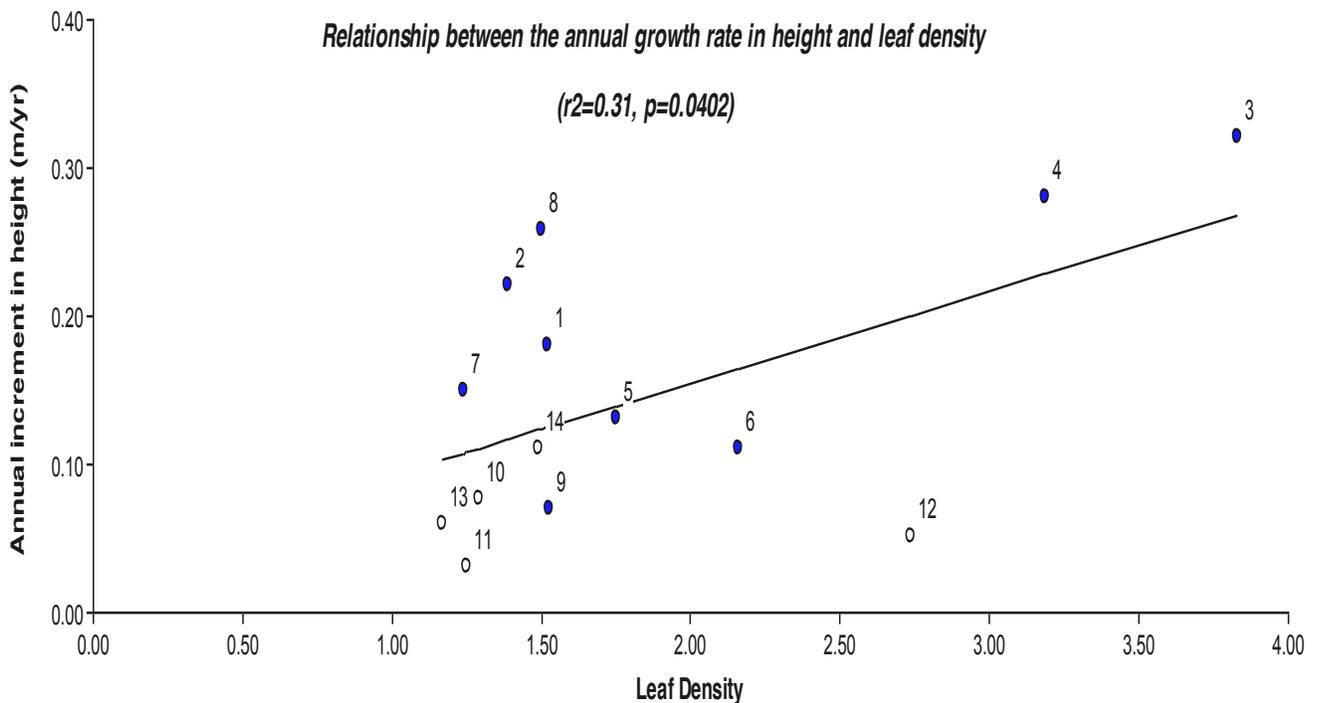
Survivorship and Specific Leaf Mass and Leaf Density

There was not a relationship between survivorship and specific leaf mass ($r^2=0.002$, $p=0.9067$) or leaf density ($r^2=0.21$, $p=0.2164$). Contrary to expected, survivorship was not related to an increase in CV of SLM ($r^2=0.28$, $p=0.1417$) or leaf density ($r^2=0.16$, $p=0.2798$). In the mature forest plot, no relationship was found between survivorship and specific leaf mass ($r^2=0.03$, $p=0.7647$) or coefficient of variation in specific leaf mass ($r^2=0.44$, $p=0.2208$) nor was survivorship related to leaf density ($r^2=0.68$, $p=0.1848$) or the coefficient of variation of leaf density ($r^2=0.58$, $p=0.1352$).

Growth and Specific Leaf Mass and Leaf Density

For all surviving saplings grouped together, overall growth was not related to specific leaf mass ($r^2=0.01$, $p=0.1986$) or the coefficient of variation in specific leaf mass ($r^2=0.01$, $p=0.1081$). No individual species presented any relationship between growth and specific leaf mass or the coefficient of variation of specific leaf mass (See Appendix). For all species, growth tended to increase as leaf density increased ($r^2=0.31$, $p=0.0402$) (Figure 7). However, there was not a relationship between the coefficient of variation of leaf density and growth ($r^2=0.04$, $p=0.5916$). In the mature forest plot for the period of 1998-2006, no relationship was found between growth and specific leaf mass ($r^2=0.13$, $p=0.5589$) or the CV of SLM ($r^2=0.40$, $p=0.2529$). Growth was not related to leaf density ($r^2=0.02$, $p=0.8169$) or the CV of leaf density ($r^2=0.22$, $p=0.4238$).

Figure 7. Relationship of the annual growth rate in height on the leaf density of 9 planted saplings (blue) and 5 saplings in the Mature Forest Plot (white).



1- *Bourreria succulenta* 2- *Bucida buceras* 3- *Bursera simaruba* 4- *Citharexylum fruticosum*
 5- *Erythroxylon aerolatum* 6- *Pisonia albida* 7- *Stahlia monosperma* 8- *Tabebuia heterophylla*
 9- *Trichilia hirta* 10- *Amyris elemifera* 11- *Bursera simaruba* 12- *Eugenia foetida* 13- *Exostema caribaeum* 14- *Gymnanthes lucida*

Discussion

Average and Coefficient of Variation of Specific Leaf Mass and Density

The results for average specific leaf mass show expected values for species growing in high light conditions like dry forest species. In this study, the average specific leaf mass for the planted saplings was 12.4 mg/cm² compared to 10.0 mg/cm² in a savannah type habitat in Brazil (cerrado). Both habitats are similar; the sites for the planted saplings are degraded dry forests that resemble savannahs. In the Mature Forest Plot, average SLM was 8.6 mg/cm² compared to 7.5 mg/cm² in a dry forest in Brazil (Neves *et al.* 2009). The difference in average SLM between the planted saplings and the species in the Mature Forest Plot might be in response due to the higher light intensities under the patchy canopies of the nurse trees compared to the denser canopy cover of the Mature Forest Plot. Species might have developed higher SLM probably to maximize resource use in leaves (Martínez-Garza *et al.* 2005).

These values, from the range of 2.28 mg/cm² to 19.2 mg/cm² with an average of 12.4 mg/cm², are higher than reported SLM values for rainforest species. In an experimental reforestation in a lowland rainforest in Mexico, species SLM ranged from 5.49 to 10.22 mg/cm² with an average of 7.6 mg/cm² (Martínez-Garza and Howe 2005). This marked difference clearly shows that species growing in high light conditions in dry forests have higher SLM than species growing in low light conditions like rainforests. This strategy of having higher SLM may maximize photosynthesis, minimize water loss (Martínez-Garza *et al.* 2005, Schulze *et al.* 2005) and are still able to photosynthesize with low precipitation (Schulze *et al.* 2005). The range for the coefficient of variation (CV) for SLM for all trees (9.2-84.8) was higher than the range for CV of SLM for the rainforest species (6.6-51.5) (Martínez-Garza *et al.* 2005) probably indicating that high intraspecific variation in SLM is an adaptation for high light conditions of dry forest species. The lack of leaf density data from other reforestation projects does not enable for comparisons, however the range of CV of leaf density for the rainforest species (2.1-30.9) (Martínez-Garza *et al.* 2005) was higher than the range for CV of leaf density for all saplings (2.0-12.5). Perhaps the lower intraspecific variation in leaf density in dry forest species might indicate that leaf density may need to be relatively stable in order to resist periods of drought.

Leaf Area Indices, Survivorship and Growth on and Specific Leaf Mass and Density

No relationship was found between specific leaf mass and leaf area index or the coefficient of variation of specific leaf mass and leaf area index in either the planted saplings or the Mature Forest Plot. No data were found in the literature for any relationship between these two traits. Contrary to expected, neither survivorship nor growth were related to SLM or an increase in CV of SLM. These results differ from those obtained from a

rainforest in southeast Mexico, where mid-canopy species with a range of CV of SLM of 2.6% to 33.3% lower than the planted saplings show increased growth rates and survival with increasing CV of SLM (Martínez-Garza *et al.* 2005). Dry forest species tend to have smaller leaves, higher SLM and lower growth rates than rainforest species with larger leaves, lower SLM and higher growth rates (Martínez-Garza *et al.* 2005). It is possible that since dry forest species do not have to go through an intense light environment change as they grow up to the canopy because of the deciduousness of many of the species, they already have the variability needed to survive and grow in a dry forest environment and increasing this variability will decrease growth and survivorship. Tree fall gaps, which are focal regeneration sites in tropical rainforest, can decrease seedling survivorship in dry forest, even for light-demanding trees because of the extreme temperatures and low humidity (Viera and Scariot 2006).

For the planted saplings, increased leaf density represented higher growth, probably indicating that thicker leaves probably developed in response to the high light conditions present at the planting sites. Leaf density is expected to increase during water-stress to enhance water holding capacity of leaves (Niinemets 2001). However, since there was no relationship between leaf density or the CV of leaf density in the Mature Forest Plot, it appears that as individuals mature under a more closed and denser canopy, leaf density tends not to relate to growth in any form. It is suggested that species with high intraspecific variability in SLM should not be used for dry forest restoration since it may lead to lower growth rates and higher mortality than species with lower SLM; however species with high leaf density should have higher growth rates than species with lower leaf density. This study shows the importance of adjusting restoration methods to the specific sites, since a reforestation tool that works in rainforests does not apply in dry forests.

Chapter 4

Conclusions

The results from the previous chapters contribute to our understanding of dry forest restoration, which unfortunately lacks specific restoration techniques, especially in Puerto Rico. The need to provide appropriate restoration techniques is critical in dry forests, since forest recovery after different land-uses will usually lead to a different species composition from the original forest (Molina-Colón and Lugo 2006). For land managers and ecologists alike, this pattern of forest response requires specific planting and management methods aimed at improving the establishment success of native dry forest tree species. The results from these studies provide new insight on the effectiveness of nurse tree reforestation as a tool to increase growth and survivorship of native tree species and the use of variability in leaf morphology as criteria for species selection in dry forest restoration.

I assessed the relationship of the light environment of the understory of the nurse trees to the growth and survivorship of ten native saplings. The light environment under the nurse trees varied, with leaf area index decreasing moving away from the nurse tree, indicating the presence of a light gradient under the nurse trees. This pattern of decreasing LAI did not affect growth of any species, suggesting that a combination of other environmental factors, mostly water availability is regulating growth. Only three species survivorship responded to leaf area index, with *Pisonia albida* and *Stahlia monosperma* having greater survivorship as leaf area index increased. *Erythroxylum aerolatum* presented the contrary response, with survivorship increasing as leaf area index decreased. Overall mortality reflected different water treatments and time of planting, with mortality being lower when planted under the nurse trees during the rainy season and watered for at least three weeks after planting. Only two species mortality responded to planting direction, with *Erythroxylum aerolatum* had lower mortality moving away from the nurse tree while *Pisonia albida* had low mortality closer to the nurse tree. Only two species mortality responded to planting direction, with *Bursera simaruba* having greater mortality at the west and *Stahlia monosperma* having no mortality at the north. *Stahlia monosperma* had less mortality under the nurse tree than in full sun while *Erythroxylum areolatum* had greater mortality under the nurse tree than in full sun. Growth varied by species, with *Erythroxylum areolatum*, *Pisonia albida* and *Trichilia hirta* having 0.13 m or less of growth and *Bursera simaruba*, *Citharexylum fruticosum* and *Tabebuia heterophylla* having an average of 0.28 m of growth or greater. In general, planting closer to the nurse tree increases growth, with the first and second planting distances closer to the nurse tree having an average of 0.10 m of higher growth than the third and fourth planting distances.

The average specific leaf mass (SLM) showed expected values for species growing in high light conditions like dry forest species. Neither survivorship nor growth was related to SLM or an increase in CV of SLM suggesting they already have the variability needed to survive and grow in a dry forest environment. Increasing variability in SLM will decrease growth and survivorship for dry forest species. For the planted saplings, increased leaf density represented higher growth rates than species with lower leaf density. Species with high intraspecific variability in SLM should not be used for dry forest restoration since it may lead to lower growth rates and higher mortality than species with lower SLM.

Recommendations

Dry Forest Management

- Planting should be performed under nurse trees during the rainy season because it would give saplings higher survival rates than when planted during the dry season.
- Saplings must be watered following planting for at least three weeks to supplement rainfall.
- *Bursera simaruba*, *Citharexylum fruticosum* and *Tabebuia heterophylla* are good species for dry forest restoration since they showed higher growth than other species.
- Planting closer to the *Leucaena leucocephala* nurse trees generally increases growth in native dry forest species.
- *Erythroxylum aerolatum* should be planted with minimum canopy cover or at full sun.
- *Pisonia albida* should be planted close to the trunk of the nurse tree.
- *Stahlia monosperma* should also be planted close to the nurse tree with the most canopy cover possible.
- Species with high leaf density should be chosen to plant because they have higher growth rates than species with lower leaf density.

Future Research

- To keep monitoring the surviving species to obtain long term data on growth and mortality.
- Evaluate the physical interactions between the planted trees and the nurse tree once they reach the nurse tree's branches.
- Do more tests with more replications with *Coccoloba uvifera*, *Pisonia albida*, *Stahlia monosperma* and *Thrichilia hirta*.
- Do more nurse trees experiments evaluating other nurse tree species, such as *Albizia procera*, *Prosopis pallida* and *Acacia* spp. among others.

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Appendix A. ANOVA table for statistical tests for leaf area index (LAI)

Variable	N	R ²	R ² Adj	CV
LAI	400	0.93	0.93	17.47

Analysis of variance table (Partial SS)

S.V.	SS	df	MS	F	p-value	Coef
Model	222.53	13	17.12	417.77	<0.0001	
Site	0.07	2	0.03	0.80	0.4523	
Distance	198.20	3	66.07	1612.38	<0.0001	
Initial height	1.1E-03	1	1.1E-03	0.03	0.8727	-0.01
Crown radius	0.13	1	0.13	3.29	0.0706	-0.05
Site*Distance	0.99	6	0.17	4.04	0.0006	
Error	15.82	386	0.04			
Total	238.34	399				

Test:Fisher LSD Alpha:=0.10 LSD:=0.04188

Error: 0.0410 df: 386

Site	Means	n
Guanica	1.14	160
Sierra Bermeja	1.16	80
CRNWR	1.18	160

Different letters indicate significant difference between location parameters ($p \leq 0.10$)**Test:Fisher LSD Alpha:=0.10 LSD:=0.04720**

Error: 0.0410 df: 386

Distance	Means	n
4.00	0.26	100
3.00	0.70	100
2.00	1.47	100
1.00	2.20	100

Different letters indicate significant difference between location parameters ($p \leq 0.10$)**Test:Fisher LSD Alpha:=0.10 LSD:=0.08377**

Error: 0.0410 df: 386

Site	Distance	Means	n
CRNWR	4.00	0.23	40
Sierra Bermeja	4.00	0.25	20
Guanica	4.00	0.30	40
CRNWR	3.00	0.68	40
Guanica	3.00	0.69	40
Sierra Bermeja	3.00	0.72	20
CRNWR	2.00	1.46	40
Guanica	2.00	1.46	40
Sierra Bermeja	2.00	1.50	20
Guanica	1.00	2.11	40
Sierra Bermeja	1.00	2.17	20
CRNWR	1.00	2.33	40

Different letters indicate significant difference between location parameters ($p \leq 0.10$)

Appendix B. Non linear regressions for LAI and survivorship analysis

Bourreria succulenta

Non linear regression

Model Mortality $\alpha/(1+\beta*\exp(-\gamma*LAI))$

Variable	N	MSError	Iteration
Mortality	40	0.23	2

Parameters	LL	PAR	UL	PAR	Start value	Estimate	S.E.	T	p-value
ALFA	-1E30	1E30			1.00	0.70	0.09	7.89	<0.0001
BETA	-1E30	1E30			0.65	1.93	4.77	0.40	0.6881
GAMMA	-1E30	1E30			1.44	9.63	16.45	0.59	0.5618

Correlation matrix of estimates

	ALFA	BETA	GAMMA
ALFA	1.00	-0.02	-0.22
BETA	-0.02	1.00	0.87
GAMMA	-0.22	0.87	1.00

Bucida buceras

Non linear regression

Model Mortality $\alpha/(1+\beta*\exp(-\gamma*LAI))$

Variable	N	MSError	Iteration
Mortality	60	0.25	2

Parameters	LL	PAR	UL	PAR	Start value	Estimate	S.E.	T	p-value	
ALFA	-1E30	1E30			1.00	299890.53	541018139.17	5.5E-04	0.9996	
BETA	-1E30	1E30			0.09	443278.87	799699045.79	5.5E-04	0.9996	
GAMMA	-1E30	1E30			-0.66	-0.08		0.14	-0.57	0.5715

Correlation matrix of estimates

	ALFA	BETA	GAMMA
ALFA	1.00	1.00	0.04
BETA	1.00	1.00	0.04
GAMMA	0.04	0.04	1.00

Citharexylum fruticosum

Non linear regression

Model Mortality $\alpha/(1+\beta*\exp(-\gamma*LAI))$

Variable	N	MSError	Iteration
Mortality	60	0.18	2

Parameters	LL	PAR	UL	PAR	Start value	Estimate	S.E.	T	p-value
ALFA	-1E30	1E30			1.00	0.81	0.09	8.89	<0.0001
BETA	-1E30	1E30			0.01	1.4E-03	0.01	0.10	0.9179
GAMMA	-1E30	1E30			-0.80	-2.24	3.98	-0.56	0.5767

Correlation matrix of estimates

	ALFA	BETA	GAMMA
ALFA	1.00	0.68	0.64
BETA	0.68	1.00	0.99
GAMMA	0.64	0.99	1.00

*Erythroxyton aerolatum***Non linear regression**Model Mortality $\text{alfa}/(1+\text{beta}*\exp(-\text{gamma}*LAI))$

Variable	N	MSError	Iteration
Mortality	60	0.22	2

Parameters	LL	PAR	UL	PAR	Start value	Estimate	S.E.	T	p-value
ALFA	-1E30	1E30			1.00	46105.27	840859732.24	5.5E-05	>0.9999
BETA	-1E30	1E30			0.01	51041.59	930903055.41	5.5E-05	>0.9999
GAMMA	-1E30	1E30			-2.85	-0.36	0.16	-2.19	0.0330

Correlation matrix of estimates

	ALFA	BETA	GAMMA
ALFA	1.00	1.00	0.39
BETA	1.00	1.00	0.39
GAMMA	0.39	0.39	1.00

*Pisonia albida***Non linear regression**Model Mortality $\text{alfa}/(1+\text{beta}*\exp(-\text{gamma}*LAI))$

Variable	N	MSError	Iteration
Mortality	20	0.23	2

Parameters	LL	PAR	UL	PAR	Start value	Estimate	S.E.	T	p-value
ALFA	-1E30	1E30			1.00	41639711.19	493813573.75	0.08	0.9338
BETA	-1E30	1E30			155.60	311514371.39	3707395530.88	0.08	0.9340
GAMMA	-1E30	1E30			2.81	0.75	0.48	1.56	0.1366

Correlation matrix of estimates

	ALFA	BETA	GAMMA
ALFA	1.00	1.00	0.28
BETA	1.00	1.00	0.34
GAMMA	0.28	0.34	1.00

*Stahlia monosperma***Non linear regression**Model Mortality $\text{alfa}/(1+\text{beta}*\exp(-\text{gamma}*LAI))$

Variable	N	MSError	Iteration
Mortality	20	0.20	6

Parameters	LL	PAR	UL	PAR	Start value	Estimate	S.E.	T	p-value
ALFA	-1E30	1E30			1.00	0.83	0.14	5.78	<0.0001
BETA	-1E30	1E30			12.25	23.78	82.75	0.29	0.7773
GAMMA	-1E30	1E30			3.21	5.79	6.46	0.90	0.3829

Correlation matrix of estimates

	ALFA	BETA	GAMMA
ALFA	1.00	-0.18	-0.30
BETA	-0.18	1.00	0.96
GAMMA	-0.30	0.96	1.00

Tabebuia heterophylla

Non linear regression

Model Mortality $\text{alfa}/(1+\text{beta}*\exp(-\text{gamma}*LAI))$

Variable	N	MSError	Iteration
Mortality	60	0.26	6

Parameters	LL	PAR	UL	PAR	Start value	Estimate	S.E.	T	p-value
ALFA	-1E30	1E30			1.00	1.71	1538040.41	1.1E-06	>0.9999
BETA	-1E30	1E30			2.53	2.95	3554281.88	8.3E-07	>0.9999
GAMMA	-1E30	1E30			0.01	1.5E-03	456.24	3.3E-06	>0.9999

Correlation matrix of estimates

	ALFA	BETA	GAMMA
ALFA	1.00	1.00	-1.00
BETA	1.00	1.00	-1.00
GAMMA	-1.00	-1.00	1.00

Appendix C. Linear regression for leaf area index and growth for *Stahlia monosperma*

Species	Variable	N	R ²	R ² Adj	PMSE	AIC	BIC
<i>Stahlia monosperma</i>	Overall Growth	12	0.46	0.41	4.0E-03	-33.38	-31.92

Regression coefficients

Coef	Est.	S.E.	LB(95%)	UB(95%)	T	p-value	CpMallows
const	0.07	0.03	2.5E-03	0.14	2.31	0.0437	
LAI	0.05	0.02	0.01	0.09	2.94	0.0147	8.97

Analysis of variance table (Partial SS)

S.V.	SS	df	MS	F	p-value
Model	0.02	1	0.02	8.67	0.0147
LAI	0.02	1	0.02	8.67	0.0147
Error	0.03	10	2.6E-03		
Total	0.05	11			

Appendix D. Contingency tables for mortality analysis

Contingency table

Frecuencias absolutas

In columns: Mortality

Site	alive	dead	Total
Guanica	75	85	160
CRNWR	147	13	160
Sierra Bermeja	28	52	80
Total	250	150	400

Statistic	Value	df	p
Chi -square (Pearson)	101.39	2	<0.0001
Chi -square (ML-G2)	114.30	2	<0.0001
Contingency Coef. (Cramer)..	0.36		
Contingency Coef. (Pearson..)	0.45		

Contingency table

Frecuencias absolutas

In columns: Mortality

Species	alive	dead	Total
Bourreria succulenta	26	14	40
Bucida buceras	37	23	60
Bursera simaruba	38	2	40
Citharexylum fruticosum	46	14	60
Coccoloba uvifera	2	18	20
Erythroxylon areolatum	37	23	60
Pisonia albida	7	13	20
Stahlia monosperma	12	8	20
Tabebuia heterophylla	26	34	60
Trichilia hirta	19	1	20
Total	250	150	400

Statistic	Value	df	p
Chi -square (Pearson)	71.75	9	<0.0001
Chi -square (ML-G2)	80.75	9	<0.0001
Contingency Coef. (Cramer)..	0.30		
Contingency Coef. (Pearson..)	0.39		

Contingency table

Frecuencias absolutas

In columns: Mortality

Site	Distance	alive	dead	Total
CRNWR	1.00	37	3	40
CRNWR	2.00	39	1	40
CRNWR	3.00	38	2	40
CRNWR	4.00	33	7	40
CRNWR	Total	147	13	160

Statistic	Value	df	p
Chi -square (Pearson)	6.95	3	0.0735
Chi -square (ML-G2)	6.54	3	0.0882
Contingency Coef. (Cramer)..	0.15		
Contingency Coef. (Pearson..)	0.20		

Contingency table*Frecuencias absolutas**In columns: Mortality*

Site	Direction	alive	dead	Total
Guanica	E	15	25	40
Guanica	N	26	14	40
Guanica	S	18	22	40
Guanica	W	16	24	40
Guanica	Total	75	85	160

Statistic	Value	df	p
Chi -square (Pearson)	7.50	3	0.0574
Chi -square (ML-G2)	7.57	3	0.0558
Contingency Coef. (Cramer)..	0.15		
Contingency Coef. (Pearson)..	0.21		

Contingency table*Frecuencias absolutas**In columns: Mortality*

Species	Distance	alive	dead	Total	
Erythroxyton areolatum	1.00	6	9	15	
Erythroxyton areolatum	2.00	8	7	15	
Erythroxyton areolatum	3.00	12	3	15	
Erythroxyton areolatum	4.00	11	4	15	
Erythroxyton areolatum	Total	37	23	60	

Statistic	Value	df	p
Chi -square (Pearson)	6.42	3	0.0930
Chi -square (ML-G2)	6.55	3	0.0876
Contingency Coef. (Cramer)..	0.23		
Contingency Coef. (Pearson)..	0.31		

Contingency table*Frecuencias absolutas**In columns: Mortality*

Species	Distance	alive	dead	Total
Pisonia albida	1.00	4	1	5
Pisonia albida	2.00	1	4	5
Pisonia albida	3.00	0	5	5
Pisonia albida	4.00	2	3	5
Pisonia albida	Total	7	13	20

Statistic	Value	df	p
Chi -square (Pearson)	7.69	3	0.0528
Chi -square (ML-G2)	9.16	3	0.0272
Contingency Coef. (Cramer)..	0.44		
Contingency Coef. (Pearson)..	0.53		

Contingency table*Frecuencias absolutas**In columns: Mortality*

Species	Site	Direction	alive	dead	Total
Bursera simaruba	Guanica	E	5	0	5
Bursera simaruba	Guanica	N	5	0	5
Bursera simaruba	Guanica	S	5	0	5
Bursera simaruba	Guanica	W	3	2	5
Bursera simaruba	Guanica	Total	18	2	20

Statistic	Value	df	p
Chi -square (Pearson)	6.67	3	0.0833
Chi -square (ML-G2)	6.27	3	0.0990
Contingency Coef. (Cramer)..	0.41		
Contingency Coef. (Pearson)..	0.50		

Contingency table*Frecuencias absolutas**In columns: Mortality*

Species	Site	Direction	alive	dead	Total
Stahlia monosperma	CRNWR	E	1	4	5
Stahlia monosperma	CRNWR	N	5	0	5
Stahlia monosperma	CRNWR	S	4	1	5
Stahlia monosperma	CRNWR	W	2	3	5
Stahlia monosperma	CRNWR	Total	12	8	20

Statistic	Value	df	p
Chi -square (Pearson)	8.33	3	0.0396
Chi -square (ML-G2)	10.18	3	0.0171
Contingency Coef. (Cramer)..	0.46		
Contingency Coef. (Pearson)..	0.54		

*Frecuencias absolutas**In columns: Mortality*

Species	Site	Distance	alive	dead	Total
Bouyeria succulenta	CRNWR	1.30	15	0	15
Bouyeria succulenta	CRNWR	4.00	4	1	5
Bouyeria succulenta	CRNWR	Total	19	1	20

Statistic	Value	df	p
Chi -square (Pearson)	3.16	1	0.0756
Chi -square (ML-G2)	2.94	1	0.0866
Contingency Coef. (Cramer)..	0.28		
Contingency Coef. (Pearson)..	0.37		
Phi-Coefficient	0.40		

*Frecuencias absolutas**In columns: Mortality*

Species	Site	Distance	alive	dead	Total
Erythroxyton areolatum	Sierra Bermeja	1.30	3	12	15
Erythroxyton areolatum	Sierra Bermeja	4.00	3	2	5
Erythroxyton areolatum	Sierra Bermeja	Total	6	14	20

Statistic	Value	df	p
Chi -square (Pearson)	2.86	1	0.0910
Chi -square (ML-G2)	2.69	1	0.1008
Contingency Coef. (Cramer)..	0.27		
Contingency Coef. (Pearson)..	0.35		
Phi-Coefficient	-0.38		

Contingency table*Frecuencias absolutas**In columns: Mortality*

Species	Site	Distance	alive	dead	Total
Stahlia monosperma	CRNWR	1.30	11	4	15
Stahlia monosperma	CRNWR	4.00	1	4	5
Stahlia monosperma	CRNWR	Total	12	8	20

Statistic	Value	df	p
Chi -square (Pearson)	4.44	1	0.0350
Chi -square (ML-G2)	4.52	1	0.0335
Contingency Coef. (Cramer)..	0.33		
Contingency Coef. (Pearson)..	0.43		
Phi-Coefficient	0.47		

Contingency table*Frecuencias absolutas**In columns:Mortality*

Species	Site	Distance	alive	dead	Total
Trichilia hirta	CRNWR	1.30	15	0	15
Trichilia hirta	CRNWR	4.00	4	1	5
Trichilia hirta	CRNWR	Total	19	1	20

Statistic	Value	df	p
Chi -square (Pearson)	3.16	1	0.0756
Chi -square (ML-G2)	2.94	1	0.0866
Contingency Coef. (Cramer)..	0.28		
Contingency Coef. (Pearson)..	0.37		
Phi-Coefficient	0.40		

Contingency table*Frecuencias absolutas**In columns:Mortality*

Species	Site	Distance	alive	dead	Total
Erythroxylyon areolatum	Guanica	1.20	4	6	10
Erythroxylyon areolatum	Guanica	3.40	9	1	10
Erythroxylyon areolatum	Guanica	Total	13	7	20

Statistic	Value	df	p
Chi -square (Pearson)	5.49	1	0.0191
Chi -square (ML-G2)	5.94	1	0.0148
Contingency Coef. (Cramer)..	0.37		
Contingency Coef. (Pearson)..	0.46		
Phi-Coefficient	-0.52		

Contingency table*Frecuencias absolutas**In columns:Mortality*

Species	Site	Distance	alive	dead	Total
Stahlia monosperma	CRNWR	1.20	8	2	10
Stahlia monosperma	CRNWR	3.40	4	6	10
Stahlia monosperma	CRNWR	Total	12	8	20

Statistic	Value	df	p
Chi -square (Pearson)	3.33	1	0.0679
Chi -square (ML-G2)	3.45	1	0.0632
Contingency Coef. (Cramer)..	0.29		
Contingency Coef. (Pearson)..	0.38		
Phi-Coefficient	0.41		

Appendix E. ANCOVA table for statistical tests for growth

Analysis of variance

Variable	N	R ²	R ² Adj	CV
LOG10 Growth	250	0.83	0.00	78.08

Analysis of variance table (Sequential SS)

S.V.	SS	df	MS	F	p-value	Coef
Model	49.44	210	0.24	0.91	0.6775	
Site>Site>Species	10.24	19	0.54	2.07	0.0267	
Site>Species	0.00	0	0.00	nd	nd	
Distance	1.78	3	0.59	2.28	0.0940	
Direction	0.03	3	0.01	0.04	0.9891	
Crown Radius	0.05	1	0.05	0.18	0.6706	-0.08
Initial height	0.07	1	0.07	0.29	0.5953	0.41
Site*Species	0.00	0	0.00	nd	nd	
Site*Distance	1.64	6	0.27	1.05	0.4079	
Site*Direction	1.28	6	0.21	0.82	0.5596	
Species*Distance	4.55	24	0.19	0.73	0.7915	
Species*Direction	6.29	23	0.27	1.05	0.4328	
Distance*Direction	2.50	9	0.28	1.07	0.4072	
Site*Species*Distance	2.74	20	0.14	0.53	0.9368	
Site*Species*Direction	2.38	16	0.15	0.57	0.8859	
Site*Distance*Direction	2.56	15	0.17	0.66	0.8085	
Species*Distance*Direction	12.33	54	0.23	0.88	0.6735	0.6735
Site*Species*Distance*Dire.	1.00	10	0.10	0.38	0.9464	0.9464
Error	10.14	39	0.26			
Total	59.58	249				

Test: Fisher LSD Alpha:=0.10 LSD:=0.15370

Error: 0.2599 df: 39

Distance	Means	n	
3.00	-0.79	64	A
4.00	-0.72	59	A
2.00	-0.56	63	B
1.00	-0.52	64	B

Different letters indicate significant difference between location parameters ($p \leq 0.10$)

Appendix F. Linear regressions for leaf density and growth

Linear Regression

Variable	N	R ²	R ² Adj	PMSE	AIC	BIC
Growth	9	0.41	0.32	0.01	-18.76	-18.17

Regression coefficients

Coef	Est.	S.E.	LB(95%)	UB(95%)	T	p-value	CpMallows
const	0.07	0.06	-0.07	0.21	1.20	0.2689	
Leaf Density		0.06	0.03	-4.9E-03	0.12	2.19	0.0651

Analysis of variance table (Partial SS)

S.V.	SS	df	MS	F	p-value	
Model		0.02	1	0.02	4.78	0.0651
Leaf Density		0.02	1	0.02	4.78	0.0651
Error	0.03	7	4.8E-03			
Total	0.06	8				