Effects of native and non-native grasses on woody species regeneration in a Puerto Rican subtropical dry forest

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ABSTRACT

Invasive non-native species can reduce native species diversity, alter ecosystem structure and produce barriers to restoration. However little is known about how native and non-native grasses may differ in their effects on woody species diversity or seedling regeneration in a subtropical dry forest. I surveyed randomly selected patches dominated by native grasses or non–native grasses throughout randomly selected 1-km^2 cells within the Guánica Dry Forest in Puerto Rico. There I assessed the effects of grass type and patch size on woody species diversity, stem diameter and stem density. Afterwards I conducted a field experiment to assess possible facilitation or inhibition effects of two grasses, one non-native (*Megathyrsus maximus*) and the other native (*Uniola virgata*), on native woody seedlings for six months. Thirty vascular families were sampled, with 58 species identified to the species level. Grass species presence was observed to correlate with woody stem density. Once this was observed I wanted to check if woody stem density was consistently different between native grasses and non-native grasses. For the native grass *Uniola virgata* woody stem density was associated with patch size. No patterns could be discerned for the other native and non-native grasses. Native woody species richness inside sampled plots was linearly related to grass patch size only for *Uniola virgata* patches. Seedlings planted near the edges of native or non-native grass clumps had a higher percentage survival than seedlings planted in bare exposed soil in the same sites. Between the two grass species, woody seedling survival was higher near native grass clumps than near non-native grass clumps, perhaps due to differences in phenology and root development that produced a more suitable microclimate near the native grass clumps. These results suggest that native grasses may be used during dry forest restoration to mitigate the negative effects of non-native grasses.

RESUMEN

Especies no-nativas y altamente invasivas pueden reducir diversidad de plantas nativas, alterar la estructura del ecosistema y crear barreras para restauración. Se conoce poco del efecto de pastos, tanto nativos y no-nativos en la diversidad de plantas leñosas nativas o regeneración de plántulas en bosques secos. Muestreé aleatoriamente parchos de pastos nativos y no-nativos dentro de celdas de 1-km de largo distribuidas por el Bosque Seco de Guánica en Puerto Rico. De este muestreo evalué el efecto del tipo de pasto y el tamaño del parcho en la diversidad de especies leñosas, diámetro de tallos y densidad de tallos. Luego llevé a cabo un experimento en el campo donde evalué el efecto de facilitación o inhibición de dos pastos, *Megathyrsus maximus,* un pasto no-nativo y *Uniola virgata,* un pasto nativo, en la sobrevivencia de plántulas de árboles nativos durante seis meses. Treinta familias de plantas vasculares fueron muestreadas con 58 especies identificadas. Se buscó si la presencia de gramíneas estaba correlacionada con la densidad de tallos nativos y la diversidad de plantas leñosas. No se encontró que la presencia de un pasto en particular fuera un factor determinante en la densidad de tallos y en la diversidad de plantas leñosas. Tan solo para parchos del pasto nativo de *Uniola virgata* fue observada una relación lineal con tamaño de parcho y diversidad de especies. Plántulas trasplantadas en el borde de pastos tuvieron mayor sobrevivencia que plántulas sembradas en suelo expuesto en ambos lugares. Entre los dos pastos sobrevivencia era mayor en el borde del pasto nativo *Uniola virgata* que en el borde del pasto no-nativo *Megathyrsus maximus*. Esto puede deberse a diferencias en fenología y desarrollo de raíces, los cuales afectan el microclima de las plántulas. Estos resultados sugieren el potencial uso de pastos nativos como herramientas de restauración de ecosistemas de bosques secos.

DEDICATION

I dedicate this to my family for being supportive of me during my academic years but specifically my parents, Juan Gilberto García-Mercado and Elaine Cancel-Plaza, for always giving the extra mile for my personal and academic betterment.

ACKNOWLEDGEMENTS

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CHAPTER 1

GENERAL INTRODUCTION AND LITERATURE REVIEW

Tropical dry forests (TDF) are one of the most abundant types of tropical forests, ~40% of tropical forests worldwide, yet these forests have suffered heavy anthropogenic influence over the course of several generations since the soil is optimal for agricultural development (Murphy and Lugo 1986). Such anthropogenic effects can be direct or indirect and can include altered disturbance regimes and the introduction of invasive species. These changes alter the frequency, intensity or magnitude of previous disturbance regimes or include novel ones.

Tropical dry forests, like many others throughout the tropics, also suffer from the introduction of invasive non-native species. Several studies have demonstrated that ecological processes such as nutrient cycling, pollination and seed dispersion have been impaired by the introduction and persistence of non-native species (D'Antonio and Vitousek 1992, Johnson and Wedin 1997, Williams and Baruch 2000). Introduced species tend to alter or outright disrupt these processes by competing with the native species for the same ecological niche or altering the ecological functioning of the ecosystem to such a degree that thresholds or environmental legacies are established (Prober *et al*. 2009). These effects in turn can reduce ecological services, which are those processes indispensable for the balanced and optimal functioning of a particular ecosystem and from which all the communities of organisms in it depend on for their survival (Suding *et al.* 2004). Once changes of this magnitude take place, moving an ecosystem to a desired state can be a costly uphill struggle.

Tropical dry forest species are adapted to survive stressful conditions associated with water limitation. Because of their characteristic low annual rainfall, ranging from 250 to 2,000 mm of precipitation, and an evapotranspiration rate higher than 1 (temperature/precipitation x 100), growth in tropical dry forest is seasonal and slow (Murphy and Lugo 1986). Furthermore, some soils in tropical dry forests have some mineral deficiencies (Van Bloem *et al.* 2004, Ceccon *et al.* 2006). Plants in TDF's have evolved several reproductive strategies to survive in this harsh environment. Some produce many light weight seeds that are wind dispersed while other plants produce larger seeds that are dispersed by animals (Hooper *et al.* 2004). Unlike in more humid tropical forests, even large fruits of TDF species are usually not fleshy and develop a hard and tough seed coat that prevents dehydration of the embryo (Khurana and Singh 2001). Local flora has evolved in these systems to enter dormancy during the pronounced dry seasons in which droughts can last up to 8 months. Seed dormancy is thus used by a wide range of plant species that wait until adequate precipitation has fallen to germinate (Khurana and Singh 2001). Although tropical dry forests species have several adaptations to deal with drought such as seasonal fruiting and deciduous behavior, they do not tend to have adaptations to deal with fire.

Fire is a novel disturbance in most neotropical dry forests and can promote the conversion of these into grasslands or scrublands in susceptible areas (Vieira and Scariot 2006, Hooper *et al.* 2004, Cabin *et al.* 2002b). Fire regimes that are novel have a more profound effect in ecosystems since the changes are unprecedented and can alter ecosystem properties (Brooks *et al.* 2004). These changes can range from altering the floristic composition at the macroscopic scale (Hooper et al. 2004) to alterations in the bacterial

communities at the microscopic level (Smith *et al.* 2008). Fires are usually promoted by invasive grass species that produce a large surface fuel load (Thaxton *et al.* 2012) and develop a profuse root system near the soil surface from which they can resprout when a fire passes (Brooks *et al.* 2004), thereby maintaining their dominance (Suding *et al.* 2004). These non-native grasses also alter soil properties to their benefit by changing physical and chemical properties of substrates (Smith *et al*. 2008) and by biotic interactions which further inhibit seedling recruitment of native flora (Cabin *et al.* 2000, Cabin *et al.* 2002b, Hooper *et al.* 2004, Daehler and Georgen 2005, Jackson 2005, Litton *et al.* 2006, Francis and Parrotta 2006, Cordell and Sandquist 2008, Thaxton *et al.* 2010, Thaxton *et al.* 2011).

Light limitation exerts a great influence in the development of plants, since plants need light for the assimilation of atmospheric carbon (Taiz and Zeiger 2002). High light levels do promote growth, yet too much ambient light stimulates the closure of leaf stomata which eventually limits plant growth and fitness. High levels of light also promote the loss of water by open stomata (Taiz and Zeiger 2002). In seasonal ecosystems where droughts are the main limiting factor in seedling survivorship (Marañón *et al.* 2004), light availability is usually not the factor most limiting to plant growth. With this in mind, several restoration efforts have been focusing on the implementation of shaded areas, which are favored as safe sites as they counteract the limited precipitation and seedling dessication (D'Antonio and Vitousek 1992, Khurana and Singh 2001, Marañón *et al.* 2004, Cabin *et al.* 2002a, Vieira and Scariot 2006, Santiago-García *et al.* 2008, Thaxton *et al.* 2011).

The use of nurse plants, such as trees and grasses, that shade seeds and seedlings, may provide a possible path towards tropical ecosystem restoration. Several studies carried out in mesic ecosystems have found the use of mature plants as nurse plants is detrimental

to the establishment of seedlings after germination (Groome 1989 as cited in Marañón *et al*. 2004). Yet this does not necessary apply to ecosystems with pronounced dry seasons, such as Mediterranean climates and tropical dry forests, or ecosystems with a significant ecological perturbation such as abandoned pasturelands (Holl 1999, Maza-Villalobos *et al.* 2011). Studies carried out in the Sierra Nevada of southern Spain have shown that the use of nurse plants increases seedling survivorship in droughts and winters (Castro *et al.* 2002). The effect of different shading regimes has also been proven to ameliorate the water stress seedlings suffer during dry seasons and increases seedling survivorship (Marañón *et al.* 2004). Yet since some sites lack the presence of nurse trees, other plants such as shrubs and grasses have also been used for restoration purposes. There has been evidence of facilitation of tree seedling emergence among grasses in abandoned pasture lands in Puerto Rico (Aide *et al.* 2000) as well as in severe drought-prone Mediterranean habitats (Maestre *et al.* 2003) and other arid systems (Franco and Nobel 1988). In contrast a study in Hawaiian dry forest with the non-native grass *Pennisetum setaceum* found that the dense shallow root system could be detrimental for the development of woody seedlings, because the grass root system aided them in the competition for water following small pulses of rain (Cordell and Sandquist 2008). Other studies carried out in South America and Australia have also shown strong evidence of these effects on local biodiversity (Baruch and Jackson 2005, Jackson 2005). *Leucaena leucocephala* is a non-native shrub that has become naturalized in the neotropics and has been shown to resprout from fires and act as a nurse plant for native woody species (Santiago-García *et al*. 2008).

The Guánica Forest is located in the southwestern part of the island of Puerto Rico, in the Greater Antilles in the Caribbean Sea ($17^o58'$ N, $65^o30'$ W). Precipitation averages

860 mm with a temperature average of 24ºC. Soils on the forest are derived from a porous limestone substrate and have a notable phosphorus deficiency (Van Bloem *et al.* 2004). This further aggravates the stress the lack of water in the forest has on the plant community. Soils typically lack a deep organic layer, suffer high solar irradiation and the rain shadow effect of the central mountain chain of the island, the Cordillera Central. Yet even so, previous to its formation as a reserve, parts of the current Guánica Forest were used for agriculture as evidenced by aerial photographs from the 1930's and soil evidence of ashes (Murphy and Lugo 1986, Molina Colón and Lugo 2006).

In Guánica Forest several grass species have been documented (Monsegur-Rivera 2009), but these tend to concentrate in the disturbed areas of the forests where the canopy is open. A common native species is *Uniola virgata* (Poir.) Griseb., a perennial grass that forms dense clumps with tangles of persistent, curled dead leaves around its base which can be susceptible to fires (Más and García-Molinari 2006) and which has been observed to produce deep roots (Thaxton *personal observation*). It is found on dry rocky coastal slopes and bluffs in the West Indies (Monsegur-Rivera 2009). A common non-native grass is *Megathyrsus maximus* which has been introduced into the neotropics as cattle feed from Africa (Williams and Baruch 2000). It is physiologically adapted to create large combustion loads which can readily be set ablaze and have a great seed production (Más and García-Molinari 2006). This grass, along with the African grass *Cenchrus ciliaris* (buffel grass), have altered the disturbance regime in the forest, changing nutrient and community dynamics in favor of fire adapted species, *e.g.* creating thatch carpets capable of easily catching fire (Thaxton *et al.* 2012). *Cenchrus ciliaris* has been shown after initial establishment by ecological disturbance (McIvor 2003) to manipulate soil properties to

favor is spread, benefit from sparse precipitation events and limit woody seedling germination (Low 1997, Daehler and Goergen 2005, Jackson 2005, De la Barrera 2008, Stevens and Fehmi 2009). Also present in small pockets in the forest is the African grass *Melinis repens* which is spreading into native *Bouteloua repens* grass dominated sites in the open shrubland. It has also been shown to have competitive and invasive characteristics in arid systems (Stevens and Fehmi 2009), making it a species of some concern.

I compared species diversity among Guánica Forest sites dominated by either native grasses or fire-promoting invasive grasses and assessed the potential for using native grasses to promote restoration of native woody species. Since fire is a novel disturbance for most neotropical dry forests, native plant species do not tend to survive fire and are not able to regenerate at a rate with could make them able competitors with the invasive fire-promoting species. Furthermore, water retention and resource allocation are key components to woody seedling survival in water stressed ecosystems. Invasive grasses monopolize water resources in the upper soil levels, thereby limiting seedling recruitment by native species. However, shade provided by grasses may have positive effects on woody seeds and seedlings, as shade has been shown to be critical to seedling recruitment in tropical dry forests. With this in mind I wanted to see if native grass species, which are drought tolerant but fire intolerant, can promote the germination of native seedlings by producing beneficial shade with less competition for water. If this could be accomplished then they could possibly be included in future restoration projects.

CHAPTER 2

Potential effects of native and non-native grasses on communities of woody species in subtropical dry forest

INTRODUCTION

Tropical ecosystems have been suffering effects of human induced ecosystem level changes, ranging from land clearance and logging for agriculture and urban development to changes in climatic patterns (Lugo and Murphy 1986). In some ecosystems these changes have become aggravated by the introduction of non-native species, which can alter ecosystem properties and services (Suding *et al.* 2004). If these changes are permanent or difficult to eradicate then the ecosystem is said to be in an alternate state (D'Antonio and Vitousek 1992), in which the ecosystem no longer provides the full range of ecological services, and is characterized as degraded with limited native biodiversity.

Tropical dry forests are a particularly hard hit biome. Although they once covered over 42% of the tropical forests of the planet (Lugo and Murphy 1986, Janzen 1988), they have been one of the most affected by logging, charcoal production, pasture formation for livestock and agriculture because of their high soil fertility and amenable climate (Van Bloem *et al.* 2004). Currently urban expansion is now a threat as the climate of these biomes appeals to people (Molina and Lugo 2004). Even if left alone these ecosystems are susceptible to non-native invasion if a novel ecological disturbance is introduced such as fires (D'Antonio *et al.* 2011, Thaxton *et al.* 2012).

Fire is a novel disturbance in most neotropical dry forests and can promote the conversion of these into grasslands or scrublands in susceptible areas (Vieira and Scariot

2006, Hooper *et al.* 2004, Cabin *et al.* 2002b). Fire regimes that are novel have a more profound effect in ecosystems since the changes are unprecedented and can alter ecosystem properties (Brooks *et al.* 2004). These changes can range from altering the floristic composition at the macroscopic scale (Hooper *et al.* 2004) to alterations in the bacterial communities in the microscopic level (Smith *et al.* 2008). Fires are usually promoted by invasive grass species that produce a large surface fuel load (Thaxton *et al.* 2012) and develop a profuse root system near the soil surface from which they can resprout when a fire passes (Brooks *et al.* 2004) thereby maintaining their dominance (Suding *et al.* 2004). These grasses also alter soil properties to their benefit by changing physical and chemical properties of substrates (Smith *et al*. 2008) and by biotic interactions which further inhibit seedling recruitment of native flora (Cabin *et al.* 2000, Cabin *et al.* 2002a, Hooper *et al.* 2004, Daehler and Georgen 2005, Jackson 2005, Litton *et al.* 2006, Francis and Parrotta 2006, Cordell and Sandquist 2008, Thaxton *et al.* 2010, Thaxton *et al.* 2011).

In the Guánica Forest several grass species have been documented (Monsegur-Rivera 2009) but these tend to concentrate in the disturbed areas of the forests where the canopy is open. The dominant native species is named *Uniola virgata* (Poir.) Griseb., a perennial C_4 grass that forms dense clumps with tangles of persistent, curled dead leaves around its base and an aboveground rhizome which can be susceptible to fires (Más and García-Molinari 2006); and which has been observed to produce deeper roots than *Megathyrsus maximus* (Thaxton *personal observation*). It is found on dry rocky coastal slopes and bluffs in the West Indies (Monsegur-Rivera 2009). The dominant non-native grass in disturbed sites is the perennial C_4 grass *Megathyrsus maximus* (Jacq.) B.K. Simon & S.W.L. Jacobs, which has been introduced into the neotropics as cattle feed from Africa

(Williams and Baruch 2000). It is adapted to create large combustion loads which can readily be set ablaze (Thaxton *et al.* 2012); with an underground stem able to resprout after fires as well as be able to produce a great seed output (Más and García-Molinari 2006). This grass, along with the African grass *Cenchrus ciliaris* L. (buffel grass), have altered the disturbance regime in the forest, changing nutrient and community dynamics in favor of fire adapted species, *e.g.* creating thatch carpets capable of easily catching fire (Thaxton *et al.* 2012). *Cenchrus ciliaris* has been shown to establish after ecological disturbances (McIvor 2003) and be able to manipulate soil properties to favor its spread, benefit from sparse precipitation events and limit woody seedling germination (Low 1997, Daehler and Goergen 2005, Jackson 2005, De la Barrera 2008, Stevens and Fehmi 2009). Also present in small pockets in the forest is the African grass *Melinis repens* (Willd.) Zizka which is spreading into native *Bouteloua repens* (Kunth) Scribn. grass dominated sites in the open shrubland (*personal observation*). It has also been shown to have competitive and invasive characteristics in arid systems (Stevens and Fehmi 2009), making it a species of some concern.

The objectives of this study were to see the distribution of grass patches throughout the Guánica Tropical Dry Forest and their effect, if any, on local native woody species abundance, diversity, and community composition in grass patches. I hypothesize that dominance of non-native grasses would cause a rapid decline in native woody species while native grasses would produce either beneficial, neutral or no effects at all.

METHODS

Study site

The Guánica Forest is located in the southwestern part of the island of Puerto Rico, in the Greater Antilles in the Caribbean Sea (17°58′ N, 65°30′ W). Precipitation averages 860 mm with a temperature average of 24ºC. Soils on the forest are derived from a porous limestone substrate and have a notable phosphorus deficiency (Van Bloem *et al*. 2004). Soils in Guánica typically lack a deep organic layer. Water stress is high due to high solar irradiation and the rain shadow effect of the central mountain chain of the island, the Cordillera Central. Yet even so, previous to its formation as a reserve, parts of the current Guánica Forest were used for agriculture as evidenced by aerial photographs from the 1930's and soil evidence of ashes (Murphy and Lugo 1986, Molina Colón and Lugo 2006).

Methodology

Woody diversity was surveyed in 22 randomly selected 1 km^2 cells across the Guánica Tropical Dry Forest (Figure 1A). Selection of cells was accomplished by overlaying a grid of cells onto maps of the forest. Each map cell corresponded to a 1 km^2 on the ground (Figure 1B and 1C). Once those areas had been selected I would then arrive at each site and select a direction with a compass. Following this azimuth I would then traverse this grid with the goal of walking one kilometer, the size of the cell grid. Along this transect I would measure the length (along the cardinal direction) of any grass patch that intersected the measuring tape (Figure 2). Measurements were also taken of the longest distances from the left and right sides of the grass patch (perpendicular to the transect direction) (Figure 2, 3, 4 and 5). With these three measurements total patch length was calculated as the sum of the initial patch length, left side measurement and right side

measurement (Figure 2). This measurement was used as a proxy for patch size. Grass patches in or right alongside trails which traverse the forest, were ignored as the trail itself is a permanent disturbance in the forest and its effects was not taken into account for this study. Survey started on February 15, 2011 and ended in May 18, 2013.

Figure 1A. Map of Guánica Tropical Dry Forest Reserve, Puerto Rico (Forest borders outlined in green). Red line indicates a distance of 1 kilometer.
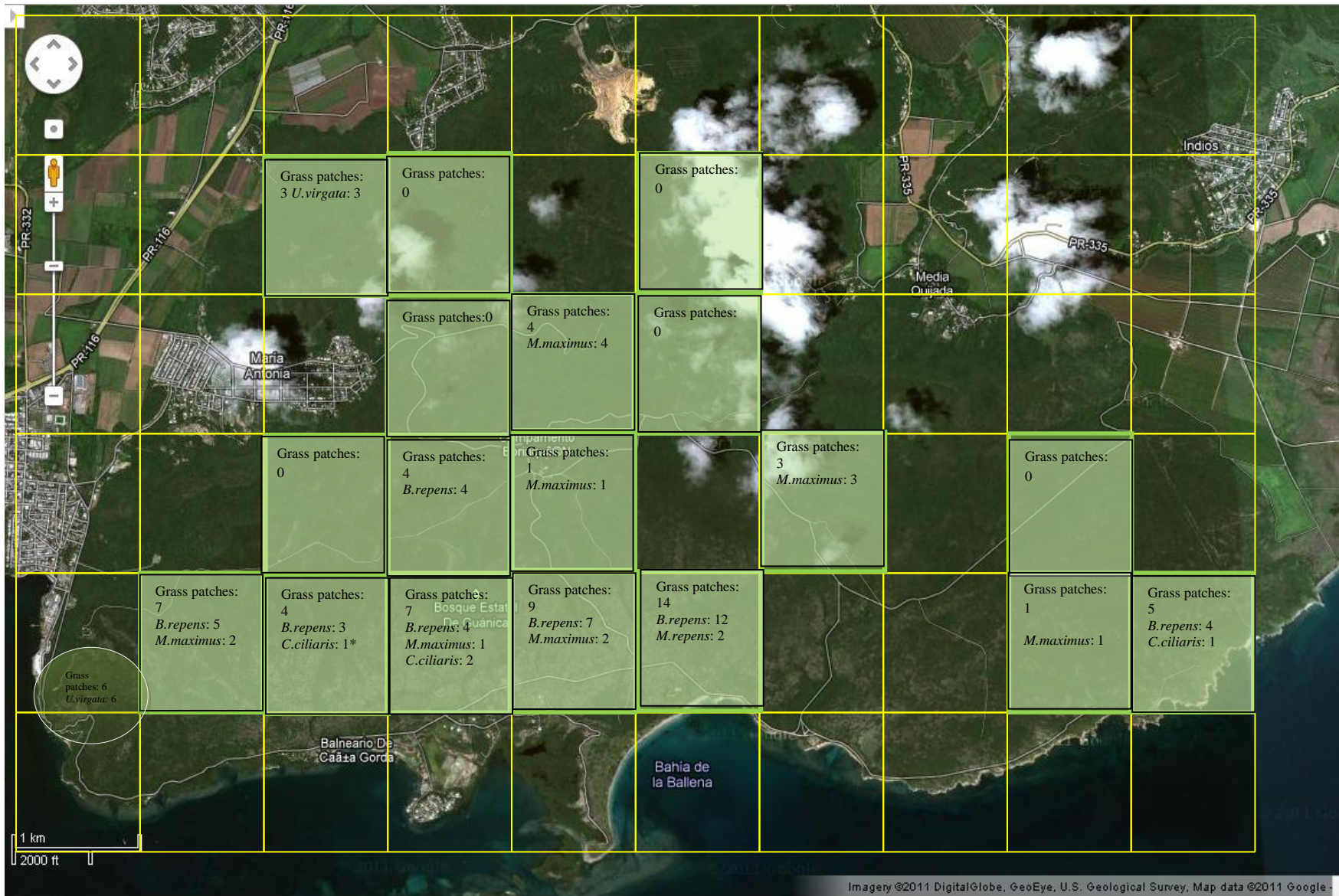
Figure 1B. Map of the Eastern portion of the Guánica tropical Dry Forest Reserve, Puerto Rico with overlaid 1 km long cell grids. Green shaded cells belonged to the randomly selected cells that were sampled. If selected cells landed on forest borders they were eliminated from the General Survey. Green ovals indicate areas that were targeted for survey after the general random survey. Number of grass patches sampled as well as grass type are included.
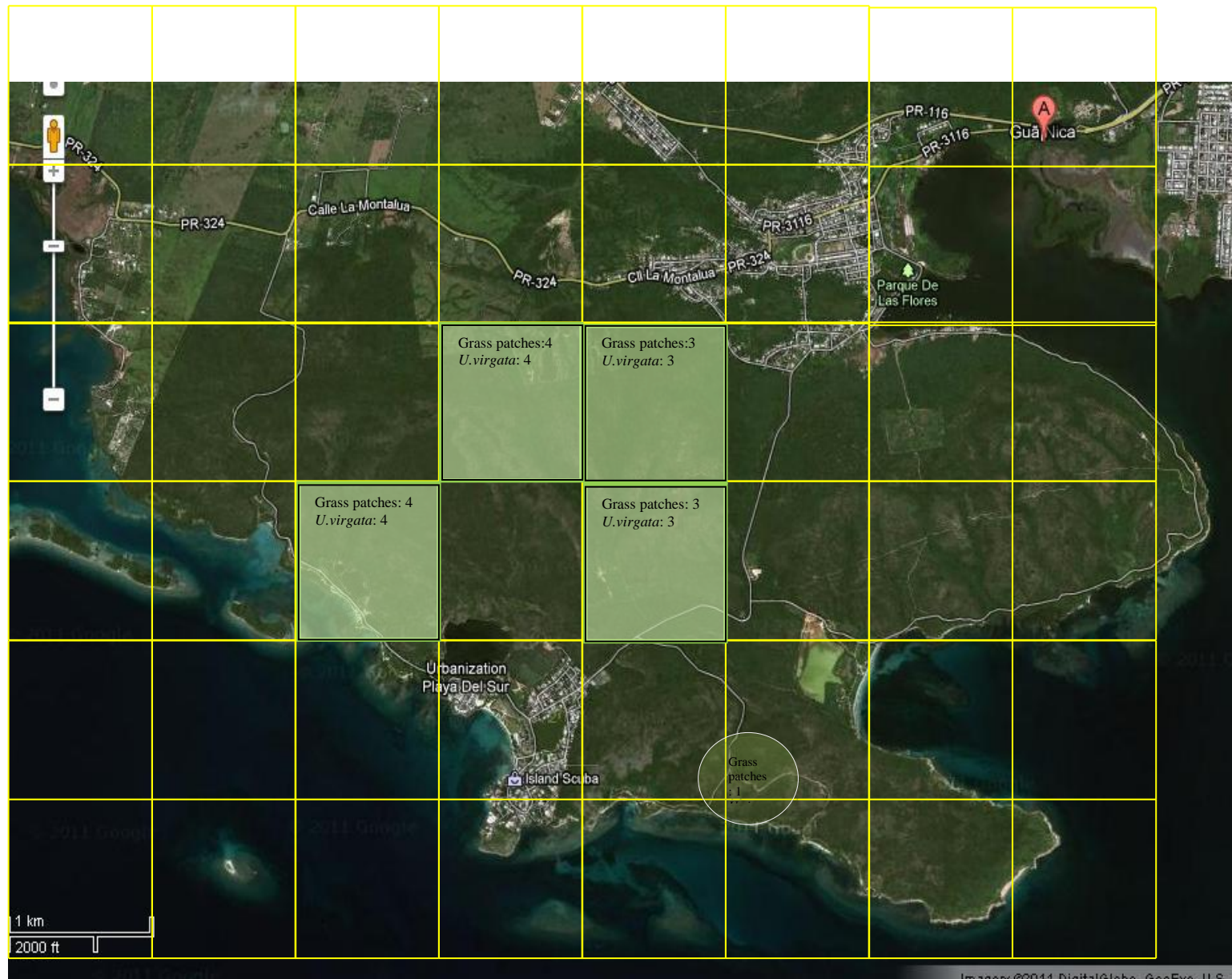
Figure 1C. Map of the Western portion of the Guánica tropical Dry Forest Reserve, Puerto Rico with overlaid 1 km long cell grids. Green shaded cells belonged to the randomly selected cells that were sampled. If selected cells landed on forest borders they were eliminated from the General Survey. Green ovals indicate areas that were targeted for survey after the general random survey. Number of grass patches sampled as well as grass type are included.
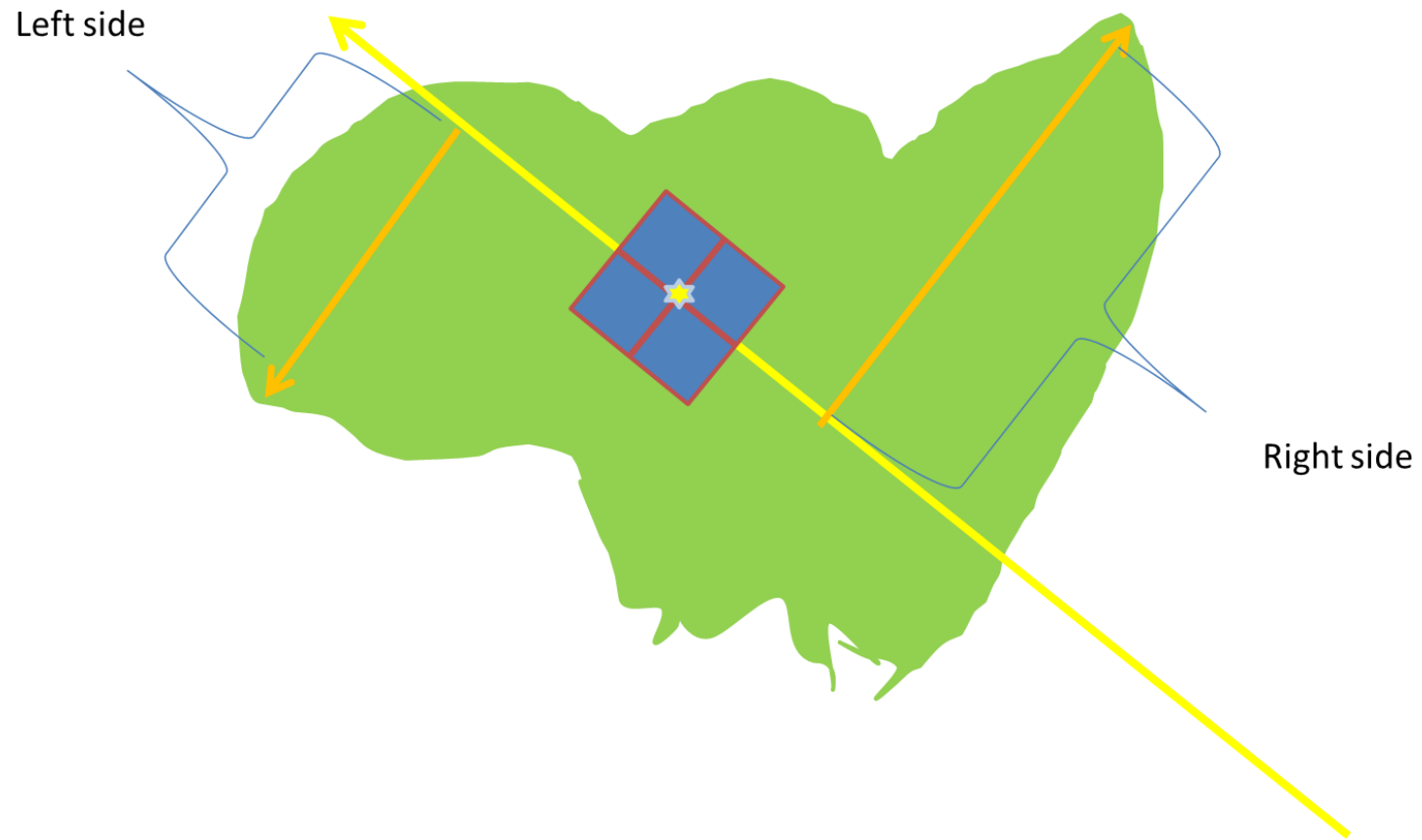
Figure 2. Experimental design established for the general field survey. Yellow arrow indicates direction from which the patch was discovered using a compass. Yellow star indicates the randomly selected point within the transect from which the 4-m^2 sampling plot would be established around it. Once data from native woody species diversity, stem density and ground basal diameter was collected, distance to the most distant right side and the left side was measured with measuring tapes. With the sum of patch length (yellow arrow) and longest left side and longest right side an estimated patch size was calculated.

Figure 3. Setting up measuring tape transecting a *Bouteloua repens* grass patch.

Figure 4. Measuring tape along *B. repens* grass patch.

Once patch length was measured, I randomly selected a point along the transect within the patch. The selected point then became the center of a 4-m^2 plot subdivided into four 1-m^2 quadrats (Figure 2). Within each plot I would then measure grass species, percent grass cover, woody species stem density and richness as well as stem basal diameter for each individual. I visually estimated grass percent cover within each 1-m^2 quadrat and averaged the values to generate one value for the entire plot (Figure 5). Identification of specimens was confirmed by Mrs. Jeanine Velez-Gavilan, curator of the MAPR at UPR-M and Mr. Omar A. Monsegur-Rivera US Fish and Wildlife biologist, Caribbean Ecological Services Field Office, nomenclature following Axelrod (2011). Of the 25 surveyed *U. virgata* patches, only 24 plots were sampled for the regression analysis since not all the patch measurements could be made by logistic constrains of size of this particular grass

patch. Of the six grass species found throughout the forest, I decided to compare *U. virgata* and *M. maximus* as they have several morphological similarities in phenology and biomass allocation and are present in areas that have burned or are prone to future burns.

Figure 5. Four 1 m^2 quadrats inside a *Bouteloua repens* grass patch.

Data were analyzed using InfoStat Student Version (DiRenzio *et al.* 2008); p-value =0.05 was use for all tests. Friedman tests were used to assess effects of grass patch type on woody species density. Using a regression analysis a relationship between woody species abundance with grass species was studied. Community level analyses were carried out using data on presence/absence of woody species with patches dominated by *Uniola virgata, Megathyrsus maximus* and *Bouteloua repens*. The sample sizes for patches dominated by the grasses *Melinis repens, Cenchrus ciliaris* and *Bothriocloa pertusa* were

too small ($\leq$ 4) and were taken out of these analyses. I used InVal analysis to find if there were any woody species that could act as indicators for the presence one of the three grass species used for this analysis. Data was then Hellinger transformed and the Euclidean distance was used for Multi-Response Permutation Procedures (MRPP) and indicator species analyses (Dufrene and Legendre 1997).

RESULTS

Within 83 grass patches surveyed, I counted 2215 woody stems from 30 families. Of these, 2108 individuals were identified to species level and situated in 58 species while only 17 individuals belonging to 15 morphospecies could not be identified (Table 1, Appendix 2). Nearly 75% of grass patches sampled were dominated by native grasses (either *Bouteloua repens* or *Uniola virgata*). The grass patch type containing the highest average woody stem density was *Uniola virgata* with 44.13 ± 7.64 stem/m^2 , followed by the non-native *Megathyrsus maximus* patches with 15.54 ± 2.34 stem/m^2 (Table 1).

Grass patches were mainly located in the southern part of the forest, which is near the coast and dominated by scrub and low-stature forest (Figure 4). Presence of grasses, mainly non-native grasses such as *Megathyrsus maximus*, *Melinis repens* and *Cenchrus ciliaris*, was observed along various trails but as mentioned in the Methods, these were not included in the survey (Figure 4 and 5, see Methods for justification). Although not sampled in the plots the presence of the African grass *Heteropogon contortus* (L.) P. Beauv. ex Roem. & Schult. was observed along road #333 in recently burned areas as well in forest trails leading from the coast, such as Vereda Ballena, Vereda Guitarra and the area

around the Guánica Cave. In Vereda Guitarra, on the east side of the forest, it was observed
to occur in association with *Bouteloua repens* grass patches

Native *Bouteloua repens* is widely distributed throughout the forest (38 of plots
sampled; Figure 1), while non-native *Cenchrus ciliaris* has been restricted to roadsides or
nearby trails (4 of the patches sampled) and non-native *Melinis repens* is uncommon in the
open rocky sites where *B. repens* dominates (2 plots sampled). *Bouteloua repens* dominated
sites, while ubiquitous throughout the open scrub, show no significant influence over native
woody species richness (p= 0.3153, Table 2). Significant patterns cannot be discerned from
the few sampled grass plots for *M. repens* and *C. ciliaris* because of their low numbers
(Table 1).

Table 1. Woody stem density in measured grass patches in the Guánica Tropical Dry Forest

Grass species	Number of patches	Average woody spp. density	SE
Bouteloua repens	38	11.32	2.34
Uniola virgata	24	44.13	7.64
Megathyrsus maximus	14	15.54	4.35
Cenchrus ciliriaris	4	1.75	0.63
Melinis repens	2	4.33	2.82
Bothriocloa pertusa	2	13.37	5.73

Comparing the four most abundant grasses throughout the survey, there was a
statistically significant difference in average woody stem density among, *Megathyrsus
maximus, Uniola virgata, Cenchrus ciliaris* and *Bouteloua repens* grass patches (P=
0.0270) (Table 2). The greatest stem density was for *U. virgata* followed by *M. maximus*
then *B. repens* and lastly by *C. ciliaris* (Figure 6)*.

Within patches of the two large bunchgrasses, *Megathyrsus maximus* and *Uniola virgata* woody stem density was statistically different (Table 3). In the fourteen *M. maximus* plots patch size was shown to have no statistically significant association with stem density (Figure 7, Adj.-R^2= 0.09, p= 0.1546). In contrast higher stem density is marginally associated with increased patch size of *U. virgata* (Adj.-R^2= 0.12, p= 0.057, Figure 8).

Multi-Response Permutation Procedures (MRPP) analysis showed that there are significant differences in species composition between *Megathyrsus maximus vs. Uniola virgata* grass patches and between *U. virgata vs. Bouteloua repens* grass patches, but not between *M. maximus vs. B. repens* grass patches (Table 4). The Indicator values analyses calculated with the Dufrêne and Legendre method showed that *Wedelia calycina*, *Crossopetalum rhacoma* and *Croton glabellus* are significant indicators of grass patches dominated by *U. virgata*, while *Stigmaphyllon emarginatum* and *Randia aculeata* are indicators of the presence of *M. maximus* dominated grass patches (Table 4). None of the woody species described showed a particular affinity for *B. repens* grass patches.

Table 2. Friedman test values from grass comparisons and posterior values. No adjustments were carried out for the posterior p-value.

Differences among grass patches	T^2	P-value		
Stem density	4.93	**0.027**		
Species Richness	1.7	0.2358		
Richness per stem	0.65	0.6014		
Stem Density:	Posterior comparisons:			
Bouteloua repens	A			
Cenchrus ciliaris	A	B		
Megathyrsus maximus	A	B	C	
Uniola virgata				D

Table 3. Values for the linear regression of stem density on patch size for different grass species. No adjustments were carried out for the posterior p-value.

	Grass type	N	Adj-R^2	P-value
Stem Density	*Uniola virgata*	24	0.12	**0.0577**
	Megathyrsus maximus	14	0.09	0.1546
	Bouteloua repens	38	0.00	0.5746
	Cenchrus ciliaris	4	0.00	0.6943
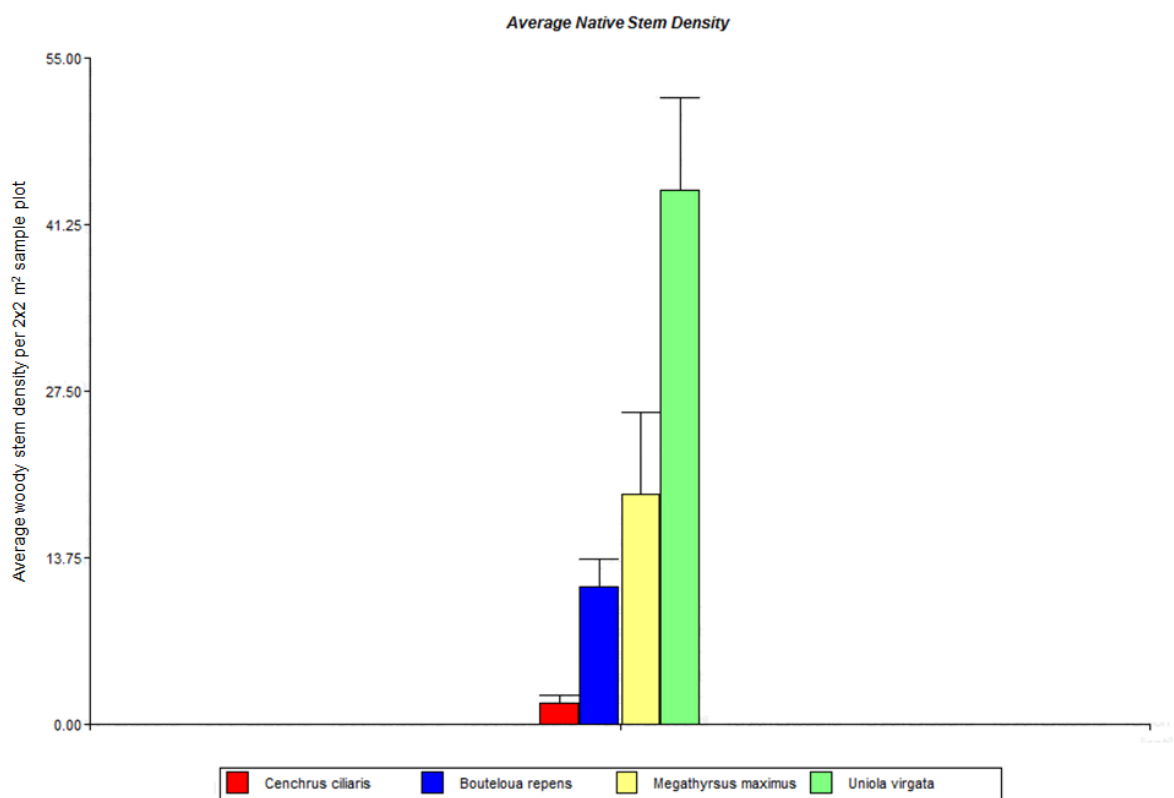
Figure 6. Average stem density in patches belonging to the four predominant grasses, the non-native *Megathyrsus maximus* and *Cenchrus ciliaris* and the native *Uniola virgata* and *Bouteloua repens.*
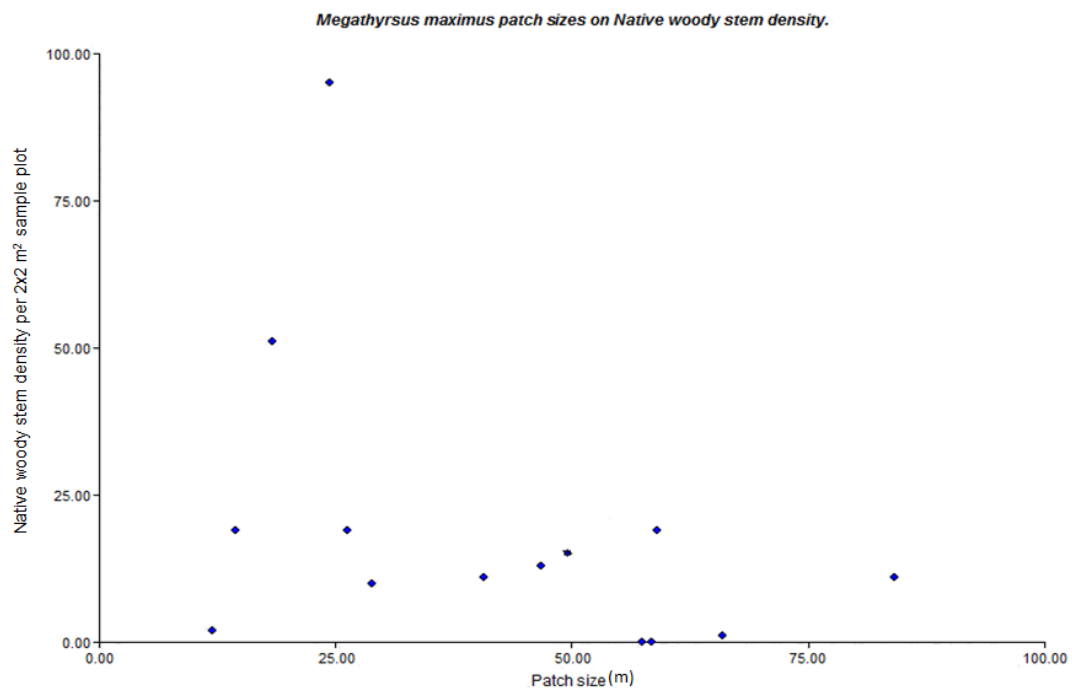
Figure 7. *Megathyrsus maximus* grass patch size index and its association with total woody stem density per sample plot.
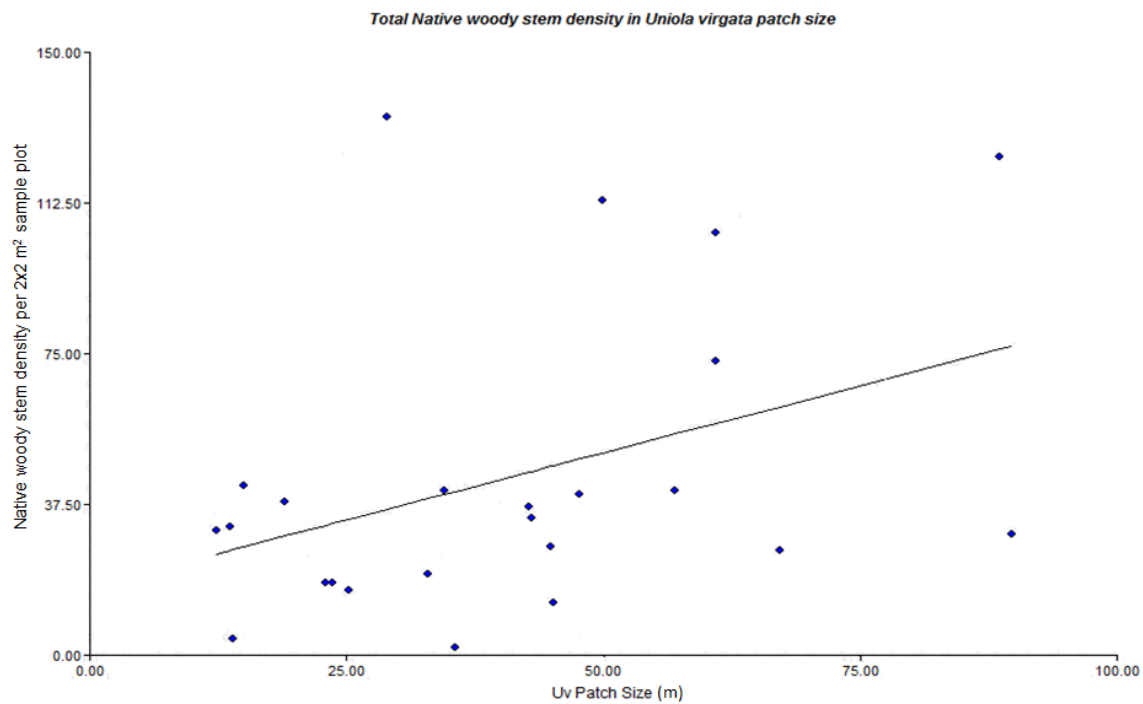
Figure 8. *Uniola virgata* grass patch size index and its association with total woody stem density per sample plot.

Table 4. Community level analyses

Multi-Response Permutation Procedures (MRPP)			
	T	A	p-value
M. maximus vs. U. virgata	-2.75200293	0.03042026	**0.01591358***
M. maximus vs. B. repens	-1.54186182	0.01040007	0.07771649
U. virgata vs. B. repens	-5.11127191	0.02445374	**0.00035578*****
Indicator values			
Indicator species	Grass type	Observed Indicator Value	p-value
Wedelia calycina	*U. virgata*	**40.9**	**0.0040***
Crossopetalum rhacoma	*U. virgata*	**25.4**	**0.0420***
Croton discolor	*U. virgata*	24	0.3964
Croton glabellus	*U. virgata*	**32.3**	**0.0270***
Krammeria ixine	*M. maximus*	8.4	0.3544
Stigmaphyllon emarginatum	*M. maximus*	**31.6**	**0.0090***
Corchorus hirsutus	*U. virgata*	14.9	0.9449
Melochia tomentosa	*M. maximus*	8.9	0.3353
Randia aculeata	*M. maximus*	**21**	**0.0400***
Mitracarpus polycladus	*U. virgata*	15.7	0.5506
Turnera diffusa	*B. repens*	29.3	0.2062
Lantana spp.	*U. virgata*	18.9	0.2523
Tamonea boxiana	*U. virgata*	8.8	0.6446

DISCUSSION

Grass patches were found throughout the forest but they were concentrated in the open scrub ecosystem in the southern slopes of the Eastern Portion of the Forest and in several places of the Western Portion of the forest (Figure 1.B and 1.C). Native grasses (led by the cespitose grass *Bouteloua repens*) in the Eastern Portion of the forest were more widespread than non-native grasses, which were located near disturbance prone sites (*e.g.* main forest trails and roadsides). In the Western Potion native grasses were also more widespread due to the native bunchgrass *Uniola virgata*. Patches dominated by this native

grass supported significantly higher native woody stem density per sampled plot and showed a marginally positive relationship between patch size and native woody species density per sampled plot. In contrast woody stem density was not related either positively or negatively to patches of native *Bouteloua repens* or non-native *Megathyrsus maximus* or *Cenchrus ciliaris.* Significant differences in woody species composition occurred among patches of the three main grass species (*B. repens, M. maximus* and *U. virgata*) were observed. Particular woody species were found to be indicators of grass species presence (Table 4).

Native *Bouteloua repens* was the grass with the widest patch distribution in the open scrub habitat, but its possible association with native woody stem density per sampled plot was not significant compared to other grass species (Tables 1 and 3). The weak association of native woody species stem density in *B. repens* sample plots may be because of species specific ceappistose growth form, which could be influencing local woody seedling recruitment. *Bouteloua repens* has been observed to inhabit a wide range of habitats that include open rocky scrub in xerophytic environments over the Americas (Herrera-Arrieta *et al.* 2004) which may suggest a correlation with their distribution throughout the Guánica Forest. *Bouteloua repens* also has an ability to produce large amounts of seeds, which have the ability to sprout 5 days after hydration yet only a limited number do so (*unpublished data*). However because of their shallow root system, roots may not be strong competitors for soil resources with deep rooted woody species. Although widely dispersed (Table 2 and Figure 1A), this cespitose grass dries up relatively quickly during the dry season, which does not make it an ideal place for seedling germination or

seedling transplantation as the roots could dry up the soil too fast with little ameliorating effect for target seedlings (*unpublished data*).

Native *Uniola virgata* was by far the grass patch type with the highest woody stem density (Table 3, Figure 8). The numbers of woody species could be related to *U. virgata*'s phenology as it could provide shade area for germinating woody seedlings along its grass edges. Yet it could also be due to the fact that *U. virgata* is not a fire prone species, and does not recover well after fires (Thaxton *et al.* 2012); with this in mind we could infer that with this lack of fire disturbance woody species are able to colonize the grass patches and accrue number of species unable to with stand fire.

Past fires could have aided in the dominance of non-native grasses such as *Megathyrsus maximus*, *Cenchrus ciliaris* and *Melinis repens*. Patches of these species were most common in areas of the forest that had history of past fire. Yet not all *M. maximus* patches were along known burned places and it has been observed along trails throughout the forest (Monsegur-Rivera 2009). This could be due to the fact that trails are a permanent disturbed habitat, which favors the introduction of non-native grasses (Veldman and Putz 2010). *Megathyrsus maximus* is also shade tolerant (Monsegur–Rivera 2009) which could suggest a more persistent presence in the forest after restoration. Other studies have mentioned *M. maximus* is a fire prone species and can regenerate after fires (Más and García-Molinari 2006) yet other studies have also mentioned its competitive nature with no need for the presence of fire by thatch formation (Williams and Crone 2006) or by using its fibrous root system to extract more water from local soil (Rojas-Sandoval and Meléndez-Ackerman 2012) which can have the effect of limiting the germination and establishment of native seedlings (Ammondt *et al.* 2012) competing for ground water.

Although the sampled plots for *Cenchrus ciliaris* were few (N=5), it has been suggested that *C. ciliaris* is an aggressive invader in arid ecosystems that limits germination of native species (Low 1997, Daehler and Goergen 2005, Jackson 2005, De la Barrera 2008) and this has been attributed to its exceptional ability to compete for water (Stevens and Fehmi 2009). Also of importance is that *C. ciliaris* does not necessarily need fire to spread (Olsson *et al.* 2012), and by simple apomictic seed production it can come dominate invaded areas (Daehler and Goergen 2005). Its limited spread to the forest might be due to its late arrival in the forest as documented with voucher specimens, collected at Caña Gorda, present in the MAPR herbarium dating to 1988 (Monsegur-Rivera 2009) and the relatively recent use of prescribed burns along road #333 to control the spread of other invasive grasses, like *M. maximus*, which favors *C. ciliaris* resprout. Also of importance yet underrepresented in the survey was *Melinis repens*, a perennial C_4 bunchgrass (Búrquez-Montijo *et al.* 2002 in Stevens and Fehmi 2009) in rocky outcrops, which has the ability to persist in the local seed bank for long periods (Cooper 2012). It has been commented that this African grass could become a potential invader in the limestone outcrops of the forest (Monsegur-Rivera 2009). This species has also been observed to readily colonize heavily disturbed areas (*e.g.* bulldozed sites) in the Forest (Jaime and Van Bloem, *unpublished data*). Thaxton and Velázquez-Rojas (*unpublished data*) observed that the biomass allocation of *Bouteloua repens*, *Melinis repens* and *Cenchrus ciliaris* share physical and biomass allocation strategies. The shared biomass allocation strategy of *B. repens, M. repens* and *C. ciliaris* for belowground growth could offer a way for studying the competition for the same rocky soil pockets in the southern half of the Eastern Portion of the Forest, between native and non-native grasses. Personal field observations suggest that this habitat is where *Bouteloua repens* patches are predominantly located as well as

other pioneering shrubs like *Croton discolor*, *Corchorus hirsutus* and *Lantana* species. Another species of *Melinis*, *Melinis minutiflora* located in the Hawaiian Islands, has been shown to limit the germination and establishment of native seedlings by rapid nitrogen cycling in the soil, the quick formation of dense litters which produce a strong shading effect they produce and by its tolerance of frequent fires (D'Antonio *et al.* 2011) which reduces native seedling germination and establishment. *Melinis repens* could become a grave concern for future conservation efforts in the forest.

Community level composition was different for the three analyzed grass species. The shrubs *Wedelia calycina*, *Crossopetalum rhacoma* and *Croton glabellus* were found to be significant, but not very high indicators of the presence *U. virgata* grass patches. All three shrub species are characterized by being present in disturbed sites (*e.g.* trails) and by being classified as pioneering species in forest succession (Monsegur-Rivera 2009). For *M. maximus* grass patches the liana *Stigmaphyllon emarginatum* and the shrub *Randia aculeata* were found to have significant values as to be indicative of this grass species. *Stigmaphyllon emarginatum* has a fast reproductive rate and its seeds are wind disperse, which has been mentioned that in other dry forest species aid in the colonization of highly disturbed areas within dry forests (Khurana and Singh 2001, Vieira and Scariot 2006). Presence of *Randia aculeata* as an indicator of *M. maximus* grass patches was a surprise since this species has been observed in a variety of habitats within the forest boundaries and outside of them and greater number of individuals were observed in native grass patches (*personal observation*). Yet it has been mentioned that *Randia aculeata* prefers open storied habitats and can recover well from moderate disturbances, such as logging and

pasture clearing (Francis 2003). Perhaps it could also survive the presence of recently established, unburned *M. maximus* patches.

Compared between themselves there was no significant difference in woody species communities between *M. maximus* and *B. repens* grass patches, but a significant difference was observed between *M. maximus* and *U. virgata* grass patches (Table 4), as well as between *U. virgata* and *B. repens* grass patches. The lack of difference between *B. repens* and *M. maximus* could be due to their co-occurrence in areas of shallow soils and similar ecological characteristics. Both species have morphological similarities in terms of a shallow root system, which could exacerbate low soil moisture availability near the soil surface thereby creating conditions that many woody species cannot tolerate. *Megathyrsus maximus* has a particularly profuse superficial root system, which can range from 45 to 152 cm in depth, depending on soil conditions (Más and García-Molinari 2006*).* Such close proximity could allow it to interact with the growing root systems of native seedlings and during droughts exacerbate parch soil conditions. During the dry season leaves of both species dry out completely, leaving more soil surface exposed to full sunlight, which can lead to higher surface temperatures and more extreme environment for seedlings (Franco and Nobel 1988).

The difference between *M. maximus* and *U. virgata* grass patches could be due as has been previously mentioned to the distinct disturbance history. *Megathyrsus maximus* sites have some fire history in the past, while *U. virgata* has basically has none (Thaxton *et al.* 2012). The fact that so much time passed between burns in *U. virgata* sites could allow enough time for propagules from nearby forest fragments or borders to come in and start the process of colonization. This could in fact explain why the woody shrubs were shown to

be indicators of *U. virgata* grass patches. Data has also shown that significant morphological differences might be present between both *M. maximus* and *U. virgata* root systems and rooting depth (Thaxton and Velázquez-Rojas, *unpublished data*) which could be a factor generating differences in rates of propagule establishment in the two grass patch types. *Uniola virgata* with its deeper root system could avoid entering into direct competition for water with native seedlings during this critical life-stage than the more superficial and fibrous root system of *M. maximus* clumps.

The significant difference between *B. repens* and *U. virgata* grass patches could also be explained by their morphological traits. *Bouteloua repens* is a shallow-rooted cespistose grass while *U. virgata* has a deeper rooting system and could be avoiding water competition with other plants in the early establishment. Aboveground phenology is also quite different, with *U. virgata* providing more partial shade to plant on its profuse edges than overexposed clumps of *B. repens*, which could be a mechanism by which woody species could survive and colonize grass patches.

CHAPTER 3

Effects of native *Uniola virgata* and non-native *Megathyrsus maximus* grasses on native woody species seedling survival and growth

INTRODUCTON

Tropical dry forests worldwide have been experiencing dramatic ecological shifts in recent centuries as human land use has transitioned from subsistence agriculture to formal industrial agriculture to urban development. Forests in this biome are preferred by people because of their high soil productivity and climate, which has periods of dryness (Murphy and Lugo 1986, Janzen 1988). Human presence also introduces the disturbance of fire into neotropical dry forests for clearing and the establishment of pasturelands (D'Antonio and Vitousek 1992). Fire is a novel disturbance in most neotropical dry forests and can promote conversion into grasslands or scrublands in susceptible areas (Vieira and Scariot 2006, Hooper *et al.* 2004, Cabin *et al.* 2002). Fire regimes that are novel have a more profound effect in ecosystems since the changes are unprecedented and can alter ecosystem properties (Brooks *et al.* 2004). These changes can range from altering the floristic composition at the macroscopic scale (Hooper *et al.* 2004) to alterations in the bacterial communities in the microscopic level (Smith *et al.* 2008). Another aspect of such high anthropogenic influence is the introductions of non-native plants and animals (Gurevitch *et al.* 2008).

Non-native plants have been introduced into tropical dry forest mainly as crops, timber or animal fodder, in the case of grasses (Parsons 1972, Williams and Baruch 2000). Non-native grasses in particular can be quite damaging as these are able to monopolize resources once a novel disturbance has been introduced into the ecosystem, even without

the active presence of fires (Olsson *et al.* 2012). Non-native grasses can limit native seedlings from germinating or establishing by creating thick thatch carpets, through direct resource (water, light or nutrient) competition or by serving as shelter for animals that are natural herbivores for the target species (Pivello *et al.* 1999, Cabin *et al.* 2002, Thaxton *et al.* 2011, Ortega-Piek *et al.* 2011, Thaxton *et al.* 2012). Many of these grasses have fibrous root systems which can enter in direct competition for water with seedling root systems (Rojas-Sandoval and Meléndez-Ackerman 2012).

In Guánica Tropical Dry Forest in Puerto Rico the most widespread non-native grass is *Megathyrsus maximus* (Jacq.) B.K. Simon & S.W.L. Jacobs (Monsegur-Rivera 2009), a perennial facultative apomictic C_4 grass which had been introduced into the Neotropics as cattle feed from Africa (Williams and Baruch 2000). It produces great amounts of seeds and tends to create large fuel loads which can readily ignite and promote fire spread (Más and García-Molinari 2006). This grass has altered the disturbance regime in the forest, changing nutrient and community dynamics in favor of fire adapted species, *e.g.* creating thatch carpets capable of easily catching fire (Thaxton *et al.* 2012).

Studies in Hawaiian dry forests with the non-native grass *Pennisetum setaceum* found that the dense shallow root system could be detrimental for the development of woody seedlings, because the grass root system aided them in the competition for water following small pulses of rain (Cordell and Sandquist 2008). Other studies carried out in South America and Australia have also shown strong evidence of these effects on local biodiversity (Baruch and Jackson 2005, Jackson 2005).

Native woody species long-term survival is diminished in grass invaded habitats (Pérez-Martínez 2007, Ramjohn *et al.* 2012, Wolfe and Van Bloem 2012), yet it is not clear

if native grasses also impose this type of barrier on native woody species germination and establishment. Within this context I addressed two main objectives. First I compared native and non-native grasses effects on seedling regeneration by transplanting seedlings into two main treatments, *Megathyrsus maximus* and *Uniola virgata* grass patches. Within these two large patches I would then partition into two additional treatments consisting of transplanting seedlings into bare soil spots and grass edges, to see the potential effect of shading in the survivorship of the seedlings. My results will contribute to an understanding of the role that native grasses may play in restoration, as catalysts for ecological succession.

MATERIALS AND METHODS

Field sites

The Guánica Dry Forest is located in the southwestern part of the island of Puerto Rico, in the Greater Antilles in the Caribbean Sea ($17^o58'$ N, $65^o30'$ W). Precipitation averages 860 mm with a temperature average of 24ºC. Soils on the forest are derived from a porous limestone substrate and have a notable phosphorous deficiency (Van Bloem *et al*. 2004). This further aggravates the effects of water stress on the plant community. Soils in Guánica typically lack a deep organic layer and experience high solar irradiation due to the rain shadow effect of the central mountain chain of the island. Yet even so, previous to its formation as a reserve, parts of the current Guánica Forest were used for agriculture as evidenced by aerial photographs from the 1930's and soil evidence of ashes (Murphy and Lugo 1986, Molina Colón and Lugo 2006).

Field Experiment

To assess the effects of grass cover on woody species seed germination and microclimate, seedlings from three woody species, *Jacquinia berteroi* Spreng, *Coccoloba krugii* Lindau and *Erythroxylum areolatum* L. were selected for this experiment. *Erythroxylum areolatum* has been suggested as a useful species for direct-to-native restoration since it is able to survive in grass invaded sites (Wolfe and Van Bloem 2012). *Coccoloba krugii* is found on exposed full light limestone substrates in the xeric forests with little disturbance history while *J. berteroi* has a widespread distribution through the forest's well drained soils (Monsegur-Rivera 2009) making both candidates for early restoration efforts in the coastal xeric habitat. Seedlings were donated by the US Fish and Wildlife Services in the Cabo Rojo Bird Refuge, Puerto Rico. These species were germinated from seeds collected in the Guánica tropical dry forest during the summer of 2011. Seedlings were grown in the greenhouses for a year and were transplanted into the field on October 26, 27 and 28, 2012. A total of 400 seedlings of each species were used in the experiment.

Twenty randomly selected grass clumps and 20 adjacent bare soil spots were chosen in native grass *U. virgata* dominated areas and non-native *M. maximus* areas. Sites were selected by the proximity to trails or roadsides, similar fire histories in the recent past (Thaxton *et al.* 2012) and the dominant presence of one the two grasses (Figure 1 A and B). Native dominated site is a slope overlooking Jaboncillo beach above road #333 and has dense *Uniola virgata* clumps intercepted with bare soil spaces (Figure 1 A). Non-native dominated site is located around the Guánica Cave, near forest trail Tamarindo (Figure 1 B). Bare soil spots were small (ranging from ~1-4m^2) and were intended to mimic the

environment seedlings would experience following a grass removal treatment. Around each grass clump five randomly selected seedlings, 2 *J. berteroi*, 2 *C. krugii* and 1 *E. areolatum* were transplanted in the field. Arrangements around each grass clump and in each bare soil site were randomized to minimize microsite effects due to aspect and orientation relative to the grass clump. To ameliorate the effect of transplantation shock, all replicates were watered every two days for two weeks following transplantation on October 26, 27 and 28, with ~95 mL of water at each watering. All seedlings were censused and measured for cotyledon retention, leaf and stem growth every two weeks until the 8th census (29 weeks post-planting). Subsequent monthly censuses were then carried out until May 3, 2013 (6 months post-planting).

I also measured microclimate conditions experienced by the seedlings during the study period. To detect if there were differences in the soil environment between treatments, 5 cm depth sensors (Decagon EC-5; decagon.com) with attached HOBO dataloggers (onsetcomp.com) were set up in the field to measure volumetric soil moisture and temperature. Soil moisture was monitored during the experiment to track if there were any difference between the bare soil and grass edges yet there with some of the probes and only data from the Jaboncillo (*Uniola virgata* site) could be graphed for the whole six month period (Appendix 2 and 3). During the experiments all points were measured for light levels using a Li-cor Line Quantum Sensor (www.licor.com).

Figure 1.A and 1.B show the selected native and non-native sites respectively. A yellow 100 meter long line has been drawn on both maps to show perspective. General area were patches were located are located inside the light green line.

Statistical analyses

Data were analyzed using the statistics program Infostat® using non-parametric Friedman ANOVA tests, since each census was treated like a repeated measure across time. Tests were measured with a set p-value = 0.05 for all tests.

RESULTS

There were no differences in overall seedling survival between transplants in *Uniola virgata* and *Megathyrsus maximus* sites (p-value > 0.9999, Table 1), however there were significant differences between bare soil and grass clump edge treatments (p= 0.0039) and a significant interplay of site by treatment (p=0.006). Overall results showed clear differences between grass edge as a safe site for woody seedling survival (33.5% ±7.21) and bare soil spots as detrimental (8% ± 9.85) during the dry season, but the magnitude of treatment differences differed by site. Higher survivorship was found to be in the grass edge of *U. virgata* grass clumps (51% ± 4.66), followed by *M. maximus* grass edge with 16% ±9.96 seedling survival. Bare soil treaments had the lowest percentages of survival with *U.*

virgata bare soil having a 12% ± 8.61 seedling survivorship and 4% ± 11.46 seedling survivorship for *M. maximus* bare soil treatment (Figure 2).

There was a statistical difference among species performance (Table 1) with higher survivorship of *E. areolatum* seedlings than *J. beteroi* or *C. krugii* seedlings (Figure 4). Final percent survival was 35% ± 6.68 for *E. areolatum,* 15% ± 9.54 for *J. berteroi* and 19.38%± 9.04 for *C. krugii* seedlings. However all species experienced highest survivorship when planted under shade of *U. virgata* (Figure 3). Among *E. areolatum* seedlings greatest survivorship was found in *Uniola virgata* grass edge (p< 0.0001), followed in descending order by *Uniola virgata* Bare soil*, Megathrysus maximus* Grass edge and *Megathyrsus maximus* Bare soil (Figure 6). Within *C. krugii* seedlings the highest survival in descending order was *U. virgata* grass edge*, M. maximus* grass edge, *U. virgata* bare soil and last *M. maximus* bare soil (Figure 4). For *J. beteroi* seedlings highest survival in descending order was *U. virgata* grass edge, *U. virgata* bare soil and similar values for seedlings under *M. maximus* grass edge and *M. maximus* bare soil threatments (Figure 6).

Light measurements from both grass edge and bare soil treatments were statistically significantly different (Table 2, p <0.0001) with bare soil locations consistently higher than grass edge. Light levels at *Uniola virgata* and *Megathyrsus maximus* grass edges were not statistically different (p= 0.6663). In contrast differences between *M. maximus* and *U. virgata* bare soil sites were found to be significant (p<0.0001) with *U. virgata* bare soil sites having higher light levels.

Sensors left at the *M. maximus* dominated site (Cueva site) were defective and data could be extracted from them. From the *U. virgata* dominated site (Jaboncillo site)two of three sensors laid on grass edges showed that soil moisture here was higher than in nearby

exposed bare soil sites. Water availability was more erratic in bare soil sites than in grass

edges (Appendix 2 and 3).

Table 1. Friedman test values for treatments and posterior values.
No adjustments were carried out for the posterior p-value.

Treatment	T^2	P-value
Site (Cueva vs. Jaboncillo)	0.00	>0.9999
Treament (Shade vs. Bare Soil)	13.91	0.0039
Site + Treatment	5.04	0.006
Species	8.97	0.0017
Site + Treatment:	Posterior comparisons:	
U.v. Bare	A	
M.m. Bare	AB	
M.m. Grass Edge	C	
U.v. Grass Edge	C	
Species:		
Jacquinia berteroi	A	
Coccoloba krugii	B	
Erythroxulum aerolatum	B	

Table 2. Friedman test values for Light Measurements and posterior values
No adjustments were carried out for the posterior p-value.

Light Measurements:	T^2	P-value
Treament (Grass Edge vs. Bare Soil)	361.00	<0.0001
U.v. Grass Edge vs. M.m. Grass edge	0.19	0.6663
M.m Bare Soil vs *U.v* Bare Soil	1.00E+30	<0.0001
Site * Treatment	63.25	<0.0001
Light Measurements:	Posterior comparisons:	
M.m. Grass Edge	A	
U.v. Grass Edge	AB	
M.m. Bare Soil	C	
U.v. Bare Soil	D	
M.m. Bare Soil	A	
U.v. Bare Soil	B	
U.v. Grass Edge	A	
M.m. Grass Edge	A	

Figure 2. Percentage of survivorship of woody species seedlings during a 6-month period during the dry season under four treatments, *Uniola virgata* bare soil (Yellow hexagons), *Uniola virgata* grass edge (green triangles), *Megathyrsus maximus* bare soil (Blue triangles) and *Megathyrsus maximus* grass edge (red squares).
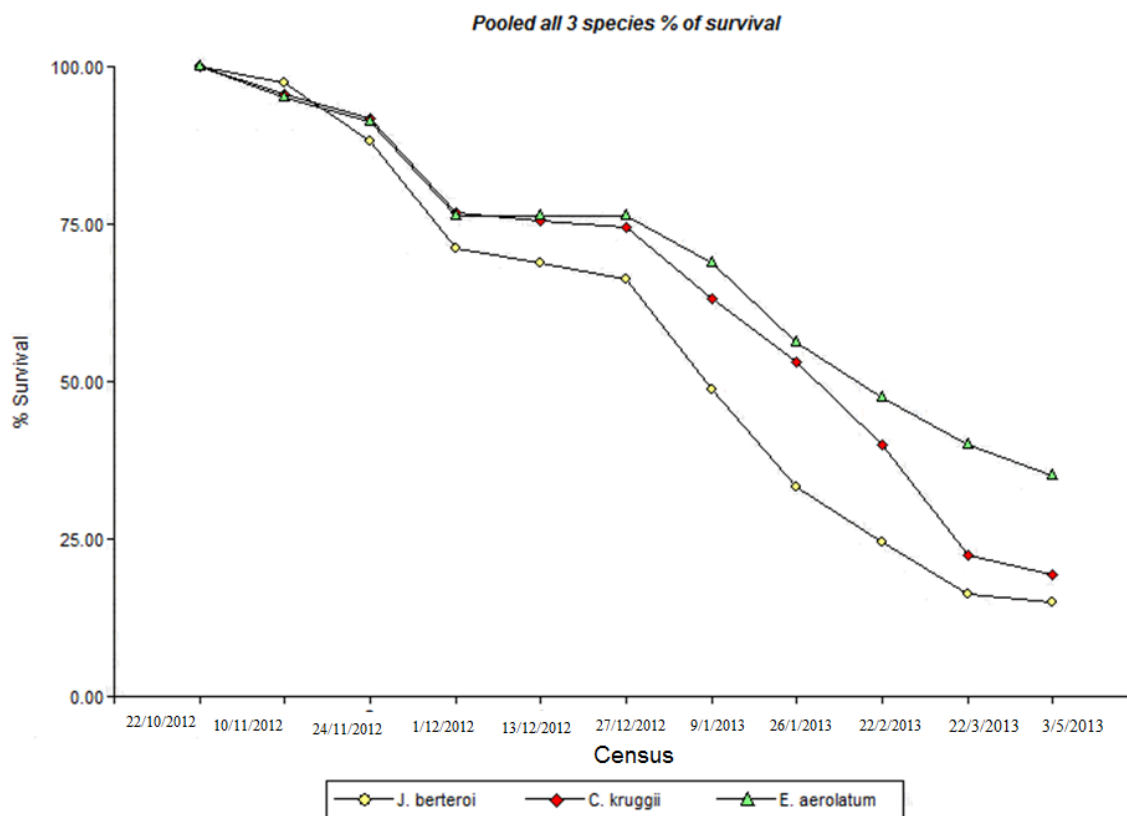
Figure 3. Percentage of survivorship of the three target species seedlings during a 6-month period during the dry season. Green triangles are *Erythroxylum areolatum*, red rhomboid *Coccoloba krugii* seedlings and yellow circles *Jacquinia berteroi* seedlings.
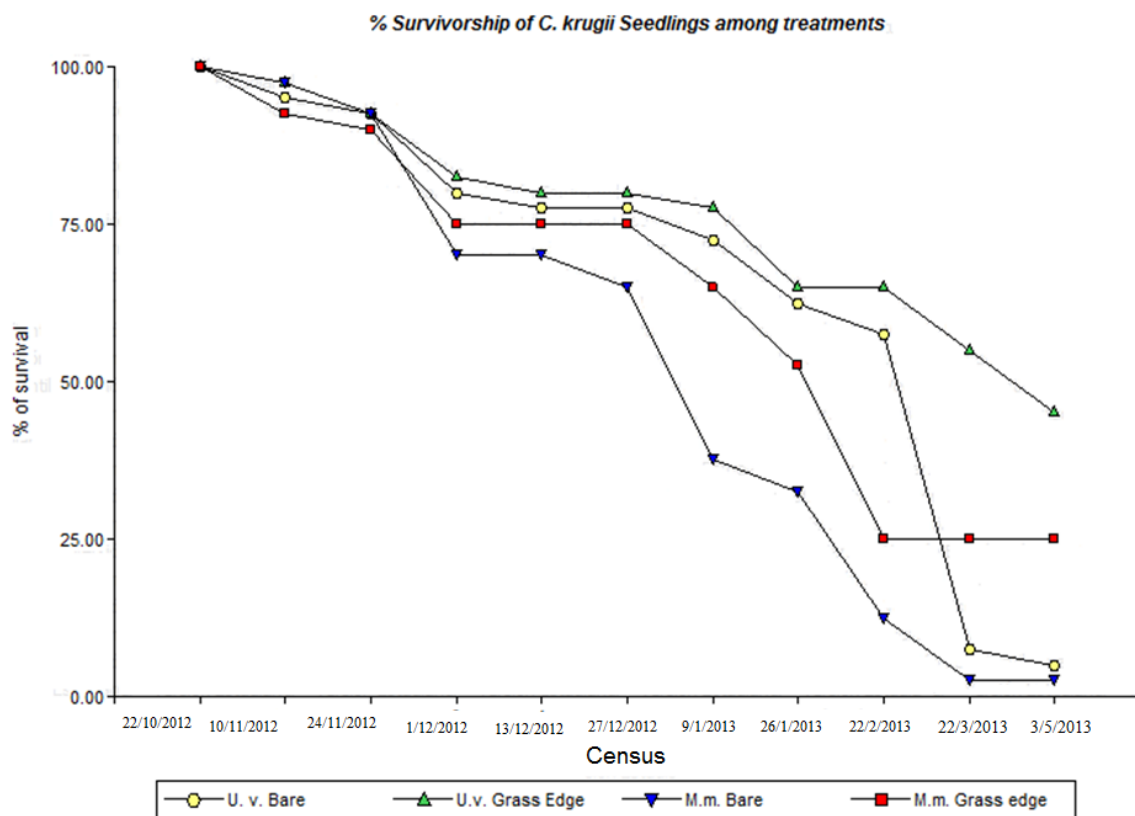
Figure 4. Percentage of survivorship of *Coccoloba krugii* seedlings during a 6-month period during the dry season under four treatments, *Uniola virgata* bare soil, *Uniola virgata* bare soil (Yellow hexagons), *Uniola virgata* grass edge (green triangles), *Megathyrsus maximus* bare soil (Blue triangles) and *Megathyrsus maximus* grass edge (red squares).
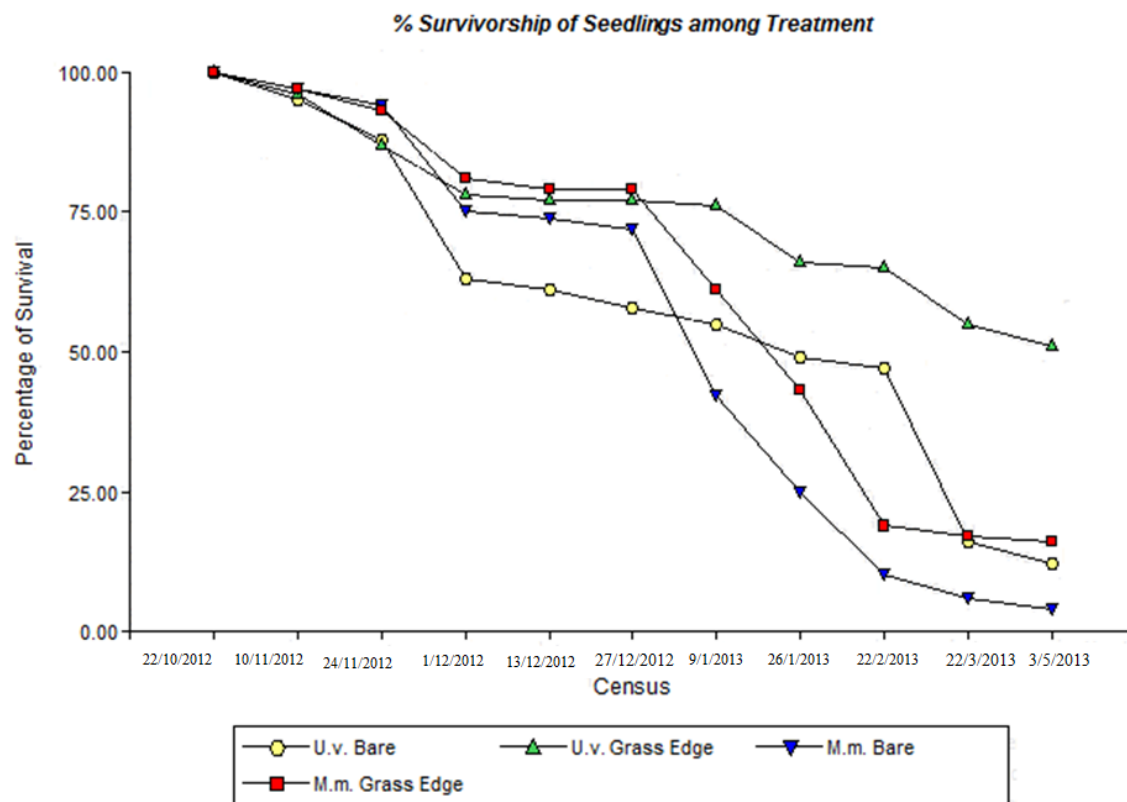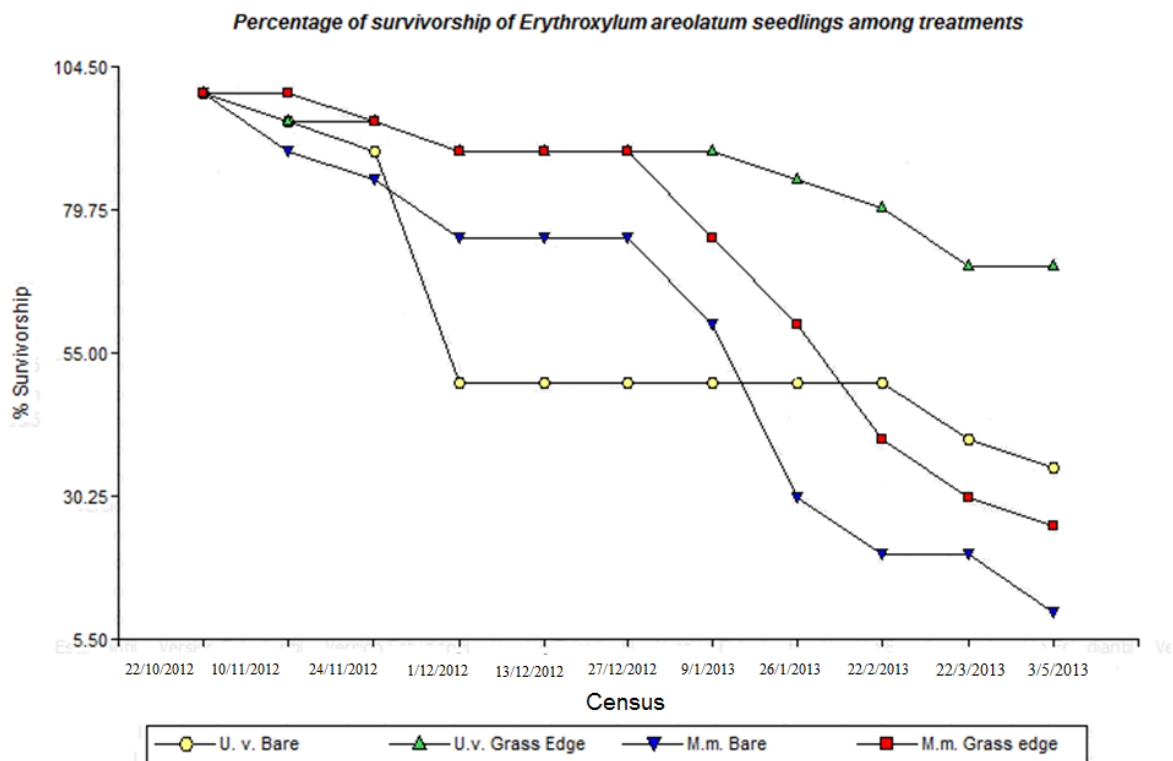
Figure 5. Percentage of survivorship of *Erythroxylum areolatum* seedlings during a 6-month period during the dry season under four treatments, *Uniola virgata* bare soil, *Uniola virgata* bare soil (Yellow hexagons), *Uniola virgata* grass edge (green triangles), *Megathyrsus maximus* bare soil (Blue triangles) and *Megathyrsus maximus* grass edge (red squares).
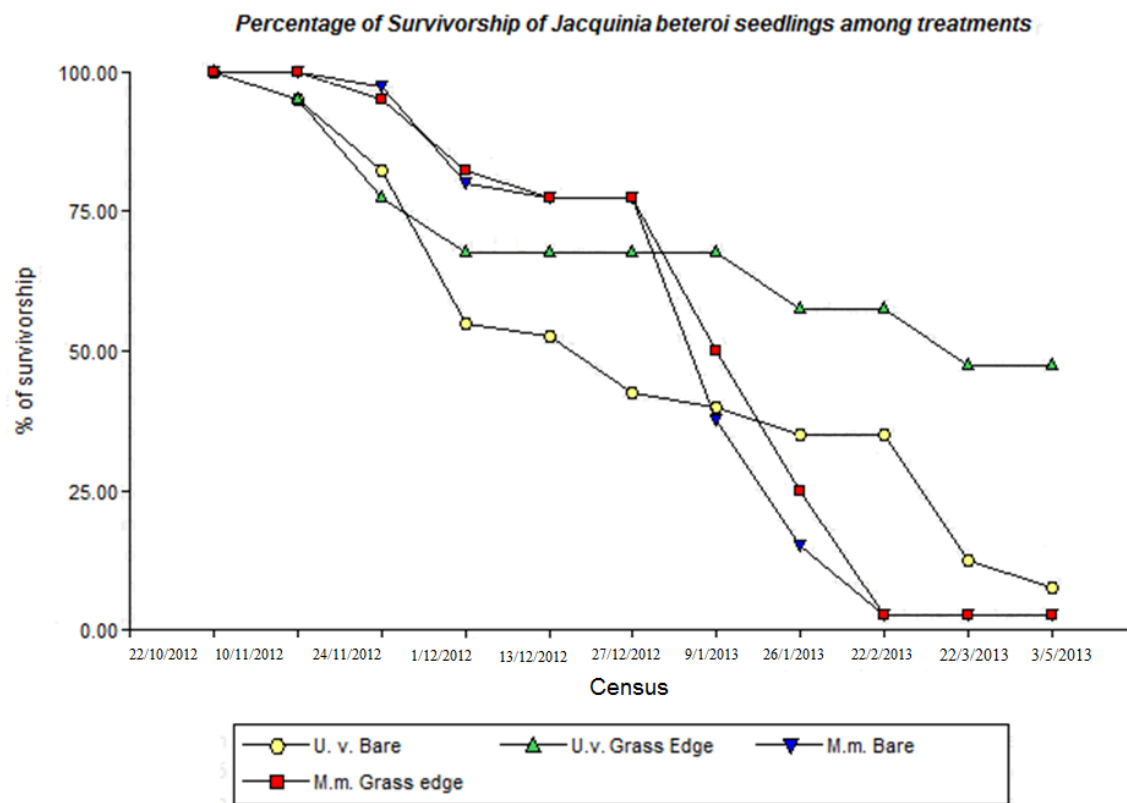
Figure 6. Percentage of survivorship of *Jacquinia berteroi* seedlings during a 6-month period during the dry season under four treatments, *Uniola virgata* bare soil, *Uniola virgata* bare soil (Yellow hexagons), *Uniola virgata* grass edge (green triangles), *Megathyrsus maximus* bare soil (Blue triangles) and *Megathyrsus maximus* grass edge (red squares).
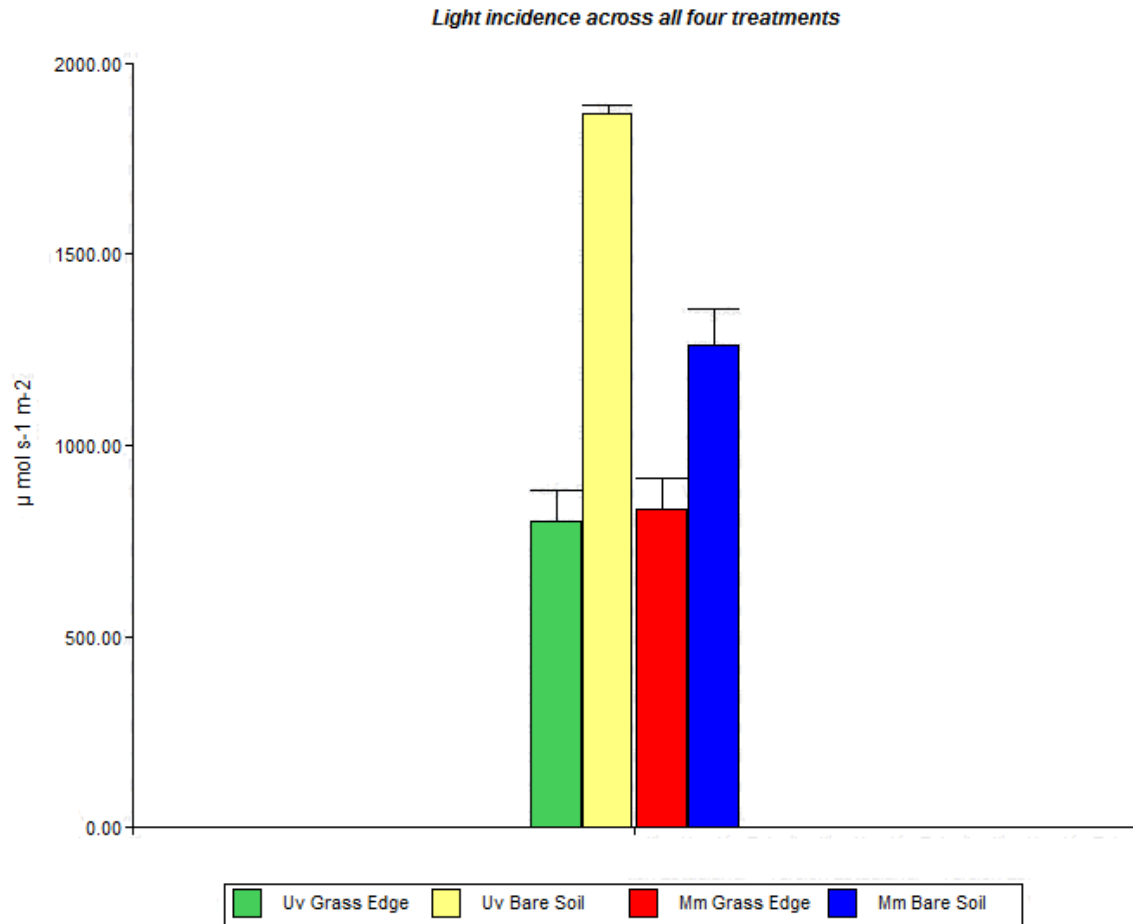
Figure 7. Averaged light incidence between all four treatments., p-value <0.0001.

DISCUSSION

Survival was affected by grass type, light exposure and soil moisture availability. This could be due to shading, because even partial shading like that of grasses can have sufficient ameliorating effect compared to open sun lit spots. Padilla and Pugnaire (2006) mention that the type of nurse plant and/or target species, as well as the time of year for the transplantation, must be taken into consideration for the successful outcome of the endeavor. Since the experiment was carried out during the most extreme of seasons, the

longest dry season of the bimodal dry seasons that the forest goes through even the small shade provided by the grasses has the potential to benefit the plants (Figure 6).

Interestingly, the light availability under *M. maximus* and *U. virgata* grass edges was not statistically different (Table 2). This may be due to the different disturbance history of the *M .maximus* site, which can include more frequent fires that could have altered the soil mineral composition. Also *M. maximus* clumps have been found to cluster closer to each other than those of *U. virgata* clumps, perhaps indicating to more intense competition for nutrients and soil moisture (Thaxton and Seguí *unpublished data*). This clustering of *M. maximus* clumps could also allow for other vegetation to have been present in the patch, exerting an influence on the light measurements. Also into consideration could be the time of day the light measurements were taken, mid-morning compared to noon in *U. virgata* site. Yet even with the influence of this extra shade appears not to have mattered and perhaps indicates that the critical mechanism might be root related or a conjecture of shade and root system interaction.

Soil moisture from *U. virgata* grass edges was not strongly indicative of clear trend, but this could be due to the position of the sensor probes on the slope which the Jaboncillo grass patch was located, or the age of the plant used. Younger plants could have roots closer to the surface and extract more surface water than older *U. virgata* plants, entering into competition with nearby woody plants. Two of the sensor probes located in the *U.virgata* grass edge showed that soil moisture here stayed relatively high during the two drought periods, the severe one from mid-December to early February and the second drought from Mid-February to March, compared to bare soil sensor probes.

When I analyzed the four treatment combinations separately (native *vs.* non-native plus bare soil spot vs. grass edges), I then observed that not all grass edges are the same. *Uniola virgata* grass edges had the highest surviving number of seedlings during the course of the experiment while the *Megathyrsus maximus* grass edge proved detrimental once the dry season started in earnest (Figure 2). This is backed by the literature. Wolfe and Van Bloem (2012) showed that native saplings in the unburned non-native grass patches, where *Megathyrsus maximus* was present, experienced higher mortality than those in the forest understory during the summer drought. This could be due not only but their dense subsurface fibrous root systems (Sandoval-Rojas and Meléndez-Ackerman 2012) but also by the lack of over story shade is probably a principal determinant in this mortality (Wolfe and Van Bloem 2012). *Uniola virgata* shade was more persistent during the dry season since its leaves, even when dead, bunch together providing a more consistent shade on its edges (*personal observation*). This could give the head start that seedlings lacked in open full light bare soil spots and in the shade of *Megathyrsus maximus* grass edges. Between the bare soil spot treatments the *Uniola virgata* sites did considerably better than the *Megathyrsus maximus* bare soil spot treatment (Figure 2). Yet by the end of the experiment seedling survivorship was also declining.

Abiotic filters are the primary determinants in seedling germination and establishment in resource poor environments (Mangla *et al.* 2011). As a tool for restoration efforts attention has been focused in recent years on plant-plant interactions emphasizing potential facilitation effects by nurse plants in arid or semi-arid ecosystems with a variety of plant life forms, trees, shrubs other grasses and cacti (Maestre *et al.* 2003, Santiago-García *et al.* 2008, Rojas-Sandoval and Meléndez-Ackerman 2012). The usefulness of

nurse plants stems from their negligible negative effects on the target species and their usually short life-spans. The strongest beneficial effects seem to occur at intermediate levels of abiotic stress (Holmgren *et al.* 2011). Several studies carried out in mesic ecosystems have found the use of mature plants as nurse plants is detrimental to the establishment of seedlings after germination (Groome 1989 and Bauer 1991 as cited in Marañón *et al.* 2004). Studies carried out by Meli and Dirzo (2012) in Los Tuxtlas, Mexico found that native sapling survival was independent of neighboring grass presence. Yet key differences must be addressed when comparing to that particular study. Precipitation at Los Tuxtlas averages 4,725 mm annually in contrast to Guánica Forest's bimodal rainy season of 860 mm of precipitation. Second their study site has no non-native grasses which and the tested subject specimens were already at the sapling stage of their development. Saplings have well developed root systems and usually can be taller than surrounding grasses avoiding any shade effect. We seek to understand the dynamics of tree establishment at its most critical life stage, that of the seedling. In this stage mortality is highest for a tree (Baudena *et al*. 2010) and can be the critical stage where non-native plants can have the greatest influence on local flora.

Yet this does not necessary apply to ecosystems with pronounced dry seasons, such as Mediterranean climates, arid ecosystems and tropical dry forests, or ecosystems with a significant ecological perturbation such as abandoned pasturelands (Holl 1999, Lugo 2004, Maza-Villalobos *et al.* 2011). In highly degraded ecosystems with a strong legacy effects in their environment the restorations of these land is an uphill battle with established thresholds (Prober *et al.* 2009, Wolfe and Van Bloem 2012). Nurse plants can ameliorate some of these abiotic stresses by creating safe sites with favorable microclimate, humidity

and/or shade for native woody species (Chinea 2002, Padilla and Pugnaire 2006, Santiago-García *et al.* 2008).

Studies carried out in the Sierra Nevada of southern Spain have shown that the use of nurse plants increases seedling survivorship in droughts and winters (Castro *et al.* 2002). The effect of different shading treatments has also been proven to ameliorate the water stress seedlings suffer during dry seasons and increases seedling survivorship (Marañón *et al.* 2004). There has been evidence of facilitation of tree seedling emergence among grasses in abandoned pasture lands in Puerto Rico (Aide *et al.* 2000) as well as in severe drought prone Mediterranean habitats (Maestre *et al.* 2003) and other arid systems (Franco and Nobel 1988). Yet not all grass species have the same root development and could have different effects in seedling germination establishment and performance. Native grasses have been observed as to have less negative impact in germination of *Agave deserti* seedlings than bare soil exposure in the Sonoran Desert (Franco and Nobel 1988).

Other studies have underscored the importance of native plants in the facilitation process of germination and establishment of native plants, acting as catalysts for further ecological succession (Cabin *et al.* 2002b, Oterga-Piek *et al.* 2011). One example comes from a study in Mona Island, west of Puerto Rico. There *Croton discolor* and *Reynosia uncinata*, both xerophytic shrubs native to the tropical dry forest of the Puerto Rican Archipelago, have been shown to act as nurse plants for the endemic cactus *Harrisia portoricensis* (Rojas-Sandoval and Meléndez-Ackerman 2012b). My results are similar to those of the previously mentioned study in that the type of shade is important. When seedlings of *H. portoricensis* were transplanted in open sites only 15% of seedling survived compared to 40% in *R. uncinata* and 30% under *C. discolor* shade. Our results show that by

the end of the experiment showed that 47% survival for seedlings transplanted under *Uniola virgata* shade 16% under Megathyrsus maximus shade, 10% *U.virgata* bare soil and 6% under *M.maximus* in bare soil. Comparisons between our open sites to those of Rojas-Sandoval and Meléndez-Ackerman (2012b) are not possible since all the seedlings under that treatment died by the second month of the experiment.

Grasses have been shown to dominate early in early successional ecological stages, paving the way for shrubs and later trees (Kennard 2002). Maestre *et al.* (2003) showed that the native grass *Stipa tenacissima* provided adequate shade for seedlings belonging to the shrub *Pistacia lentiscus*, balancing the negative effect of *S. tenacissima* plants' own water uptake in the soil. The major problem faced with using grass species as nurse plants is the interaction of root systems sharing the same soil level, creating the conditions for direct competition between the nurse plant and the target (Franco and Nobel 1988). This is not necessarily the case as the root system of *U. virgata* is deeper than that of other grasses (Thaxton and Velazquez-Rojas, *unpublished data*) and does not automatically enter into direct competition for water with woody seedlings transplanted in its edge.

Native deep rooted grasses could act as potential tools for restoration of highly degraded lands outside of the forest periphery. Once established the *Uniola virgata* clumps could act as safe sites for the germination and/or establishment of native woody species. It must also be considered the type of target plant. *Jacquinia berteroi* seedlings proved too susceptible to transplant shock and consequently their survivorship drop in the non-native sites and well as the bare soil native site which could be due to the age of the seedlings since many of them still had their cotyledons when transplanted and afterwards (Figure 6). *Coccoloba krugii* seedlings survivorship pattern was the highest mortality in bare soil sites

regardless of native or non-native status and the grass edge treatments fared better but always *U.virgata* producing the largest number of survivors (Figure 4). *Erythroxylum areolatum* seedlings were the fewest plant (N= 80) yet they had higher percentage of overall survivorship (Figure 5). This could be due to several reasons, perhaps the most important one is the fact that *E. areolatum* has a dense fibrous root system early in development, allowing it to absorb more water quickly and would have roots less exposed to damage during transplantation. Also *E. areolatum* occurs in a wide range of habitats (Monsegur-Rivera 2009) and it is deciduous (Santiago-García 2010), which could be a survival strategy to conserve water during the driest periods. In contrast to Santiago-García (2010) who mentions that during his experiment mortality was highest under nurse tree treatment, our *E. areolatum* survival was highest under nurse plant treatment. This could be attributed to the type of nurse plant used, since for that study the non-native *Leucaena leucocephala* was used, while here we used the native grass *U. virgata*. With the projected drying climatic patterns for the Caribbean (Neeling *et al.* 2006) in the future the role of nurse plants is likely to increase. Education of local communities and people in general should focus in ecosystem services provided by this forest type in issues like erosion control and aquifer recharge, or global ones like carbon sequestration (Ramjohn *et al.* 2012).

CHAPTER 4

CONCLUSIONS

Grass species have a particular distribution on the Guánica forest, associated more with the open storied scrublands where frequent disturbance regimes (*e.g.* historically hurricanes and now the addition of human induced fires) and limestone substrate limit the formation of closed canopies. In the eastern half of the forest the widest distribution belongs to the native grass *Bouteloua repens* and the highest stem density from the overall general survey was achieved by the native *Uniola virgata* grass patches. Non-native grasses are still restricted to main forest trails or roads, yet their encroachment on the forest borders is beginning to be noticed as the number surveyed *Megathyrsus maximus* patches show. Yet the most worrying aspect could be the presence of *Cenchrus ciliaris* on the roads and main trails, as well as *Heteropogon contortus*, dense mat forming species with several fire adaptations that can severely reduce native woody species by fire, inhibiting seedling establishment and intense water competition.

Grass edges had higher percentage of survivorship than bare soil spots at the end of the experiment. Yet the key difference could be in what type of grass to use as each grass species may have different root and aboveground biomass allocation strategies. These in turn affect the availability of shade and soil water, key in the establishment of native woody species.

In conclusion *Uniola virgata* should be used in restoration efforts in other tropical dry forest areas outside the forest boundaries to increase their range and that of woody species as well as lower the potential for local extinctions and better improve ecosystem services in such degraded areas. Since most of the woody flora of tropical dry forests has

evolved to invest heavily in below ground biomass they might make it more resilient to future climate change.

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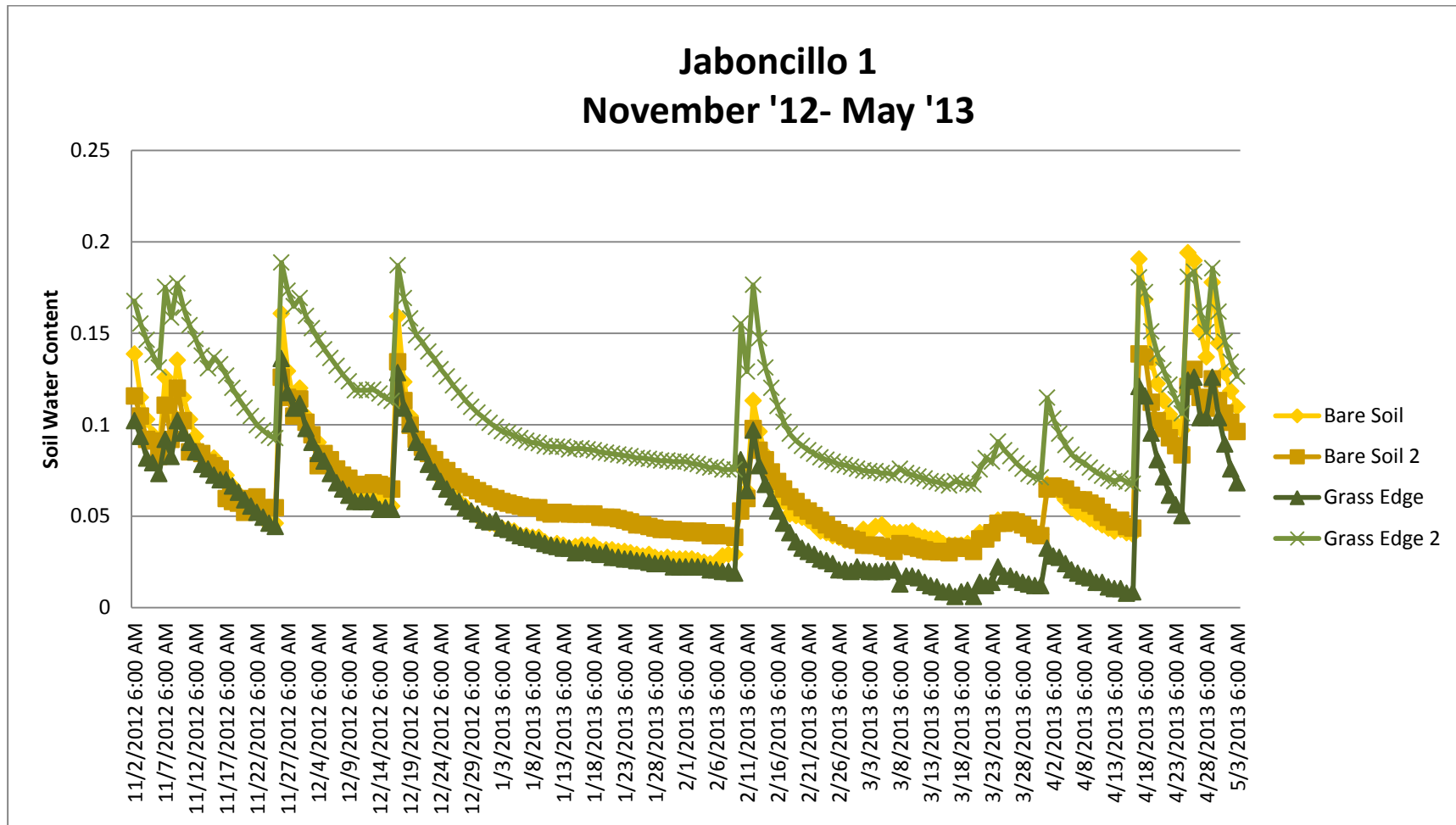
APPENDIX

Appendix 1. Table 1. Woody species found in grass patches in Guánica Forest. The presence of each species within the six grass patch types in the forest is indicated as well as total patch level frequency. Plant families identified to their lowest taxonomic identification. Present also is Frequency which is the number of patches divided by total number of patches (83 total).

Family	Sub-family	Species	Native or exotic	U.v.	M.m.	B.r.	C.c.	M.r.	B.p.	Total Frequency
Arecaceae		*Thrinax morrisii*	N	x						0.02
Anacardiaceae		*Comocladia dodonea*	N	x	x	x				0.14
Annonaceae		*Plumeria alba*	N		x	x				0.06
Asteraceae		*Wedelia calycina*	N	x						0.11
Bignoniaceae		*Tabebuia heterophylla*	N	x						0.02
Boraginaceae		*Bourreria succulenta*	N	x	x				x	0.07
Burseraceae		*Busera simaruba*	N	x	x	x		x		0.08
Capparaceae		*Cynophalla flexuosa*	N		x					0.024
Celastraceae		*Crossopetalum rhacoma*	N	x		x				0.12
		Schaefferia frutescens	N	x	x					0.036
		Elaeodendrum xylocarpum	N	x						0.012
Combretaceae		*Bucida buseras*	N		x					0.024
Erythroxlaceae		*Erythroxylum areolatum*	N	x						0.024
		Erythroxylum rotundifolia	N	x	x					0.06
Euphorbiaceae		*Croton astroites*	N		x					0.012
		Croton discolor	N	x	x	x				0.38
		Croton glabellus	N	x	x	x	x		x	0.27
		Croton spp.	N		x	x	x			0.07
Fabaceae	Caesalpinoideae	*Chamaecrista lineata*	N	x						0.012
		Haematoxylum campechianum	E		x					0.036
Fabaceae	Faboideae	*Pictetia aculeata*	N	x			x			0.06
Fabaceae	Mimosoideae	*Leucaena leucocephala*	E	x	x			x		0.07

Family	Sub-family	Species	Native or exotic	U.v.	M.m.	B.r.	C.c.	M.r.	B.p.	Total Frequency
Fabaceae	Mimosoideae	*Pithecellobium unguis-cati*	N		x					0.012
		Zapoteca portoricensis	N		x					0.012
	Unidentified	*Acacia sp.*	-		x					0.012
		Fabaceae tree	-			x				0.012
		Fabaceae unknown	N		x					0.012
Krameriaceae		*Krameria ixina*	N	x	x	x			x	0.07
Malpighiaceae		*Stigmaphyllon emarginatum*	N		x	x	x			0.13
Malvaceae		*Corchorus hirsutus*	N	x	x	x				0.3
		Malvacea #1 Donato	N		x					0.036
		Melochia tomentosa	N		x	x			x	0.06
Meliaceae		*Swietenia mahogani*	E		x					0.04
Myrtaceae		*Eugenia axillaris*	N		x					0.024
		Eugenia foetida	N	x	x					0.04
		Eugenia ligustrina	N			x				0.024
		Eugenia sp.	N	x						0.012
		Mosiera xerophytica	N	x						0.012
Nyctaginaceae		*Pisonia albida*	N	x						0.04
Polygonaceae		*Coccoloba microstachya*	N		x					0.024
		Coccoloba diversifolia	N						x	0.012
		Coccoloba krugii	N	x						0.012
		Coccoloba spp. #1	N	x						0.012
		Coccoloba sp. #2	N		x					0.012
Rhamnaceae		*Colubrina arborescens*	N	x						0.012
		Colubrina sp.	N	x						0.012
		Reynosia uncinata	N	x		x				0.024
		Reynosia uncinata o vivesiana	N					x		0.012
Rubiaceae		*Catesbaea melanocarpa*	N	x	x					0.07
		Exostema caribeaum	N	x	x	x	x			0.12

Family	Sub-family	Species	Native or exotic	U.v.	M.m.	B.r.	C.c.	M.r.	B.p.	Total Frequency
Rubiaceae		*Mitracarpus polycladus*	N	x		x				0.22
Rutaceae		*Amyris elemifera*	N		x	x				0.024
Sapindaceae		*Thouinia portoricensis*	N	x	x	x			x	0.15
Theosphrastaceae		*Jacquinia sp.*	N	x						0.012
Turneraceae		*Turnera diffusa*	N	x	x	x				0.38
Verbenaceae		*Lantana spp.*	N	x	x	x			x	0.19
		Tamonea boxiana	N	x		x				0.12
Zygophyllaceae		*Guaicum officiale*	N		x					0.024
Unknown		Unknown # 2	-		x					0.012
		Unknown # 4	-		x					0.012
		Liana #1	-		x					0.012
		Unknown liana Patch #6	-			x				0.012
		Unknown Spiny Woody	-			x				0.012
		"Malvastrum americanum"	-	x						0.036
		Unknown tree; leahery leaf	-	x						0.012
		Bo. La Luna known woody	-	x						0.012
		Unknown #1	-			x				0.012
		Unknown # 2 (II)	-	x						0.012
		Unknown 3	-	x						0.012
		Unknown #2 (III)	-	x						0.012
		Unknown #4 (II)	-	x						0.012
		Unkown from la Jungla	-	x						0.012
		Unknown seedling	-	x						0.012

Appendix 2. First Water Logger data station in Jaboncillo site, native *Uniola virgata* dominated site. X-axis indicates date of sensor reading at 6:00 AM from November 2012 until June 2013, while Y-axis indicates soil water content values.
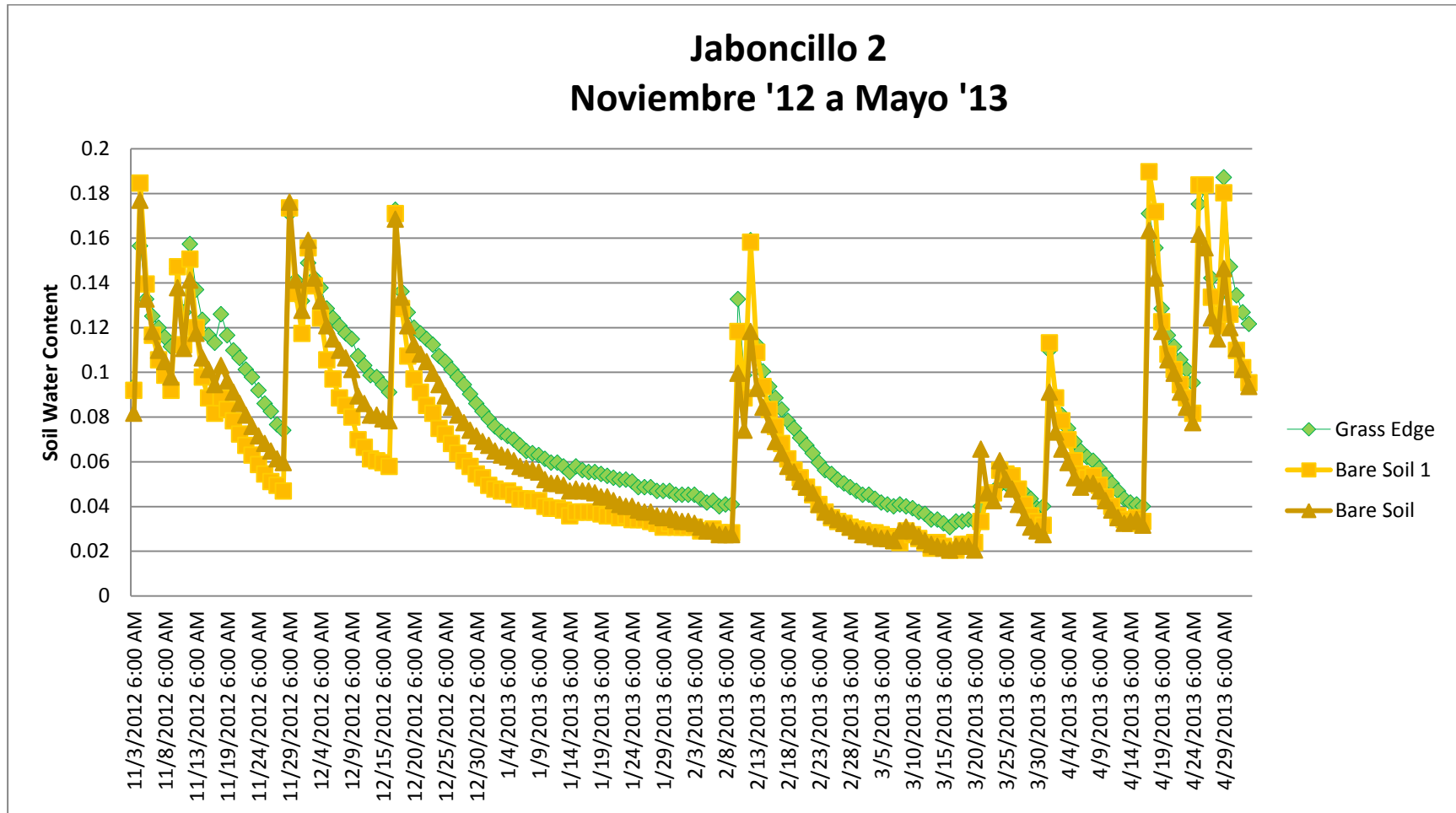
Appendix 3. Second Water Logger data station in Jaboncillo site, native *Uniola virgata* dominated site. X-axis indicates date of sensor reading at 6:00 AM from November 2012 until June 2013, while Y-axis indicates soil water content values.