NEOTROPICAL DRY FORESTS OF THE CARIBBEAN: SECONDARY FOREST DYNAMICS AND RESTORATION IN ST. CROIX, US VIRGIN ISLANDS

By

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A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

2010

To my wife, Jennifer, for supporting me in this and in all things.

ACKNOWLEDGMENTS

Thank you to my parents, William and Tricia Daley, for giving me the fundamental tools and building blocks I needed to accomplish this. Thank you to my lovely wife, Jennifer, for helping me use those tools properly while also being my best friend. I would also like to thank Ariel Lugo for challenging me to try and prove my beliefs and for providing generous institutional support to make it possible.

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LIST OF ABBREVIATIONS

ETM+	Enhanced Thematic Mapper. An 8-band multi-spectral scanning radiometer associated with Landsat 7. The primary new feature added to the ETM+ scanner is the multispectral band with a 15 m spatial resolution.
GIS	Geographic Information Systems. A computer software program that stores and processes spatial and other data.
TM	Thematic Mapper. An Earth observation sensor associated with the Landsat 4 & 5 platforms. The sensor has a total of 7 bands, 6 spectral reflectance bands with a 30 m spatial resolution and a single temperature band

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May 2010

Chair: Daniel J. Zarin
Major: Forest Resources and Conservation

Neotropical dry forests exist today mainly as secondary forests heavily influenced by exotic plants. This project analyzes land–cover change and secondary dry forest dynamics in three distinct phases (land cover change, secondary forest succession and forest rehabilitation), using St. Croix, US Virgin Islands as an example. Using Landsat satellite images and other data layers, I created classified land cover maps of St. Croix for 1992 and 2002. Forest was the dominant (56%) cover type on both dates, followed by development, grassland/pastures and water. A land cover change analysis comparing the two images revealed that 15% of the study area experienced a change either to (8%) or from (7%) forest. Grassland was the cover most likely to change and decreased from 16% to 11%, converted primarily to development. The overall result is a landscape trending toward younger forests, and increased forest fragmentation and development. In a second study, vegetation data from a chronosequence of secondary forests was analyzed for changes to forest structure, species composition and presence of exotic species. The leguminous exotic tree *Leucaena leucocephala* was by far the most frequently observed tree and dominated all stands, except those over 50 years old. Species diversity was significantly (p <0.001) higher for forests in the two oldest

age classes and there was a strong trend toward increasing canopy complexity with increased age. However, age class accounted for only a small portion of variability in species diversity, indicating other influencing factors. Slope, elevation, aspect and soil were not significant and sites with long histories of intensive agricultural land-use remained low in species diversity and dominated by exotics >50 years after abandonment. In a third experiment, a ‘gap planting’ method for establishing four rare native tree species was tested on a site experiencing arrested succession. All four species successfully established at >69% survival in 3m diameter gaps artificially created in exotic tree stands. A mulch treatment significantly (p <0.01) increased survival, but not growth. This study demonstrates on St. Croix forest is the primary land cover type and secondary forests are predominant forest type. The species composition of these forests is dynamic, but they tend to be dominated by exotic tree species and over 50 years of natural succession is insufficient time for secondary forest stands to advance beyond the earliest successional stages. These results can be applied to jump-start native forest succession and rehabilitate degraded secondary forests.

CHAPTER 1
INTRODUCTION

Secondary Dry Forests

The dry forests of the Caribbean are one of the world's biodiversity hot spots due to their species richness and their high level of endemism. Despite their high species diversity and being spread over a large part of the Earth, dry forests remain far less studied and less protected than tropical rainforests (Quesada et al., 2009). Dry forests account for approximately 42% of the world's tropical forests, but tend to occur in areas where there are high density human populations, which makes them susceptible to clearing for agriculture and human development and makes conservation more challenging (Murphy & Lugo, 1986). In their map of the global distribution of tropical dry forests, Miles et al. (2006) estimate that just over 1 million km^2 of closed canopy tropical dry forest remain. Habitat loss and invasive species remain as significant threats to biodiversity (Vitousek et al., 1997). The basic mechanisms delivering the threats are considered to be; climate change, forest fragmentation, fire, conversion to agriculture and other pressures from high human population (Miles et al., 2006). Roughly 66% of dry forests have already been converted to other uses throughout their global range (Portillo-Quintero & Sanchez-Azofeifa, 2010) and mature dry forests are predicted to effectively disappear in the next few decades (Quesada et al., 2009). Only 23,000 km^2 (4.5%) of dry forest in the Americas in protected, and much of that is considered to be secondary forest. However, Caribbean Island nations protect a higher percentage of their dry forest than do countries in Central and North America (3.9%) (Portillo-Quintero & Sanchez-Azofeifa, 2010).

Secondary forests form as a result of human activity and account for over 40% of the forests in the tropics and continue to expand in global range (Brown & Lugo, 1990). They are highly dynamic and variable in their structure and function and likely represent the forests of the future (Quesada et al., 2009). Secondary forests extend throughout the Caribbean region and are the dominant forest cover type in many of the Caribbean islands. The three main US Virgin Islands (St. Croix, St. Thomas and St. John) are approximately 60% forested with subtropical moist forest in the higher elevations and subtropical dry forest in the lowlands. The US Forest Service describes the forests as generally young and undeveloped stands that reflect historic and current land uses (Brandeis & Oswalt, 2007). St. John has the highest percentage (20%) of mature secondary forest due to the protection by National Park Service while 8% of stands in St. Thomas are mature. The younger forests have low amounts of downed woody debris, standing snags and trees of the large trunk diameters (>45 cm dbh) (Brandeis & Oswalt, 2007). St. Croix, the largest of the three US Virgin Islands and the site of this research project, has a centuries long agricultural tradition and the current landscape is a matrix of agriculture, residential and urban development. These dynamics and the relatively recent introduction of exotic agricultural weed species make the secondary forests of St. Croix an ideal laboratory for studying secondary dry forest succession.

Succession

Forest succession is defined as the directional change through time of the species composition and structure of a forest stand where other outside environmental factors remain effectively constant (Finegan, 1984). It is perhaps the most studied process in forest ecology. Primary succession refers to colonization of newly created land, such as lava flows or land exposed by receding glaciers and secondary succession occurs after a natural or human disturbance. The study of Neotropical secondary forest succession focuses on the revegetation of land after anthropogenic stand clearing disturbances, such as land cleared for agriculture and then abandoned. It is difficult to make generalizations about a protean process like succession. However, the process is generally thought of as a series of stages and the pattern of species replacement frequently moves in a somewhat predictable way from the simple to more complex and diverse (Guariguata & Ostertag, 2001). Severely disturbed forests typically go through four stages of regeneration; 1) stand initiation, 2) thinning or exclusion, 3) transition or understory regeneration, and 4) steady-state or old-growth (Kozlowski, 2002). The actual species composition of a stand may not be predictable and will remain dynamic, but the change comes from predictable, describable sources both allogenic and autogenic. Some of the most widely accepted aspects of succession are that plants compete for a finite amount of resources and that differential response among species leads to changes in stand composition. The most basic functional groups in this competition have traditionally been considered sun-loving pioneer species and shade tolerant forest trees, including forest emergents (Finegan, 1996), although more recent work has demonstrated success in classifying plants into more detailed functional groups based on growth characteristics (Chazdon et al., 2010).

Invasive Exotic Species

Exotic species are those that are introduced by humans to a new area outside of their historical native range. It would be impossible to determine the actual number, but the vast majority of species introductions result in the individual dying without reproducing and going unnoticed outside of cultivation. In more rare cases a species is able to successfully produce off-spring unassisted and becomes naturalized to a new area. In the most extreme cases the introduced species thrives, reproduces in large numbers, spreads and causes ecological damage to the new ecosystem. The damage can include reduced ecological function, altered disturbance regimes, or large-scale exclusion/replacement of native species. In cases where the new species quickly spreads its range to the detriment of native species or the whole ecosystem, the organism is considered invasive. Invasive exotic species are becoming increasingly common as humans move plants and animals, (intentionally and accidentally) around the Earth and now represent the second greatest threat to global biodiversity. Invasive plants are often characterized as aggressive, fast growing species whose establishment and spread is favored by ecologically open and disturbed sites (Barnes et al., 1998). The presence of invasive species in an area however, may reflect poor health of that environment rather than characteristics of the invading plant (Lugo, 1992). In the Neotropics, forest conversion for agriculture and subsequent abandonment creates a condition where agricultural weeds are frequently present at the start of the secondary succession.

In the US Virgin Islands the most common woody plant in regenerating pastures is locally referred to as tan-tan (*Leucaena leucocephala*). The fast-growing, nitrogen-fixing, leguminous tree is believed to have been introduced to the US Virgin Islands in the 1940s for pasture improvement. It thrives in full sun and low-nutrient soils, tolerates heavy defoliation and grazing, resprouts from stumps and roots and plants begin copiously producing long-lived seeds in as little as one year. *L. leucocephala* can grow in all altitudes and soil types on St. Croix except for beach sand. The variety of *L. leucocephala* most pervasive in the Virgin Islands is the “Hawaiian-variety” native to

Mexico described by Pound and Cairo (1983) as producing many seeds and having the ability to become an aggressive weed. Today it is the single most common plant in St. Croix and the other US Virgin Islands (Brandeis & Oswalt, 2007). Its distribution however is patchy indicating some limiting factor. The plant's intolerance to shade and initially weak seedlings (Pound and Cairo, 1983) are characteristics which do not aid in colonizing the shaded understory of a healthy forest and likely limits its spatial distribution.

Influence of Exotic Plants on Succession

A heavy influence of invasive species in an area can sometimes result in slowed or even arrested succession (Sarmiento, 1997; Chapman et al., 1999; Roth, 1999; Hau & Corlett, 2003). In these cases the plants that initially colonize the site dominate and somehow prevent forest species from establishing. There are many studies in Puerto Rico that focus on secondary forest development as a chronosequence on abandoned pastures or other agricultural sites of varying ages (Aide et al., 1995; Rivera & Aide, 1998; Aide et al., 2000; Pascarella et al., 2000; Zimmerman et al., 2000; Lomascolo & Aide, 2001; Rudel et al., 2001; Bernard, 2002; Weaver & Chinea, 2003; Lugo, 2004; Francis & Parrotta, 2006). Many of these studies concluded that introduced species can function to stabilize the local microclimate, facilitate the establishment of native forest species in their understory and eventually give way to species rich secondary forests. Though the Virgin Islands have many environmental similarities to Puerto Rico, the land-use history and conditions are unique and studies of secondary forest succession are far fewer. For example, Ray and Brown (1995a) found that 50 year old sites in St. John were dominated by *L. leucocephala* while 125 year old forest surrounded by protected park land no longer had the species as a dominant member of the forest canopy or the understory. The Nature Conservancy property in St. Croix was used for intensive agriculture for decades and was abandoned and unmanaged since 1960. A forest inventory of the 10 ha. site found that *L. leucocephala* was the most abundant canopy species accounting 39% of the stems/ha and 36% of the basal area (m^2/ha). Forty-five years after abandonment invasive species accounted for 46% of regeneration in the understory and the population of native species was comprised almost entirely of only three primary successional species (Adam & Ryan, 2003). The authors concluded that forest regeneration through succession did not seem to be occurring and that this site appeared similar in composition, structure and function to many other sites on the island and around the Caribbean.

Summary

St. Croix may be on the leading edge of a region-wide phenomenon as other islands also make the shift toward tourism and industrialized economies. This study is the analysis of the secondary forests in St. Croix and was conducted in three distinct parts. First I measured the extent of secondary forests and other land covers on an island-wide scale. Geographic Information Systems (GIS) are ideally suited to measure landcover change at this spatial scale. To show change, land cover maps were created using a combination of Landsat satellite data from 1992 (TM) and 2002 (ETM+) and other spatial data layers, and then compared. The 10 year time period is sufficient to record actual changes in land cover across the landscape (Lambin, 1999; Lambin et al., 2001) that are not simply temporary fluctuations, such as seasonal changes or changes in land-use intensity within a land cover class. I evaluated if St. Croix is gaining or losing total area for forest, grassland/agriculture and development as well as identify the spatial distribution of that change. Analysis of the switches between one land cover class to another, combined with additional ancillary data sets, helped to identify drivers and trends in the landscape.

A comparative analysis of the structure and species composition of secondary forests of varying ages evaluated the overall state of secondary forests in St. Croix. Field data was collected from a set of both random and purposefully selected sites and interviews conducted with property owners were used to confirm land-use history and actual stand age. The main objective was to quantify the rate that secondary forests increase their species diversity and canopy structure. Likewise, an increased frequency of exotic species in stands of varying ages is an indicator of a slowed rate of secondary forest recovery through succession. Stand age is unlikely the only factor determining the rate and extent of recovery of secondary forests. Additional abiotic factors were analyzed by combining spatial layers (including slope, elevation, aspect and soil) with field observations of vegetation in a GIS.

For highly impacted sites dominated by invasive species succession can become stalled or arrested and some form of intervention is required to restore secondary forests. I assessed experimental forest rehabilitation methods on such a site on St. Croix, owned and managed by The Nature Conservancy. If managed properly, these secondary forest sites have the potential to both regain their ecological function and to serve as refugia for rare or endemic species. Four species of native tree seedlings were grown from seed and planted in artificially created gaps in canopies of exotic trees. One half of the plants were randomly assigned a mulch treatment. Plant survival, plant height, canopy closure and rainfall were measured to determine the performance of each species in varying light conditions and the effect of the mulch treatment on growth and survival. The method was successful overall and could be used to jump-start succession in undeveloped secondary forests in St. Croix and other parts of the Caribbean.

CHAPTER 2
LAND COVER CHANGE ANALYSIS USING LANDSAT SATELLITE IMAGERY FOR ST. CROIX, US VIRGIN ISLANDS

Introduction

Caribbean islands offer a unique setting for studying land cover change because they have high population densities in topographically complex landscapes within fixed boundaries. In the Caribbean, where land area is limited and human population density is high, secondary forests are the most important and most rapidly expanding forest cover type (Lugo & Helmer, 2004). The rate and causes of tropical deforestation have traditionally received considerably more attention than forest cover increases and declines in the rate of forest loss (Mather & Needle, 1998), despite increases in forest area from places as diverse as Costa Rica, China, and India (Mather & Needle, 1998; Rozelle et al., 2000; Foster & Rosenzweig, 2003; FAO., 2006). In the western hemisphere forest increase results from historic economic shifts away from land intensive agriculture to manufacturing and is often accompanied by out-migration of agricultural workers from frontiers to urban centers (Rudel et al., 2005). Caribbean islands of Puerto Rico and the Dominican Republic have also experienced landscape wide reforestation in conjunction with a shift agriculture to industrialization (Rudel et al., 2001; Grau et al., 2003). The vast majority of secondary forests arising from agricultural abandonment are not planned or managed, yet occur at the landscape level.

Forest Transition Theory (FTT) describes a process where a trend of forest loss in a region slows and eventually results in a net gain in forest area (Mather, 1992). FTT assumes that land owners act in a rational way that brings the greatest financial reward (Angelsen, 2007). The single fundamental factor driving the transition is adjustments to the agriculture sector over time, but other factors can strengthen or weaken the process

(Mather & Needle, 1998). This usually means a decrease in the agricultural sector results in abandoned farmland becoming forested and is also frequently associated with an outmigration of agricultural workers from rural areas to urban areas. St. Croix has transitioned from an almost completely forested landscape, to almost completely deforested during the height of sugar cane production, to modern times where these data indicate there is a steady-state of over 50% forested landscape.

Forest Transition Theory relies largely on macro-economic factors to explain how large scale changes in forest cover can occur at the landscape level. Specifically, how industrialization and population migration can lead to large scale increases in forest cover as a result of abandonment of agriculture (Mather & Needle, 1998). Rudel (2005) and others have thoughtfully applied the Forest Transition Theory to several regions of the world to reveal consistent patterns in several countries and distinct trends that are unique to the east and west hemisphere.

Changes in St. Croix's forest cover have not been studied until relatively recently and there are few quantified details available on forest cover change over time in the Virgin Islands. The island's economy was once agricultural, focused primarily on growing sugar cane, cotton and tobacco (Weaver, 2006), and today in more industrialized. Neighboring Puerto Rico is 40 times greater in land area than St Croix (only 215 km^2) but has similar climate, land-use history, forest types and is the site of extensive forest cover research studies. Forest cover in Puerto Rico increased from 8% to 50% over 50 years that coincided with industrialization of the economy and landscape level abandonment of agricultural sites (Grau et al., 2003; Helmer, 2004; Marin-Spiotta et al., 2007).

Many Caribbean islands in the Lesser Antilles chain are similar in size to St. Croix and the Virgin Islands and share similar colonial histories, economics, land-use patterns and forest types. Unfortunately there has been little to no land cover mapping in most of these islands. Results from an experimental method of mapping land cover and forest structure using Landsat ETM+ and course-resolution lidar are now available for the U.S and British Virgin Island (Kenneway et al., 2008). Also, preliminary estimate of land cover change have been conducted for some of the Windward Lesser Antilles (St. Kitts, Nevis, St. Eustatius, Grenada and Barbados) indicating the same trend of increasing forest cover as land under cultivation has declined and development and construction increased in the lowlands (Helmer et al., 2008).

I examined landcover change in St. Croix to address three objectives (1) To create accurate classified images of St. Croix for two dates (1992 and 2002) using a combination of remotely sensed and ground-truthed data. These snapshots describe land cover on the island at two specific points in time and are the starting point for change detection. (2) To quantify and describe the changes that occur during the 10 year time period, using Forest Transition theory to put those observations into context (Mather & Needle, 1998; Rudel et al., 2005). Ten years is considered an appropriate time period for understanding the processes that lead to forest loss and degradation (Lambin, 1999). (3) To identify the drivers effecting this change. Determining which land covers interact will identify which human land uses lead to the changes observed in the landscape. I hypothesis that land cover change increases as proximity to roads increases. When roads provide accessibility to a previously isolated area, anthropogenic disturbance and land cover increases in Amazonian frontier (Laurence et al., 2002; Asner et al., 2005) and tropical mountain landscapes (Southworth & Tucker, 2001). However, St Croix and other Caribbean islands have high population densities within a finite space and inelastic borders.

Methods

Study Area

The island of St. Croix (17°47' N 64°45' W) is among the Leeward Caribbean Islands, is the largest of the three main US Virgin Islands and is the easternmost possession of the United States. St. Croix is 10 km from north to south and 35 km from east to west, encompassing roughly 215 km^2. The terrain in the north has rugged hills and steep slopes while the south is characterized by rolling lowlands and the coast is fringed with coral reefs. Virgin Islands soils are generally molisols derived from volcanic and marine parent material. One of the most common soil types is locally referred to as 'caliche', which is white in color, has slow drainage and a pH. >8.0. Soil in the north tends to be shallower and eroded while deeper soil and the most productive agricultural land are concentrated in the central valley and the south (Davis, 2000).

Trade winds blow from the east all year and are most prominent in the winter months. The warm Caribbean Sea stabilizes air temperatures so that diurnal temperature changes approximate annual fluctuations. There is a pronounced east-west rainfall gradient similar to many of the less mountainous islands of the Lesser Antilles, where the east end receives less than 75 cm annually and the west end over 150 cm. Rainfall tends to be distributed irregularly throughout the year and between years. The variable rainy season is from September to December but rainfall can be concentrated during tropical storms and hurricanes. Prolonged periods of drought occur in most years, typically from March to July.

The majority of the island is considered to be of the subtropical dry forest ecological life zone while the hilly, northwest portion of the island is subtropical moist forest (Ewel & Whitmore, 1973). The first European to arrive in St Croix was Christopher Columbus in 1493, who described a completely forested island landscape with a small population of Carib Indians. There were sporadic small scale agriculture and timber extraction under French and other European rule for the next 250 years. Real change began in 1733 under Danish rule when the island was divided into a grid system, and cleared for agriculture; sugar cane became the primary crop. By the end of the 1700s St. Croix's remaining forests were in more isolated hilly areas and wood was being imported to fire mills that processed cane and made rum.

Image Processing

To detect changes in St. Croix's landcover over a 10 year period, classified landcover maps were created using two satellite images; August, 1992 Landsat TM and January 12, 2002 Landsat ETM+ image. The classifications for each date were conducted separately. Precipitation differences between the two dates were addressed by considering rainfall data at three months and three weeks before each image date and determining the potential effect this could have on classifying vegetation types (Jensen, 2005). The 10 year time period was selected to minimize detection of short-term changes such seasonal fluctuations in forest or agricultural fields being freshly cleared or temporarily left to fallow and to capture meaningful change such as forest clearing and secondary forest regeneration. All image processing was conducted using Erdas Imagine software (ERDAS, 2003). Both images were separately georectified to 1:48,000 scale USGS topographic maps using a polynomial model with 150 point pairs resulting in a root mean squared error (RMS) of 0.7 pixels (<23 m) for each. This level of error is acceptable for detecting changes (Wang et al., 2004), especially in a semi-arid environment (Townshend et al., 1992). Careful visual inspection of the overlaid images confirmed there was minimal misregistration. Appropriate atmospheric corrections were made (Song et al., 2001) including those for atmospheric variation, solar angle (Jensen, 2005) and radiometric calibration using dark object subtraction (Chavez, 1996). Using the layer stack function, I added seven additional spectral and spatial layers. NDVI (Normalized Difference Vegetation Index) is derived in Landsat from bands 1 and 2 (visible red and near infrared) and is used to measure plant health or detect differences in vegetation types. The final spectral layers were the three principle components layers resulting from a texture analysis of the Landsat image for both dates. The three non-spectral layers elevation, slope (United States Geological Survey, 2007) and a soils layer (Natural Resources Conservation Service, 2000) were also added so the classification was not based solely on reflectance values, thus improving class seperability. Pixels in cloud cover were treated as having no data and any pixels with no data were not used in the change analysis. Clouds account for 6% of the 1992 image and 8% of the 2002 (and are noted in the classified images for each date) and account for a combined loss of 12% of the total study area in the two date change images.

Image Classification and Ground-truthed Point Data.

A ground-truthed data set were created in 2004 and used to train the classification model and to assess accuracy of the resulting images. A total of 246 points were randomly distributed across St. Croix, uploaded into GPS units, and training sample data were collected at each point. Land use and land cover characteristics were collected at each point and additional vegetation characteristics were collected for the forested sites (Lu et al. 2004) such as canopy structure and species composition. All of the points were later assigned to one of four land cover classes; forest, grass, developed and water. Other minor cover types are included in these general headings and a complete description is in Table 2-1. The 246 points were overlaid on the stacked images and data extracted from pixels contacting the points in all layers. Data from one half of the points were used to create a unique signatures for the class and the other half used in accuracy assessment (Jensen, 1996). All pixels in the images were compared to the signatures and assigned to a class using Erdas Imagine's supervised classification technique. The same 246 points were overlaid on a 1992 black and white digital orthophotograph to classify the 1992 Landsat image because field verification for that date was impossible. Basic aerial photo interpretation techniques were used to assign the points to a single cover class. The same signature creation technique and classification process was used for both dates.

Accuracy of the classified images was assessed by overlaying the other half of the field verified points on the classified images for each date and tallying the correct and incorrect classifications. Results are expressed in a confusion matrix that includes an overall accuracy, producer error (errors of inclusion) user error (error of exclusion) and for each class on each date, as well as an overall kappa coefficient that measures accuracy relative to random chance (Foody, 2002). There is no universally accepted measure for assessing classification accuracy that is appropriate for all situations, but calculating multiple accuracy terms, as done here, is preferable.

These land cover classification results were further verified by comparing them with three other independent estimates of forest cover on St. Croix. One is a land cover classification mapping project (University of the Virgin Islands, 2002) completed through traditional photo-interpreting techniques of a 1999 aerial photograph. Secondly, the US Forest Service first Forest Inventory Analysis (FIA) was conducted in 2004 (Brandeis & Oswalt, 2007) via intensive field data sampling and resulted in a ground-truthed map of forest cover types. Finally, results from multiple years of the US Department of Agriculture's Census of Agriculture were used for comparison of changes in area to the agricultural sector (National Agricultural Statistics Service, 2005; National Agricultural Statistics Service, 2009). These data are interesting and uniquely independent because they are derived through interviews and surveys with farmers and are not spatially explicit.

Land Cover Change Analysis

Change detection was conducted to determine the nature, spatial extent and pattern of land cover change (MacLeod and Congalton, 1998). I show the results in a cross-tabulation change matrix to effectively quantify persistence, change and the type of change observed (Pontius et al., 2004). The matrix describes (1) net change in each category, (2) gain, loss and swap by class, and (3) stability or persistence in each class. Water was retained as a separate class although there is very little fresh water on St. Croix. Pixels changing to or from water were few and represent either tidal change or ephemeral water fluctuation and not anthropogenic cover change. The results of the changes in forest and grass area are described within the context of the Forest Transition Theory (FTT), the change from forest loss to forest expansion for a given geographic area that occurs as a consequence of broader demographic, economic, and/or political changes (Mather, 1992).

Fragmentation

Landscape metrics were calculated with the software Fragstats 2.0 for the classified images of the two dates. Fragstats provides a suite of spatial statistics and descriptive metrics at the patch, class and landscape level. I used several measures of area, edge and shape determine the fragmentation of each class. The variables Area, Largest Patch Index (LPI), and Average Patch Size (APS) measure the entire area occupied by a class, the area of the largest patch within a class, and the average area of the patches within a single class. Number of Patches (NP) is a simple count and a direct measure of fragmentation where more patches within a fixed area means increased fragmentation. Landscape Shape Index (LSI) is a unitless measure of the overall complexity of the class shape. Clumpiness and Interspersion-Juxtaposition Index (IJI) are measures of whether patches from a single class are clustered together or intermixed with other class types. Taken together these measures give a detailed picture of the spatial characteristics of land cover types in a landscape and are an effective measure of fragmentation (Nagendra et al., 2003; Southworth et al., 2004). The landscape size is equal for the two dates, so comparisons are simple to interpret. Fragstats was also used to calculate these same metrics for the change image that compares the differences between the two dates. In this way the spatial characteristics of stable patches can be compared with patches that experienced change.

Forest Cover Change and Roads

The amount of forest cover change in an area is frequently associated with roads. Because roads provide increased human access, the change is presumed to be anthropogenic. I tested this relationship in St. Croix by overlaying a layer of primary roads on 1992-2002 forest cover change layer. The roads were buffered in a GIS to create eight distance classes (0-100, 100-200, 200-300, 300-400, 400-500, 500-700, 700-1000, and 1000+ m). These distances were chosen so that each contained at least 1,000 terrestrial ha^2. Water was excluded from the analysis because it is not associated with anthropogenic change in St. Croix. The percentage of stable land cover and forest change were analyzed to determine if change area decreased with increased distance from roads.

Results and Discussion

Classified Images

The four-class images for 1992 and 2002 (Figure 2-1) show that forest is the dominant cover type and that land cover class distribution patterns are relatively stable between dates. Forest covers the rugged slopes of the northwest and higher elevations along the north coast and eastern hills. Large grassy pastures are concentrated along the south eastern coast with smaller pastures occurring in a mixed matrix throughout the lowlands. The south central coast is a designated industrial zone where the airport, an oil refinery and other commercial enterprises are located. Other development is concentrated in patches throughout the central valley. Water encircles the coast and the only inland bodies of water are the ephemeral salt ponds in the east and west ends of the south shore.

Producer and user accuracy for each class, overall accuracy and kappa statistics are given in Table 2-2. There were two main sources of classification error. Some pastures on forest edges or within mature patches of woody regrowth were misclassified as forest, while patchy coastal scrub forest in the dry east end was occasionally misclassified as either pasture or even developed (bare ground). The second type of error was between low density residential and forest. Accuracies for

1992 and 2002 of 72% and 75% were achieved, with kappa statistics of 61% and 66%. These levels may be acceptable for individual image dates, but are lower than the preferred 85% accuracy for images in a change analysis (Thomlinson et al., 1999). However, calculating user and producer accuracy levels and kappa statistics allows us to use these data with knowledge of their strengths and weaknesses and is the current best method for measuring accuracy of classified images (Foody, 2002).

Because forest cover change is the focus of this study, the images were further simplified to focus on forest change and to improve accuracy. A raster recode process combined the developed class with grass cover. The new Forest/Water/Other image was assessed for accuracy, which improved to 83% and 91% for 1992 and 2002, respectively. These data are used in forest cover change analysis throughout this study (Table 2-3). Water is retained as a separate class because it is easily distinguished from other cover types.

These classified images describe St. Croix as being 56% forested in both 1992 and 2002. The forest cover estimate by the Rapid Ecological Assessment (University of the Virgin Islands, 2000) used different methods the calculations, but concluded that St. Croix had 53% forest cover in 1999 and a similar distribution of cover types, with the majority of forests concentrated in the hilly northwest portion of the island. The results of the FIA conducted in 2004 found St. Croix to be 53% forested, though the definition of forest was more liberal to include areas of potential forest (Brandeis & Oswalt, 2007). The authors characterized the forests as largely secondary stands in early successional stages and often dominated by a single exotic plant species, *Leucaena leucocephala*. The most mature secondary stands were found to be concentrated in the hills of the northwest part of the island. These comparisons corroborate the finding in this study that St. Croix is slightly more than 1/2 forested and there was little net change in forest area between 1992 and 2002

Land Cover Change

Class by class comparison was conducted here using a cross tabulation matrix (Table 2-4). Results quantify two types of landscape change between categories; gross change for each class and net change and swap (Pontius et al., 2004). The net change among classes between 1992 and 2002 reveals a largely steady-state forested landscape with a distinct trend of increasing human development and a proportional decrease in cultivated grassland for pasture (Figure 2-2). Forest cover remained stable at 56%, (10,540 in 1992 to 10,590 ha in 2002) as did water (1,290 ha and 1,250). Grass cover, however declined substantially (over 1,000 ha or 34%) and there was a simultaneous increase in developed area by the same amount. There are no naturally occurring grasslands in St. Croix and the vast majority of grass cover is pasture for grazing cattle sheep and goats.

An independent, non spatial data set was used to corroborate this finding of rapid change in grass cover during the 10 year study period. The Virgin Island Department of Agriculture conducts an Agricultural Census every five years in conjunction with the US Department of Agriculture. These data are collected through surveys and interviews with farmers and the dates closely approximate the time period covered in this study. USDA data shows that between 1998 and 2002 (National Agricultural Statistics Service, 2005) the area in pasture in St. Croix decreased from 4,050 to 2,880, a 29% decrease in pasture area. Although not confirmed through site visits nor assessed for accuracy, this independent data demonstrates the same trend in pasture loss gives additional confidence to these findings. It is interesting to note that St. Croix’s largest dairy farm has declared bankruptcy and closed since the time this data was collected likely perpetuating the trend of pasture land coming out of production and converting to either secondary forest or being developed.

A more detailed look at land cover change is achieved analyzing gross change within categories and swap (Figure 2-3). Water, for example, remained stable at 7% for both dates, but spatial change within the class is visible, primarily with the two ephemeral salts ponds on the south coast of the island (Figure 2-1). These sites are a combination of salt flats, sand, water and mangrove forest, and the water level varies with tides and rainfall. The salt pond in the south west corner of the island changed from developed to water while the brackish Great Salt Pond in the south east drained, exposing mangroves and sand. The developed class also includes bare soil and sand because they have similar spectral signatures (Table 2-1). These changes in forest, developed and grass are either to or from water and are considered natural annual fluctuations of the coastal environment, therefore, they are not included in the analysis of anthropogenic change.

Forest cover experienced no substantial net change, but there was approximately 1,500 ha gain and loss of forest area. Forest gain primarily came at the expense of grass cover, as 1,040 ha of grassland reverted to secondary forest during the 10 year study period. The other 500 ha came from the developed class and careful visual inspection confirmed this findings. The spatial distribution of all the stable classes and all types of change is depicted in Figure 2-4. A percentage of this change can be attributed to error as development is generally considered a permanent cover type. However, the majority of changes from developed to forest occurred in the mixed coastal scrub forest of the dry east end. The steep slopes have patches of bare rock and were classified as developed in the 1992 image. The change likely represents real forest development. However, a possible contributing error factor is that 40% more rain fell in the three months prior to the 2002 image than the 1992 image. Such a rainfall increase can cause denser, fuller tree canopies and result in pixels that are a mixture of grass and scrub being classed as grass during drought and as forest during high rain. The other noteworthy location is the highly patchy cluster of small patches around a large residential neighborhood. These patches are lots cleared to bare ground for development and allowed to regenerate into a low patch of woody cover during an extended building process.

Forest Change

A primary objective of this study was to determine the extent and distribution of forest cover change. To focus on forest change only, the classified image was recoded to a Forest/Non-forest classification by combining the pasture and development classes into a single group. Water was detected highly accurately and changes within the water class represent natural changes, such as tidal fluctuation and variation in ephemeral water bodies. Mangrove forests, for example, frequently appear to fluctuate between water and forest cover during change detection. The 1992 and 2002 images were recoded into three classes (forest, water, other) and assessed for accuracy resulting 82.88% and 91.43% respectively and no single class less than 70% for users or producers error (Table 2-3). Comparing the two images resulted in a change matrix with nine possible categories.

Over the 10 year period gross forest area remained stable, at 56% of the study area. Of the 19,000 ha in the study area, 9,200 ha (48%) were stable forest and 5,500 ha (29%) were stable non-forest areas. Non-forest areas include both developed and grass. Stable water and pixels swapping to or from water are combined into a single category because they account for a relatively small total area (7%) and represent natural change rather than anthropogenic change. The spatial distribution of forest gain and forest loss is shown in relation to stable land covers in Figure 2-4.

Changes in population, worker wages and government programs can have profound effects on the agricultural sector that drives Forest Transition. A generalized graph of the historical changes in forest cover on St Croix appears in Figure 2-5 and is similar to that described for many other countries in the western hemisphere. In St. Croix, land prices and workers' wages have increased sharply in recent decades, making agriculture a much less attractive option for land owners. St. Croix is small enough that when workers discontinue farming on their family land and take wage-paying jobs, it does not result in the out-migration frequently discusses in FTT because workers can simply commute by car. However, Virgin Islands Department of Agriculture programs give 95% property tax exemptions for properties registered in agricultural production. The least labor intensive type of agriculture is pasture/livestock. The result is St. Croix's agricultural sector is comprised mainly of infrequently maintained pastures where property tax exemption is more important than earnings from actual livestock production. Larger commercial farms close due to changing economic realities, while the smaller land holders maintain their agriculture exemptions in order to avoid property taxes. Evidence of this is found in the USDA Census of Agriculture which finds the average pasture farm in St. Croix decreased in size from 54 ha in 1992 to 33 ha in 2002. Many of the smallest pastures are infrequently maintained and fluctuate between grassy pasture and advanced woody regrowth. Data from this study captures this phenomenon, finding that during the 10 year time frame, almost 15% of the island was converted either from forest to pasture or from pasture to forest. This indicates that total forest area in St. Croix may have achieved a post-FT steady state, but that the spatial distribution of forest remains a dynamic, shifting mosaic. The current reality is strongly influenced by the territorial government's tax incentive and forest area would almost certainly experience a sharp increase if this incentive were to discontinue.

Fragmentation

Fragstats metrics for the three terrestrial classes in 1992 and 2002 are given in Table 2-5, as well as data for forest gain and forest loss. Grass cover experienced a large decrease in area, Number of Patches (NP), and a 13% reduction in the Average Patch Size (APS) as well as a decrease in average complexity of the shape of the class (LSI). While forest area remains stable between the two dates, the NP increased by 156, a strong indication of forest fragmentation. Forest LPI decreased slightly and the APS decreased by 29%. These numbers describe a stable net area of forest becoming divided into a greater number of smaller patches. Interestingly, as forest becomes fragmented, developed areas are growing and merging together. The total area and average patch size of the developed class increased substantially while the NP decreased by over 100. The spatial distribution of all types of forest change is shown in Figure 2-7 with colors distinguishing between the cover type the area changed from/to. Both reforestation and deforestation are concentrated in the lower elevations, away from slopes and patches of both types of change are frequently found in association with each other. Visual inspection at finer spatial resolution reveals that deforestation is usually the result of specific human activities such as construction or clearing fallow fields and reforestation results from cessation of human activity (the maintenance of pastures) and fields reverting to fallow. Although one can differentiate between reforested and deforested areas during this time period, it is more meaningful to consider both types of change as parts of a single dynamic fluctuation process. This change is brought about by human activity and pasture management and residential development are the core drivers.

Spatial analysis using Fragstats indicates that reforestation and deforestation patches are highly similar in terms of average patch size, largest patch and edge density. Change patches have a smaller maximum size and average size than stable patches as well as a higher edge density than other patch types. An Interspersion and Juxtaposition Index (IJI) was calculated for each of the 6 classes. The index provides a measure (0 – 100) of intermixing of patch types by looking at each patch and what patch type is adjacent to it. A score of 1 indicates a class is adjacent to pixels of a single cover type and a 100 score means a class is equally adjacent to all other types. Reforestation and Deforestation both had IJI=37 while stable forest (45.6), stable water (53.5) and stable development (63.1) all scored higher.

Forest Cover Change and Roads

Roads frequently serve as a proxy for the presence of human activity in land cover change studies and land at greater distances from roads is considered less accessible. I hypothesized that a small island like St. Croix with a high population density would not show the traditional pattern of increasing cover change with decreasing distance to roads because the entire island can be considered part of the urban/wildland interface. In other words, humans have access the whole island, so forest cover change will not vary with road distance. I tested this by using eight road buffer classes to determine if any observed changes occur gradually.

The results indicate that forest gain and forest loss occurred in conjunction with each other spatially and that gain and loss occurred in equal proportions within each distance category. Contrary to predictions, the proportion of the land experiencing forest change decrease as distance to roads increased (Figure 2-7). However, the trend only becomes observable at the 500-700 m distance class and over 73% of the island falls within 500 m of a primary road and 94% is within 1,000 m. The variation on St. Croix occurs suddenly over a relatively short distance as previous studies have reported the findings over distances of >130 km (Laurence et al., 2002; Southworth et al., 2004). At a similar spatial scale, Helmer (2004) found that newly developed areas in Puerto Rico occur closer to roads although even Puerto Rico is over 40 times greater in area than St. Croix. I interpret this to mean that only a very small percentage of St. Croix is inaccessible enough to humans that land cover change patterns differ.

Together these data describe a shifting mosaic of land covers undergoing change in a post-agricultural context. St. Croix's landscape is roughly 50% forested, consisting of primarily young, secondary forest stands (Brandeis et al., 2009) by forest cover and livestock production in pastures is the most dominant agricultural practice. The Department of Agriculture Census data shows a sharp decline in revenues and land area for almost all types of agriculture, especially livestock and pastures. Grass cover area also declined sharply between the 1992 and 2002 images and there was a corresponding increase in development. However, there was no net increase in forest area indicating St. Croix may have achieved the new steady state in forest area predicted by FT theory (Mather & Needle, 1998). There may be some unique characteristics due to the size of the island. With only 215 km^2, there are few inaccessible areas and migration to urban areas does not occur due to declines in agriculture. Spatial analysis of the forest change areas indicates that patches of forest gain and forest loss have similar sized patches and both occur in lowland areas and in transition zones where all three terrestrial cover types tend to be mixed (as indicated by low measures for Clumpiness and IJI in Table 2-5). The net effect is increased fragmentation of forest cover, trending away from large patches of stable forest and toward smaller patches of young secondary forest.

If the trends identified in this study continue, St. Croix will see the continued spread of development on prime agricultural lands and forest land becoming increasingly young, fragmented and relegated to hillsides. This is surely a daunting prospect for an island that already imports the overwhelming majority of its food and is currently advertising itself in the tourism industry as “The Nature Island”. If St. Croix is to maintain a percentage of green space or forested areas around residential developments, efforts must be made to protect land as it comes out of agricultural production and before it becomes developed. St. Croix does not yet have effective zoning and development regulations and the territorial government is ineffective in maintaining protected areas or creating new ones. A recent example is the territorial senate acting to lease protected coastal land to a casino developer, despite passage of a voter referendum to block the move. The federally funded Forest Legacy Program and Forest Stewardship Program offer realistic ways for land-owners to take their properties out of agricultural production while maintaining both their tax exempt status and forest cover. It is still uncertain if these programs will be effective in the Virgin Islands.

Conclusion

These classified images provide accurate, spatially explicit descriptions of land cover on St. Croix on two dates. The change analysis describes a forest dominated landscape (56%) experiencing a high degree of change. Total forest area remained stable, but there was substantial change within the class and a strong trend toward younger secondary forest and increased forest fragmentation. Approximately 1,500 ha of forest were lost, with the majority converted to development and 1,500 ha of forest were gained, the majority coming from regenerating grassland.

Over 5% of the island changed from grassland to developed during the 10 year time span. The loss of grassland was corroborated by independent non-spatial data collected by the Virgin Islands Department of Agriculture. These findings indicate St. Croix is still experiencing Forest Transition and economic realities favor increased urbanization at the expense of grassland while net area of forest remained stable.

I tested the hypothesis that changes in forest cover decrease with increased distance to roads and conclude that forest change area only varies at the greatest distance values. The pattern is not as pronounced as in other studies and occurs over a smaller spatial scale. Also, patches of both forest gain and forest loss are spatially (patch size, location and distribution) similar and are two parts of the same process where small patches of land are irregularly cleared and then left fallow. The process is driven by macroeconomic changes (increasing worker wages, population density and real estate prices) and re-enforced by local policies offering property tax exemption to land that is registered as agriculturally productive in name only.

Table 2-1 Names and descriptions of the four land cover classes used in the land cover classification of 1992 and 2002 Landsat images of St. Croix, U.S. Virgin Islands

Cover Class	Description
Forest	All forest types with >25% canopy coverage including coastal scrub, early successional stands, secondary dry forests and mature multi-layered moist forest.
Grass	Pastures, regenerating pastures with patches of woody regrowth covering <25% woody regrowth, recreational fields, golf courses and large lawns.
Developed	Urban, mixed residential, paved roads, parking lots, bare ground, beach sand and mud flats.
Water	Coastal sea water, salt ponds and estuaries.

Table 2-2. Overall accuracy assessment of the four-class images for 1992 and 2002. These images are the base layers utilized in fragmentation analysis.

Class name	Reference total	Classified total	Number correct	Producer accuracy	User accuracy
1992					
Forest	52	45	29	55.77%	64.44%
Grass/pasture	14	20	11	78.57%	55.00%
Developed	24	26	20	83.33%	76.92%
Water	21	20	20	95.24%	100.00%
TOTAL	111	111	80		
Overall Accuracy	72.07%				
Overall Kappa	61.35%				
2002					
Class name	Reference total	Classified total	Number correct	Producer accuracy	User accuracy
Forest	52	53	36	69.23%	75.00%
Grass/pasture	14	16	10	71.43%	62.50%
Developed	20	18	15	75.00%	83.33%
Water	19	18	18	94.74%	100.00%
TOTAL	105	105	79		
Overall Accuracy	75.24%				
Overall Kappa	66.41%				

[Producer accuracy (# correct/reference total) measures errors of exclusion and User accuracy (# correct/classified total) measures errors of inclusion.]

Table 2-3. Accuracy assessment for the three cover classification used to detect forest cover change. These images serve as the base layers for land cover change analysis.

Class name	Reference total	Classified total	Number correct	Producer accuracy	User accuracy
1992					
Forest	52	45	39	75.00%	88.64%
Non-forest	38	47	33	86.84%	70.21%
Water	21	20	20	95.24%	100.00%
TOTAL	111	111	92		
Overall Accuracy	82.88%				
2002					
Class name	Reference total	Classified total	Number correct	Producer accuracy	User accuracy
Forest	52	52	48	92.31%	92.31%
Non-forest	34	35	30	88.24%	85.71%
Water	19	18	18	94.74%	100.00%
TOTAL	105	105	96		
Overall Accuracy	91.43%				

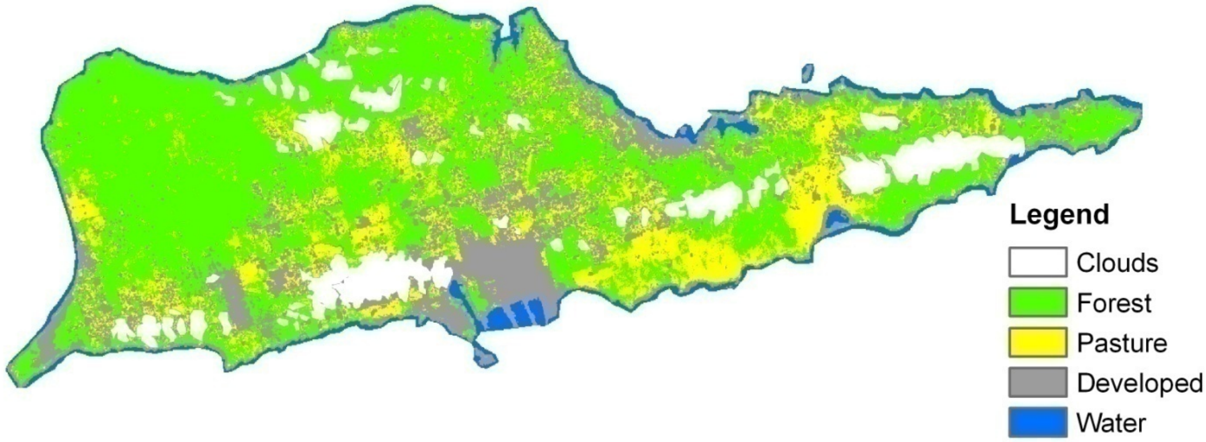
[Producer accuracy (# correct/reference total) measures errors of exclusion and User accuracy (# correct/classified total) measures errors of inclusion.]

Table 2-4. Cross-tabulation matrix comparing classified images for 1992 and 2002 expressed as a percentage of the total study area.

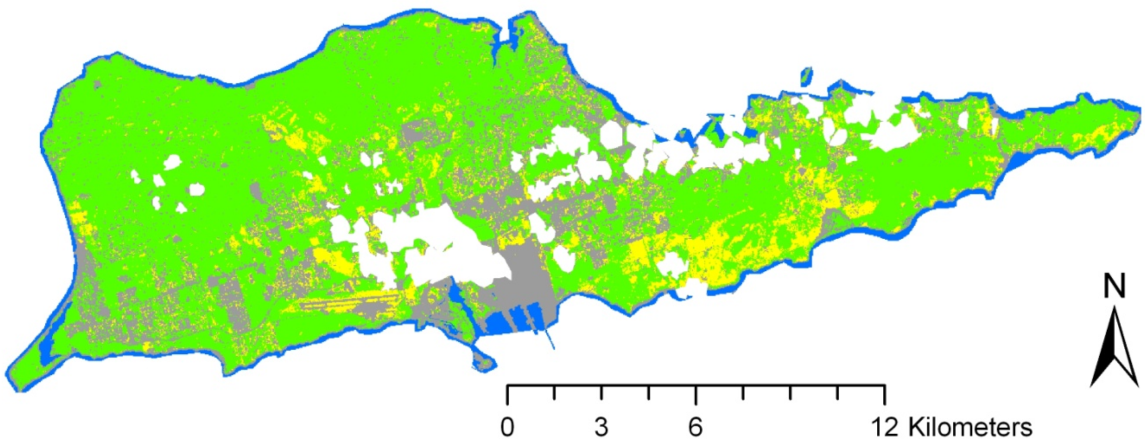
		2002				**Total 1992**	**Loss**
		Forest	Grass	Developed	Water		
1992	Forest	47.78%	3.17%	4.86%	0.00%	55.80%	8.03%
	Grass	5.49%	6.36%	4.12%	0.00%	15.97%	9.61%
	Developed	2.75%	0.95%	17.07%	0.62%	21.40%	4.33%
	Water	0.03%	0.00%	0.79%	6.01%	6.83%	0.82%
Total 2002		56.05%	10.48%	26.83%	6.63%		
Gain		8.28%	4.12%	9.77%	0.62%		

Table 2-5. Seven landscape metrics [Area (% of total area), LPI (Largest Patch Index), NP (Number of Patches), APS (Average Patch Size), LSI (Landscape Shape Index), Clumpiness and IJI (Interspersion and Juxtaposition Index)] that describe fragmentation for the three terrestrial land cover classes on both image dates.

DATE	CLASS	AREA %	LPI (%)	NP (#)	APS (ha)	LSI	CLUMPINESS	IJI
1992	DEVELOPED	21.29	4.39	1063	4.16	39.99	0.89	77.09
	GRASS	16.07	2.91	1376	2.41	39.42	0.88	60.50
	FOREST	56.00	38.27	783	5.84	28.03	0.91	70.71
2002	DEVELOPED	26.83	4.34	946	5.60	39.56	0.88	85.20
	GRASS	10.52	2.45	1010	2.09	31.53	0.87	60.72
	FOREST	56.19	37.55	939	4.16	28.87	0.91	75.22
1992-2002	FOREST TO NON-FOREST	8.18	<0.1	2183	0.71	NA	0.78	37.47
	NON-FOREST TO FOREST	7.32	<0.1	2080	0.67	NA	0.77	37.51



A 1992



B 2002

Figure 2-1. Classified land cover maps for St. Croix, A) 1992 and B) 2002. Green=forest, yellow=grassland/pasture, grey=development, blue=water and white= no data (normally as a result of clouds).

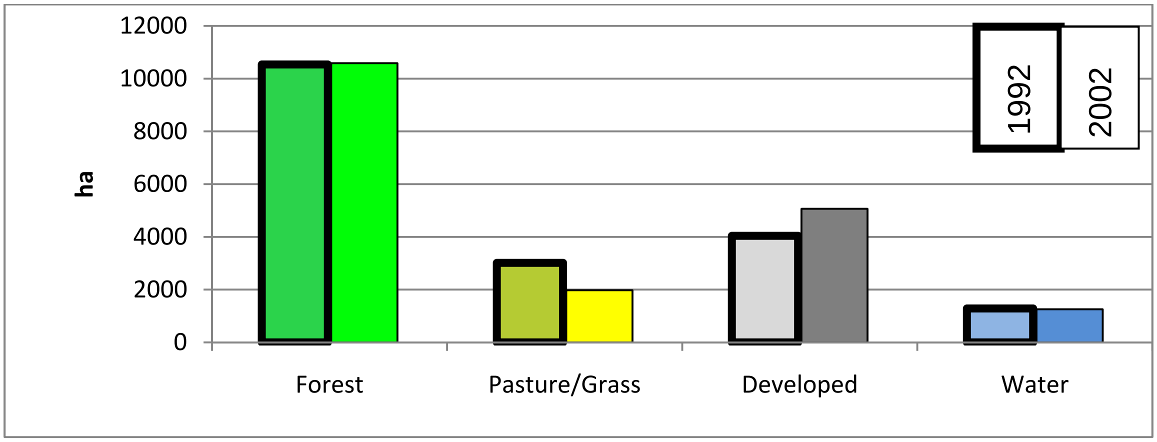
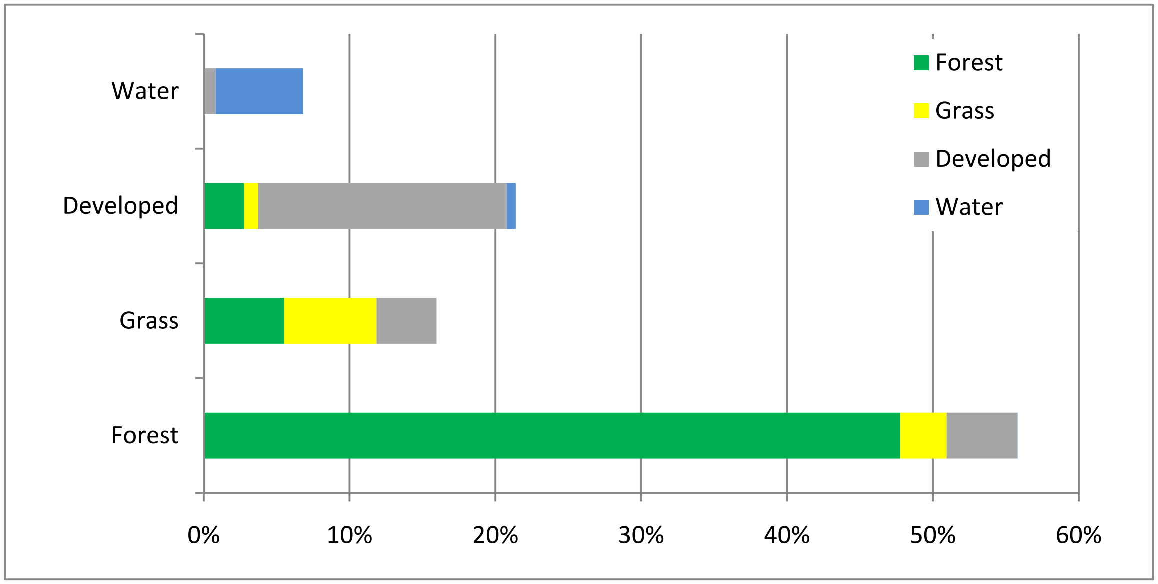
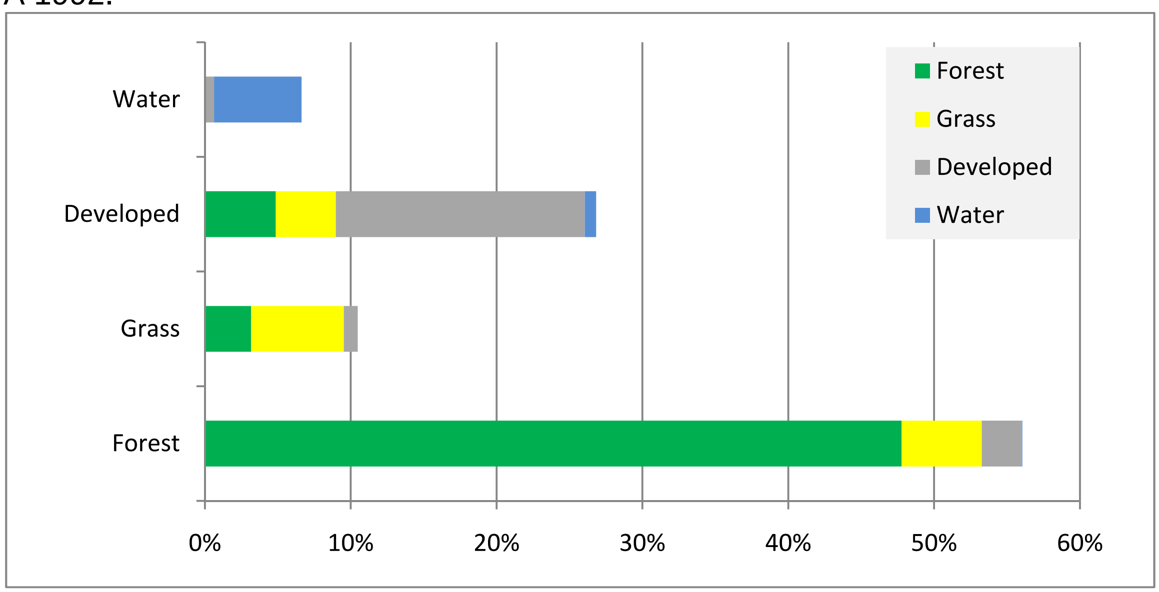


Figure 2-2. Total area of four land cover classes in 1992 and 2002 in St. Croix, U.S. Virgin Islands. Values for 1992 appear on the left hand side for each of the cover types and 2002 values appear on the right.



A 1992.



B 2002.

Figure 2-3. Transition within each of the four land cover classes during the 10 year study period. 4A) Horizontal bars represent the total area in each of four land cover classes in 1992. The colors within the bars indicate how that same area became classified in 2002. 4B) horizontal bars represent the total area in each of four land cover classes. The colors within the bars indicate how that same area was classified in 1992. Note that the total area in forest remains stable between the two dates while developed increases and grass decreases.

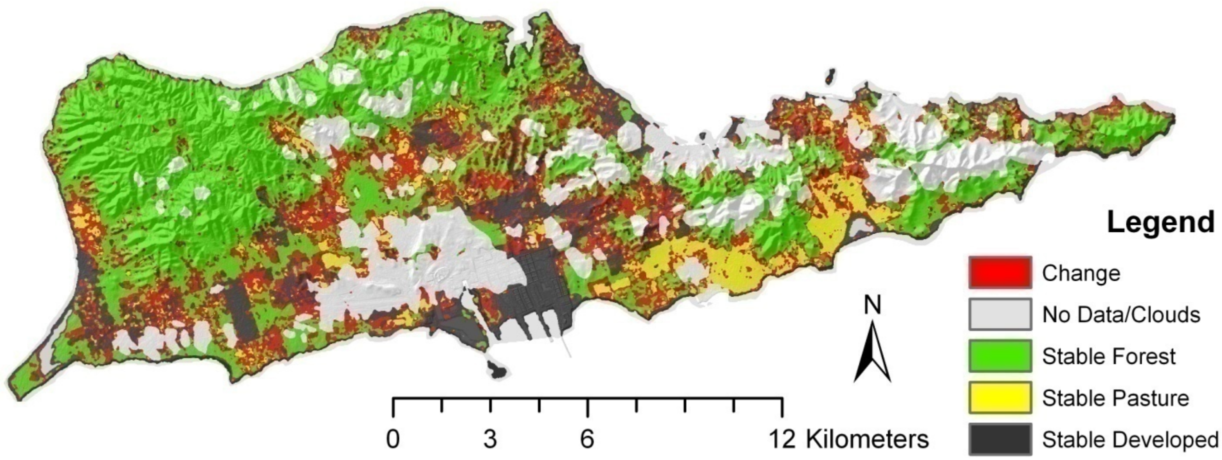


Figure 2-4. Spatial distribution of areas experiencing change (shown in red) between 1992 and 2002 relative to the three stable land cover types.

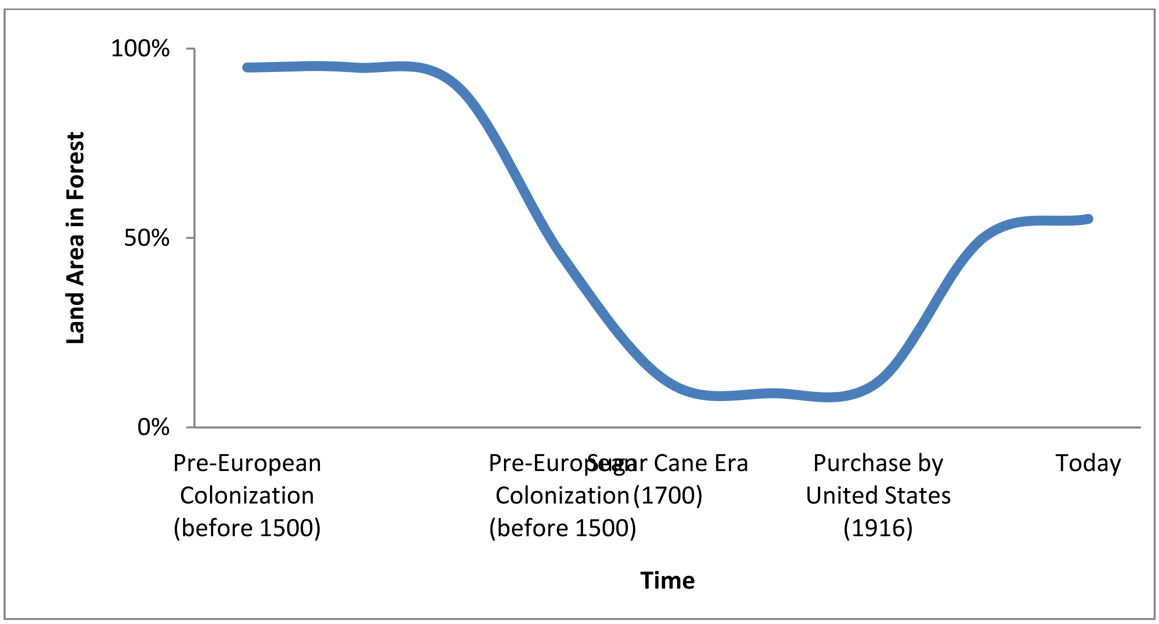


Figure 2-5. An idealized graph of the percentage of forest cover on the island of St. Croix through time.

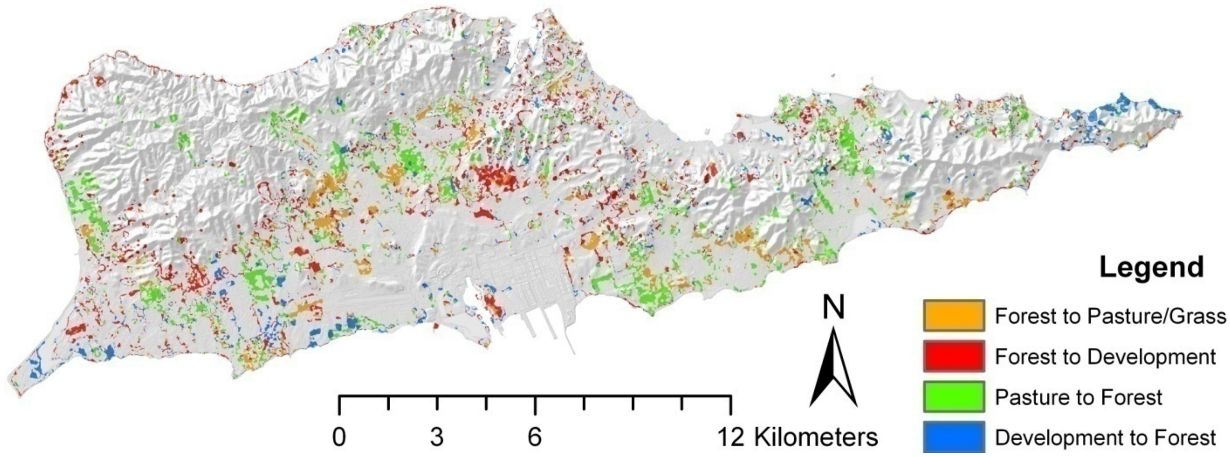
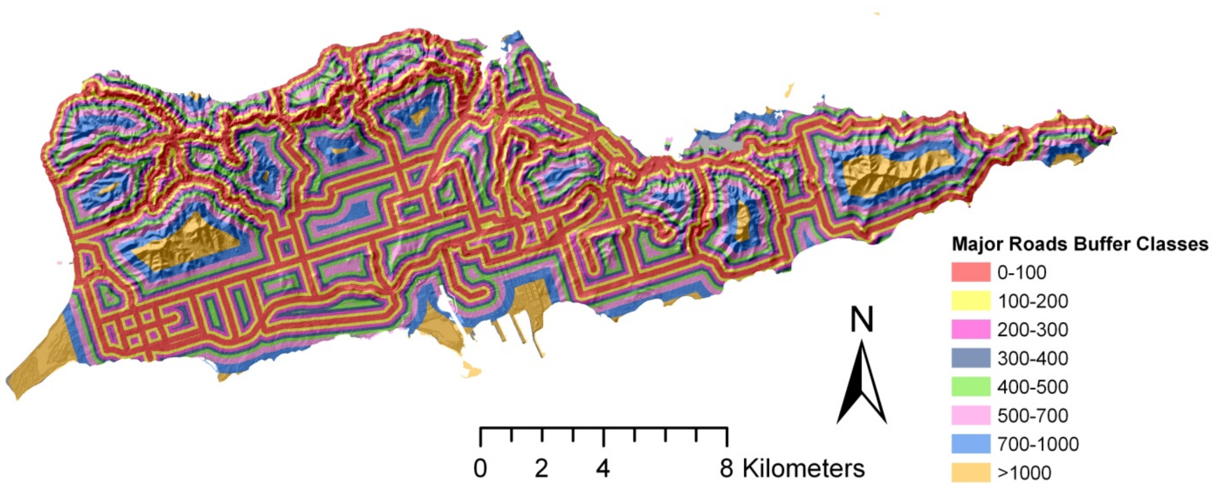
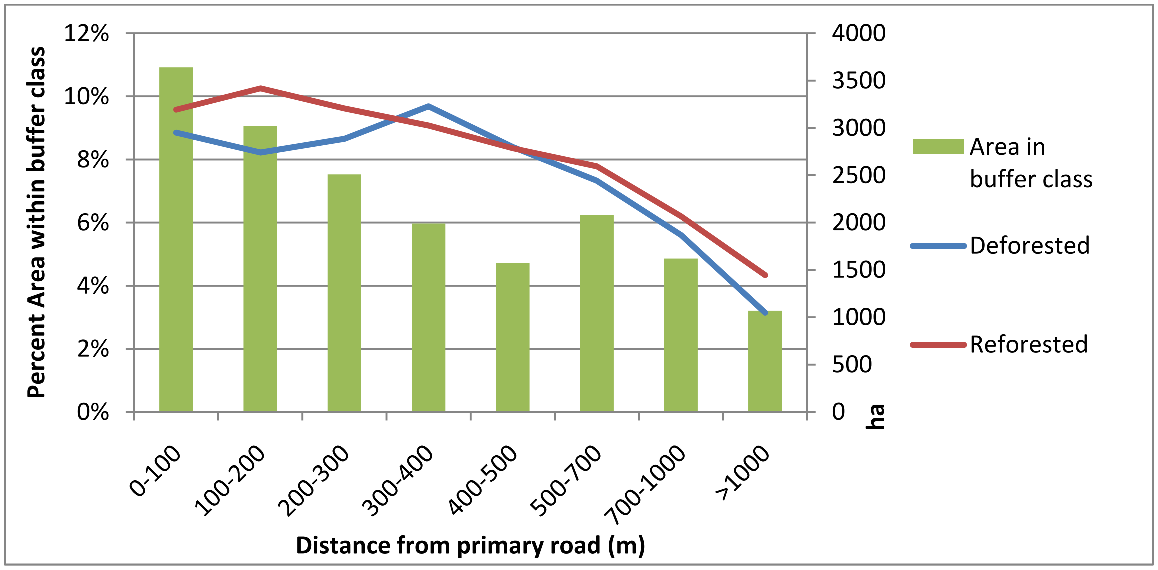


Figure 2-6. Distribution of forest gain and forest loss from 1992 to 2002 shown in relation to topography. Forest loss to forest appears in red and loss to grass in indicated by orange. Forest gain from pasture is indicated with green and forest gain from developed class is blue. Much of the forest gain from the developed class was previously bare ground, sand or mud flats and does not represent urban development converted to forest.



A



B

Figure 2-7. Change area relative to the distance from main roads in St. Croix. A) The spatial distribution of the six road buffer distance classes and B) the percent land area in each distance class occupied by forest gain and forest loss.

CHAPTER 3
DIVERSITY AND STRUCTURE OF SECONDARY FORESTS OF VARYING AGES

Introduction

Native tropical and sub-tropical dry forests are high in species diversity and endemism and are becoming increasingly rare across the world. Forests are lost primarily due to conversion of forestland to agriculture. Subsequent abandonment leads to creation of secondary forests, which have been the dominant forest cover type in the tropics for decades (Brown & Lugo, 1990) accounting for over 60% of all tropical forests and increasing (FAO, 2006). These secondary forests form under unique conditions that often include altered disturbance regimes, and harsh localized climatic and edaphic conditions which results in stands with novel species compositions. Secondary forests will likely play an increasing role in conservation of forest biodiversity (Chazdon et al., 2009) especially in fragmented landscapes.

There is a decline in global net rate of forest loss, attributed primarily to an increase in secondary forests in certain regions of the world (FAO., 2006). The species composition of secondary forests often contains a mix of pioneer and mature forest trees as well as native and exotic plants which reflects the unique conditions under which they were formed (Lugo & Helmer, 2004). Native mature forest species are frequently not present if there are few remnant trees standing after disturbance and the modified environmental conditions inhibit seed dispersal of large-seeded species. Introduced exotic species play an increased role and agricultural weeds are especially common in the earliest stages of regeneration. Forests combining aspects of mature forests and young secondary stands can be considered hybrid systems, including secondary forests with remnant mature patches, stands with severe a reduction in mature forest trees such as heavily thinned stands, and with elevated presence of exotic species (Hobbs et al., 2008). Tropical secondary forests can provide a wide range of services in addition to conservation of biodiversity including fuel wood, small game (Roth, 2001) and sites for agroforestry practices (Vieira et al., 2009). As these spontaneously regenerating, frequently unmanaged secondary forests become increasingly common, so has the desire forest rehabilitation strategies that return ecological function to the systems A land manager could facilitate establishment of desirable species to produce a relatively stable system that provides ecological goods and services (Seastedt et al., 2008; Jackson & Hobbs, 2009).

Secondary forests can be dynamic and resilient, quickly replacing species over time and developing structure and diversity (Brown & Lugo, 1990). Human land use history is among the most important factors determining the rate and extent of forest recovery. The duration and intensity of the previous land use greatly influence the rate of recovery as well as the structure and species composition of the secondary forests that follow abandonment. Unfortunately, intensity of land use is a difficult variable to measure and quantify. Recovery can be rapid if the previous land use was not intense and a propagule source is nearby (Guariguata & Ostertag, 2001; Weaver & Chinea, 2003). The secondary forests that regenerate can recover similar levels of ecological function and species diversity over decades (Lugo & Helmer, 2004), but tend to have unique species composition with fewer native species and greater dominance by exotic species (Marin-Spiotta et al., 2007; Brandeis et al., 2009). When native forests are cleared and new species introduced, a novel ecosystem can arise, comprised of a completely new combination of species (Hobbs et al., 2008) Forests cleared for agriculture have recovered species diversity, stem density and basal area after 50 years of abandonment in Puerto Rico, New England and elsewhere without any human intervention (Grau et al., 1997; Martin et al., 2004), though other estimates predict nearly 200 years may be required to reach mature forest basal area and biomass values, even on lightly used land (Saldarriaga et al., 1988). Succession is influenced by *in situ* factors as well as the conditions of the surrounding landscape. Intact soil seed banks and stump sprouting lead to diverse forest that can resemble the species diversity of original stands. Human altered disturbance regimes, such as the introduction of fire can eliminate soil seed sources and stump resprouts. Repeated burns reduce soil nutrient levels such a nitrogen and phosphorous and significantly slow rates of forest regrowth as well as cause the system to be more susceptible to future fires (Zarin et al., 2005).

In Puerto Rico, studies of secondary forests regenerating on abandoned agricultural land suggest that the least impacted sites (coffee and fruit production) recover species diversity more quickly and contain more rare and endemic species than sites with high impact forms of pasture and agriculture (Rivera & Aide, 1998; Pascarella et al., 2000; Thompson et al., 2002). The recovery rates and process in these studies are important for St. Croix and the rest of the Lesser Antilles because of their proximity, similarity in ecotypes, forest species composition and relatively similar land-use history. However, the differences between St. Croix and these studies in also noteworthy. St. Croix is only 1/40 the size of Puerto Rico and has simpler topography and fewer ecotypes. Many secondary forest succession studies there are in the higher mountain regions where land use was low intensity (such as shade coffee production and fruit orchards) for short time periods. St. Croix has few high mountains, making most of the island accessible for human activity. Burning and tilling were part of intense agricultural production of sugar cane and cotton practiced throughout the lowlands of St. Croix for centuries (Weaver, 2006). Intensity of land-use history is known to have long lasting on forest recovery rates and species composition (Thomson et al., 2002). In addition, studies in mountain areas with high rainfall, surrounded by protected forest area (Pascarella et al., 2000; Thompson et al., 2002) are likely to experience faster recovery than the mosaic of former pasture and agricultural fields in the lowlands of St. Croix.

Most studies of succession in secondary forests tend to focus of specific study sites and studies examining the effects on land use across the entire range of environmental gradient are uncommon (Brandeis et al., 2009). The Forest Inventory Analysis (FIA) in Puerto Rico and the Virgin Islands are utilized in this study because they are island wide, although the FIA does not address land use history or intensity. Studies of secondary forest on abandoned agricultural sites in nearby island such as Jamaica indicate early site conditions select against native tree establishment (McLaren & McDonald, 2003). Prolonged intense agriculture followed by persistent low-level disturbance to regenerating forests in the Dominican Republic resulted in severely hampered or arrested succession, even (Roth, 1999). Simple stands dominated by invasive species persist after the disturbance is eliminated. A similar type of arrested succession has also been described on former pastures in fragmented mountain landscape of South America (Sarmiento, 1997) and Africa (Chapman et al., 1999). Other studies similar to the abandoned pasture in the dry sub-tropical forest in St. Croix have been in Puerto Rico (Aide et al., 2000: Zimmerman et al., 2000: Lugo & Helmer, 2004). The sites in these studies contain plant communities with a highly altered species composition where exotic invasive species represent a large percentage of the stems and aboveground biomass. These provide high level of detail on a small area over fairly uniform environmental conditions and none have a comprehensive sampling to incorporate island wide conditions.

The goal of this study is to determine the extent to which native forests are regenerating in St. Croix, U.S. Virgin Islands and how exotic invasive plants may influence the process. I assess the composition and structure of secondary forests in St. Croix, across a temporal gradient (stand age) and the full spectrum of land-use gradients on the island. Secondary forest stands ranging in age from two to fifty years are analyzed to determine how species richness changes over time and are also compare to some of the most mature stands. If secondary forests can recover their structure and composition over time than non-interference can be a low-cost method of achieving forest restoration in targeted areas. In the Virgin Islands, however, forests occur in a highly fragmented mosaic of agriculture and development where invasive plants play a prominent role in succession. Do these newly introduced plants function in the ecological role of pioneer species just as the native pioneers do, or do they have a longer lasting influence on succession? I assess this by determining: 1) what suite of plant species are present in recovering forests of varying ages? 2) How does species diversity of a site vary with age? 3) How do other factors, such as land-use history, slope and soil type influence the pattern of forest recovery?

Methods

Study Area

St. Croix in the U.S. Virgin Islands provides an excellent opportunity to study post agricultural secondary forests. The small size (215 Km^2) and relative isolation of an oceanic island limit some of the confounding factors (such as the influence of pollutants or native/exotic organisms from neighboring systems) inherent in studying forest ecology in an uncontrolled environment. St. Croix experienced widespread forest clearing for agriculture, primarily sugarcane, cotton and pastures, during the colonial period starting in the 1500s and eventually resulted in native forests remaining in only isolated fragments (Weaver, 2006). Like neighboring Puerto Rico, economic changes starting around the 1950s resulted in widespread agricultural abandonment and forest regeneration (Helmer, 2004). Secondary dry forests are by far the most dominant forest cover type in St. Croix and represent the future forests of the territory (Brandeis & Oswalt, 2007). This study analyses if St. Croix's secondary forests are able to recover their native species diversity over time without human intervention.

Field Data Collection

I collected field data during the summers of 2004 and 2005. Random points from a previous land cover classification study were used to select a portion of the vegetation sampling sites. However, many of the points both were difficult to physically access and a challenge to determine the actual age of the forest stand. Therefore, additional sites were purposefully selected in accessible locations where land use history and stand age could be accurately determined through personal knowledge of the property, property owner interviews and field data. Land owner interviews and 1992 black and white aerial photographs helped determine stand age at each site. The secondary forests sampled were assigned to one of five age classes (Table 3-3). Vegetation data was collected along a total of 50 transects measuring 3 x 50 m (as described by Aide et al., 2000) on 30 sites (*n*=30). The transects were broken into 10 m segments and presence/absence was recorded for all tree species, which were identified to the species level (Figure 3-1). Canopy height and structure, percent ground cover, presence of vines, lianas, orchids and epiphytes were also recorded (Figure 3-2). Waypoints were recorded at the start and end of each transect using a Garmin, *e*-trex GPS unit.

Data Analysis

The vegetation data from the transects were analyzed in SAS 9.1 using a generalized linear mixed model (proc GLIMMIX) that treated sites as a random effect and transects as spatially auto correlated. Data was summarized by age class and compared for differences. Simple linear regression was performed to determine the effect stand age had on species diversity of the secondary forest sites. In addition to age, spatial data were also analyzed (proc GLIMMIX) relative to species diversity and the location of age classes.

These field data and their geographic attributes were combined in a geodatabase using a Geographic Information System (GIS) where additional layers were added, including soils, slope, and elevation using the GIS software package ArcGIS 9.1. Results from the 2002 land cover classification of St. Croix (see Chapter 2) and results from the 10 year land cover change analysis were also included in the geodatabase and used to help confirm details on site land-use history. Field data from this project were cross referenced with the results of the Forest Inventory Analysis (FIA) conducted in 2004 by the U.S. Forest Service (Brandeis & Oswalt, 2007). Sampling density for the Virgin Islands FIA was increased because of the small land area in the territory and contains detailed information on forest species composition, stem density, basal area, above ground biomass, downed woody debris and other data on the sites sampled. Exact locations of FIA data points are kept confidential, so transect locations and forest cover polygons were sent to the Forest Service FIA lab where they produced summary tables use in this analysis.

Results

Across all sites, a total of 101 woody species were identified. Table 3-1 lists the most common species and their frequency (number of observations where the species occurred divided by the total number of observations). The vast majority are tree species while some of the most common lianas and woody shrubs are also included. The most frequently encountered tree species by far was the exotic invasive *Leucaena leucocephala*, found in 67.5% of the sample segments (Table 3-1). *Capparis indica* is a medium sized tree, ubiquitous to the Virgin Islands dry forest, and was the most frequently (27%) encountered native among all age classes. The thorny, exotic *Acacia macracantha* is a common pasture weed found in 24% of the plots sampled. Although native, *Cordia alba* is considered a weedy tree and *Lantana camera* is an early successional shrub associated with highly disturbed sites and each were found in roughly 20% of all sites. *Borrarea succulanta, Guapira fragrens* and *Eugenia monticola* are among the most common native trees of St. Croix's dry forest and were also found in approximately 20% of samples among all age classes. Like *C. indica*, they are medium sized trees that produce berry-like fruit containing animal dispersed seeds.

Figure 3-3 presents species diversity trends across age classes for three plant groups. Sun-demanding exotic tree species like *L. leucocephala*, *A. macracantha* and the larger *Albizia lebbeck* generally had high frequencies peaking in younger age classes and decreasing sharply in older forest stands. The shade-tolerant *Triphasia tripholia* invades mature forest and establishes in the understory. It has a patchy distribution but with extremely high density where it occurs. Native trees generally tended to increase in frequency with stand age, like the most common species listed in Figure 3-3B. *Tabebeuia heterophylla* is a notable exception to the trend. It is an early colonizer, fairly long-lived, medium-sized tree with small, paper-like, and wind-dispersed seeds. These results indicate it may be intolerant of dense shade as it was rarely found in older stands. Several other woody species also demonstrated distinct trends, such as *Capparis flexuosa*, a liana that can also grow as a low shrub and is so common in St. Croix that it is listed separately. Other liana species are grouped into a single category. These and the shade tolerant native shrub *Erythroxylum brevipes* increased in frequency with increasing stand age (Figure 3-3C). Native, shade-intolerant plants such as *Lantana camara* and *B. simaruba* were found is small numbers in all age classes, but especially in young forest.

Species rank order and relative frequency varied when sites were analyzed by age class. The most frequently encountered species in age classes 1-4 was the invasive exotic *L. leucocephala* which was found in 90% of segments in Age Class 1 (Figure 3-3). The second and third ranked species in Age Class 1 (0-5 years) were the fast-growing, sun-demanding shrubs, *L. camera* and the euphorbia, *Croton flavens.* Two of the first native trees to colonize secondary forests are *C. alba* which ranked 4th and was found in 22% of Age Class 1 segments and *C. indica*, ranked 9th (8%). In Age Class 2 (5-10 years) , *L. leucocephala* still ranked 1, but its frequency decreased to 69%

(Figure 3-3). The 2nd and 3rd ranks were held by the larger and longer lived pioneer trees *A. lebbeck* (53%) and *C. alba* (24%). Age Class 3 (10-20 years) sites up to 20 years old still had *L. leucocephala* as the most frequent (65%) species, followed by the *A. macracantha* (34%). Longer lived, shade-tolerant trees like *B. succulanta* (24%) and *Swietenia mahogoni* (18%) factored prominently in these stands. The three youngest forest classes shared other characteristics; canopies tended to have a single layer and were often patchy, the liana *C. flexuosa* was found in roughly 16% of the segments and four of the ten most frequently encountered species were exotic.

Age Class 4 (20-50 years) stands still had *L. leucocephala* ranked 1 (62%), however, indicator species *C. indica* (48%), *B. succulanta* (43%) and *E. monticola* (34%) all factored prominently in the stands. The stands were still somewhat patchy, but tended to have two distinct layers with shrubs *L. camera* (41%), *Tecoma stans* (31%) and *Croton discolor* (24%) dominating brightly lit portions of the understory. Age Class 5 (>50 years) stands were the only sites where native *C. indica* (79%) ranked 1 instead of *L. leucocephala*. Exotic species accounted for only one of the top ten ranked species, but the aggressive and shade-tolerant *T. tripholia* was found in 60% of Age Class 5 segments. The plant thrives in the forest understory and produces copious amount of sweet, juicy berries with bird dispersed seeds throughout the year. The percentages in this class are likely skewed somewhat due to a smaller sample size within the class due to the limited number of sites with 50 year old forest and known land-use histories.

In addition to variation in species composition, age classes also differed significantly in species diversity (average number of species encountered per segment).

Results from the GLIMMIX procedure indicated a significant difference ($p < 0.001$) in species diversity between age classes (Table 3-2). The trend was for species diversity to increase as stand age increased. Post hoc mean separation using the Bonferroni procedure for multiple tests of inequality indicated that age classes fall into two groups. Classes 1, 2 and 3 did not differ from each other and class 4 and 5 do not differ from each other (Figure 3-4).

As expected, species richness generally increased with stand age but there are other factors influencing species diversity for age classes. Species diversity within Age Class 4 and 5 ranged from 5 to 25 species per segment. One 50 year-old transect at The Nature Conservancy was dominated by *L. luecocephala* and *T. trifolia,* with one or two individual native trees per segment. For some sites it was difficult to determine exact stand age because information from land-owners seemed to conflict with either field conditions, the aerial photographs or both. Stand age did not account for the high degree of variability in the older age classes. In fact, there are several transects in age classes 4 and 5 with the same diversity as the youngest sites in the study. There are other mechanisms influencing successional pathways to cause the unexplained diversity results. Segments in age class 4 and 5 with less than six woody species in a 30 m^2 and with all of those species considered invasive exotic or primary successionary species is a strong indication of severely hampered or arrested succession.

Results from the GLIMMIX procedure indicated no significant ($p < 0.05$) difference between stand age for variables elevation and aspect (Table 3-3). For slope, Age Class 5 stands differed significantly from other sites while there was no detectable trend among the younger forest classes. Previous studies have found that forests, especially older forests, tend to occur at higher elevations and on steeper slopes. The explanation for the trend is that steep slopes are low quality sites for farming or development and higher elevation translates to more difficult access. Finding that this trend does not apply in St. Croix is surprising, at first and one possible explanation is that site selection was not completely random and therefore not representative of all conditions. A more likely explanation relates to spatial scale. It is likely that St. Croix's small size makes all parts of the island accessible. In the land cover change analysis in the first chapter of this document, I tested whether or not land cover change tended to occur more frequently in areas located closer to roads, a phenomenon commonly demonstrated in continental systems over large areas. My results gave evidence for the trend, but only at the greatest distances measured, which accounted for only 5% of the island area. I concluded that increased distance from roads in such small increments did not translate to decreased human accessibility; therefore change remained relatively constant at almost all distances. Results from the land cover change study also indicated that forest areas had a higher average elevation and slope than developed or grass areas. However, with the methods used in this study I was unable to find significant differences ($p < 0.05$) between age classes within the forest land cover.

Discussion

The goal of this study was to determine the extent to which native forests are regenerating in St. Croix, the influence exotic invasive plants have in forest succession and for how long. Almost all of St. Croix's forests are considered to be secondary forests (Little & Wadsworth, 1964) and results from Chapter 2 indicate that >8% of the island may be covered in forests less than 10 years old. Results from this study indicate that species diversity within young secondary forests of St. Croix is relatively low and there is a high degree of dominance by a single invasive plant, *L. leucocephala.* The canopies tend to be patchy, less than 5 m tall, and have no emergent trees. Older secondary stands have higher species diversity and an increased presence and diversity of native trees, however even after 50 years *L. leucocephala* is still the most common species.

Four common native trees should be considered indicator species for successfully recovering native secondary forests; *Capparis indica*, *Bourreria succulanta*, *Guapira fragrens* and *Eugenia monticola*. Abundance of *C. flexuosa* and other lianas was lowest in young stands and increased with stand age, and may also be an indicator of improving forest health. Studies in rainforest tree gaps have found lianas to be positively correlated to pioneer tree abundance and frequently resulted in liana-dominated gaps with stalled forest succession (Schnitzer et al., 2000). This is not the case in St. Croix. These indicator species also tolerate a wide range of conditions and are potential candidates for reintroduction when rehabilitating the most degraded secondary forest sites.

The FIA found *L. leucocephala* to be the most abundant tree in St. Croix and assigned it the highest importance value of any tree species (Brandeis & Oswalt, 2007). (The Forest Service classifies the species as native, although locally the species is considered to have been introduced by the US Department of Agriculture during the 1950s.) Brandeis and Oswalt (2007) concluded *L. leucocephala* stands were distinct in that they were undeveloped, even-aged, largely monospecific with high stem density (4,235 stems/ha) and classified them as ‘reversions’, a cover type that was not found in the other U.S. Virgin Islands or in any of the United States. These FIA findings support my finding that the plant shows an unusual degree of dominance in St. Croix that alters the succession process.

Relative to continental forest systems or large islands with diverse topography and life zones, St. Croix would naturally have lower species diversity and comparisons between sites should be made with this in mind. In nearby Puerto Rico, a study of The Cartajena Lagoon Wildlife Refuge recorded species diversity in a secondary dry forest two years and 10 years after fire and grazing were excluded from the area (Weaver & Chinea, 2003). The Cartejena Refuge (CR) has similar soil, rainfall, slope and elevation gradients to those found across St. Croix. The survey found a total of 103 tree species with *L. leucocephala* being the most common and showed a high degree of dominance by a small suite of exotic species on both dates. Of the 103 tree species identified, 43 combined to account for only 2.2% of the stems. The 10 most common species in St. Croix (Table 3-1) occurred in a similar number of plots in CR, the notable differences being the common vine (*C. flexuosa*) and the shrub (*L. camera*) were nearly absent in the Puerto Rico site. Despite these similarities, species diversity was far greater in CR, which had 23 common tree species (defined as being found in >10% of plots) compared to 14 common tree species in St. Croix. Dominance by a single species was also greater in St. Croix as *L. leucocephala* was found in 67% of plots and only 33% of plots in CR.

It was not possible to compare *L. leucocephala* dominated stands with regenerating forest comprised of primarily native tree species because none could be found. In a matter of decades St. Croix seems to have transformed from having no *L. leucocephala* in forests to having little to no forest regeneration without it. The ramifications of this on succession are difficult to determine. The young stands in this study are compared to >50 year old forests that began regenerating when *L. leucocephala* was not as prevalent on St Croix or may have been absent.

By comparison, St. John of the US Virgin Islands has roughly 66% of it land area protected by US National Parks Service. An inventory of five secondary forest stands within the park boundaries, ranging in age from 35 to 125 years, found that the youngest stand was similar to those in St. Croix, with a long agricultural history and a short, simple secondary forest structure dominated *L. leucocephala* (Ray & Brown, 1995a). The three sites over 100 years old also had long histories of intense agricultural use, but their abandonment may have predated the introduction of *L. leucocephala.* The shade intolerant legume was not found in any of >100 yr St. John sites, which could be the result of either successional exclusion or that the plant was never present.

Studies of forest succession on abandoned agricultural sites are many and have indicated that tropical forests are potentially resilient and can recover structure and species diversity quickly (see reviews by (Brown & Lugo, 1990; Guariguata & Ostertag, 2001; Chazdon et al., 2009). When the intensity and longevity of human land use is mild, forest recovery can be quite rapid (Aide et al., 2000). Forest recover is further enhanced by close proximity to healthy forest patches and other seed sources. Regardless of the speed of recovery, secondary forests bear the legacy of previous human land use in their unique species compositions

St. Croix likely represents the most extreme setting for testing the lessons learned from the previous studies. Historical land uses were intense as in sugar cane production that frequently utilized fire for pest control. After productivity decreased land was maintained as pasture for centuries, in many cases. However, the greatest difference between the previous studies and St. Croix (and the rest of the Lesser Antilles) is an issue of scale. St. Croix's small size made almost the entire island accessible to humans, resulting in a high percentage of forest removal (Little & Wadsworth, 1964). The island is also distant from continental sources of genetic material and has a relatively simple topography, causing a relatively low species diversity and higher degree of endemism. Finally, the introduction of invasive organisms seems to have further reduced the forest's ability to regenerate. The cumulative result of these facts is secondary forests with a relatively low rate of recovery

A state of arrested succession has been suggested in other secondary forests dominated by exotic species, including tropical dry forests (Sarmiento, 1997; Chapman et al., 1999; Roth, 1999; Sandor et al., 2003; Kalacska et al., 2004). The results from this study indicate a higher degree of dominance from exotic species for a longer period of time than in other studies. In fact, study sites such as the >50 year old secondary forest stand sampled at The Nature Conservancy in Estate Little Princess posses forest structure and diversity indicative of a five to ten year old stand. Sites like this are common and require human intervention as natural succession does not occur under the present conditions.

Conclusions

During the entire field data collection process for this study not a single site was found where St. Croix's Caribbean dry forest was regenerating without the heavy influence of exotic species. The current reality is that, young secondary forests are completely dominated by exotic species, regardless of location, previous land use or any biotic or abiotic factors. After 50 years without disturbance other aggressive exotic plant species are still present, but no longer dominate forest canopies in some sites. These results indicate that secondary forests of St. Croix tend to recover species diversity and canopy structure over time. However, multiple sites in this study exhibited strong signs of arrested succession, including undeveloped canopies, low species diversity and dominance by exotic species. An additional confounding factor is that 60-70 yr old secondary forests began regeneration under conditions that did not include island-wide domination of *Leucaena leucocephala* and the this has had on successional pathways cannot be easily determined.

Stand age accounted for only a portion of the variability in species diversity in this study. Land use history can play an important role in the rate of forest recovery, but quantifying severity of previous land-use is challenging, even with detailed information from land owner interviews. Attempts to correlate slope, aspect and elevation to stand age were inconclusive. The secondary forests arising from abandoned agricultural sites on St. Croix have novel species compositions where exotic species play a major role even half a century after abandonment. The most likely explanation is the small spatial scale of the island has caused the forests to reach some type cross some threshold of resilience from where they are no longer able to recover unassisted. St Croix is likely on the leading edge of this phenomenon as dozens of small islands in the Lesser Antilles are transitioning out of agricultural and into manufacturing and tourism-based economies that will likely lead to forest transitions under similar circumstance to St Croix.

Table 3-1. Tree species encountered during field sampling in St. Croix with, botanical names, species code, species origin (N= native to St. Croix before European settlement, I= introduced) life form (T=tree, S=shrub, L=liana and P=palm) and frequency (expressed as a percentage of the number of segments where the species was observed over the total number of segments).

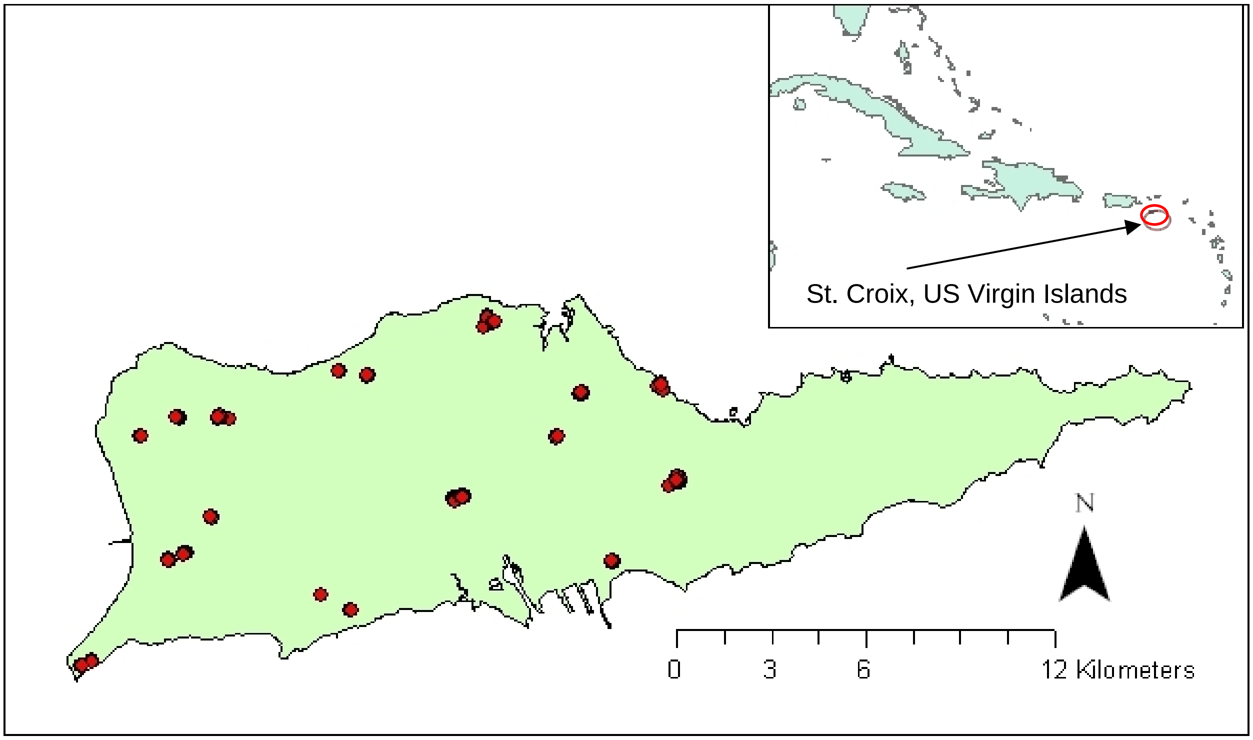
Genus	Species	Code	Origin	Life Form	Frequency
Leucaena	leucocephala	leu leu	I	T	67.5%
Capparis	indica	cap ind	N	T	27.0%
Acacia	macracantha	aca mac	I	T	24.2%
Capparis	flexuosa	cap fle	N	L	21.0%
Lantana	camera	lan cam	N	S	20.0%
Bourreria	succulanta	bou suc	N	T	19.0%
Cordia	alba	cor alb	N	T	18.7%
Albizia	lebbeck	alb leb	I	T	15.9%
Guapira	fragrens	gua fra	N	T	15.5%
Eugenia	monticola	eug mon	N	T	15.1%
Swietenia	mahagoni	swe mah	I	T	14.7%
Croton	flavens	cro fla	N	S	13.9%
Tecoma	stans	tec sta	I	S	13.5%
Triphasia	tripholia	tri tri	I	S	12.7%
Erythroxylum	brevipes	ery bre	N	T	12.3%
Eugenia	rhombia	eug rho	N	T	11.1%
Randia	aculeata	ran acu	N	T	9.9%
Eugenia	biflora	eug bif	N	T	9.1%
Tabebeuia	heterophylla	tab het	N	T	8.7%
Eugenia	foetida	eug foe	N	T	7.9%
Genipa	americana	gen ame	I	T	7.9%
Casearia	sylvestris	cas syl	N	T	7.5%
Eugenia	aeruginea	eug aer	N	T	6.7%
Croton	discolor	crot dis	N	T	5.6%
Psidium	guayava	psi gua	I	T	5.6%
Swietenia	macrophylla	swi mac	I	T	5.6%
Faramae	occidentalis	far occ	N	T	5.2%
Krugiodendron	ferrum	kru fer	N	T	5.2%
Coccoloba	uvifera	coc uvi	N	T	4.7%
Crossapetalum	rhacoma	cros rha	N	S	4.3%
Andira	inermis	and ine	N	T	4.3%
Capparis	baduca	cap bad	N	T	3.9%
Coccothrinax	alta	coc alt	N	P	3.9%

Table 3-2. Description of the number of observations and the mean species diversity (number of species observed per segment) with standard error for each of five age classes of secondary forests in St. Croix, U.S. Virgin Islands. Totals are given for the experimental design and plant species. Significant differences (p<0.001) for species richness are indicated with unique letters. Age classes without differences are marked with the same letter.

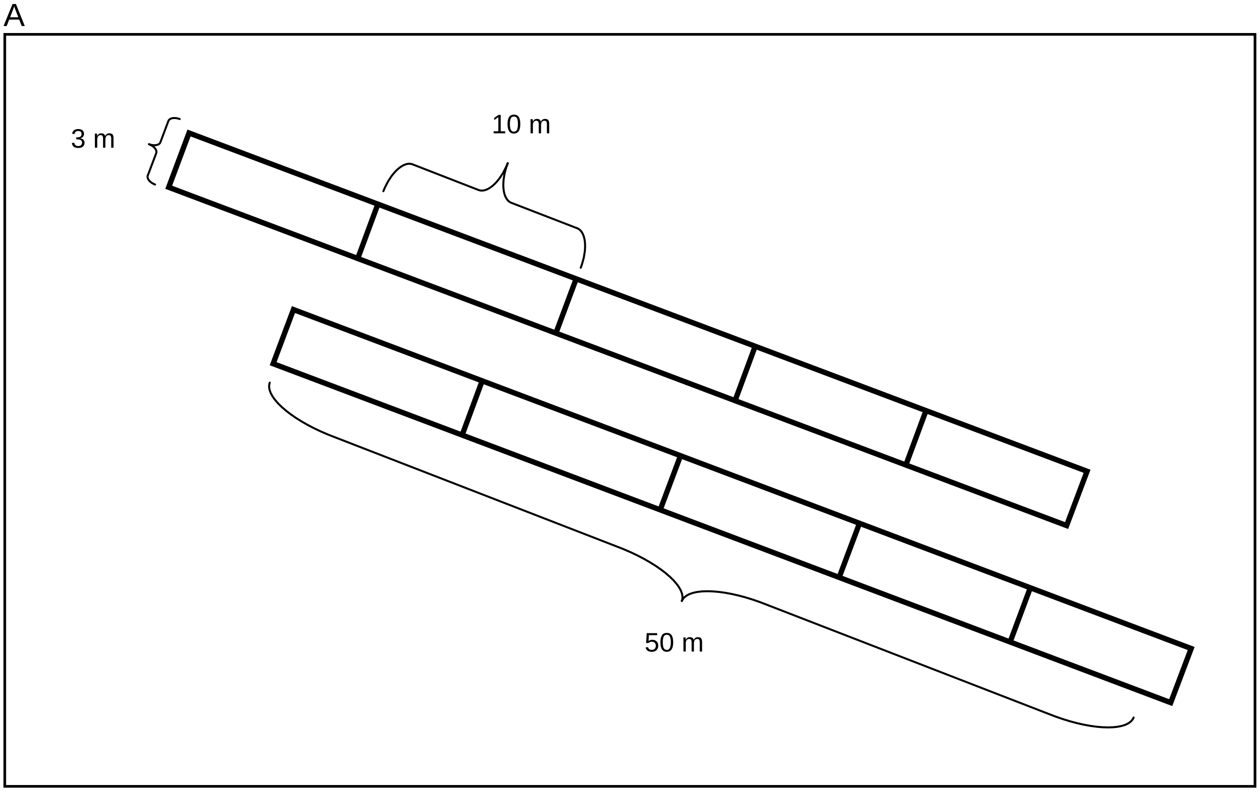
Age Class	**Unique sites (*n*)**	**Transects**	**Segments**	**Mean Species**	**SE**
1	9	12	60	3.15 b	1.63
2	3	9	45	3.82 b	1.89
3	7	13	65	4.17 b	2.43
4	8	11	55	8.17 a	2.56
5	3	5	25	10.79 a	4.62
Total	30	50	250	5.42	3.58

Table 3-3. Age ranges (yr) of five forest cover classes and the average elevation (m), aspect (º), and slope (º) and corresponding standard error of the means. Significant difference (*p* <0.032) between age classes for the variable are indicated with *. Results are derived from 250 observations in 30 independent samples (*n*=30).

Age Class	**Age yrs**	**Elevation (m)** $\bar{x}$	**SE**	**Aspect (º)** $\bar{x}$	**SE**	**Slope (º)** $\bar{x}$	**SE**
1	0-5	59.5	118	201.8	32.6	7.7	3.2
2	5-10	145	204.3	204	39.6	10.7	5.1
3	10-20	48.2	204.3	275.1	48.7	9.5	5.4
4	20-50	42	125.1	162.6	33.1	5	3.4
5	>50	113.4	104.5	210	36.1	21.1 *	3.8



A

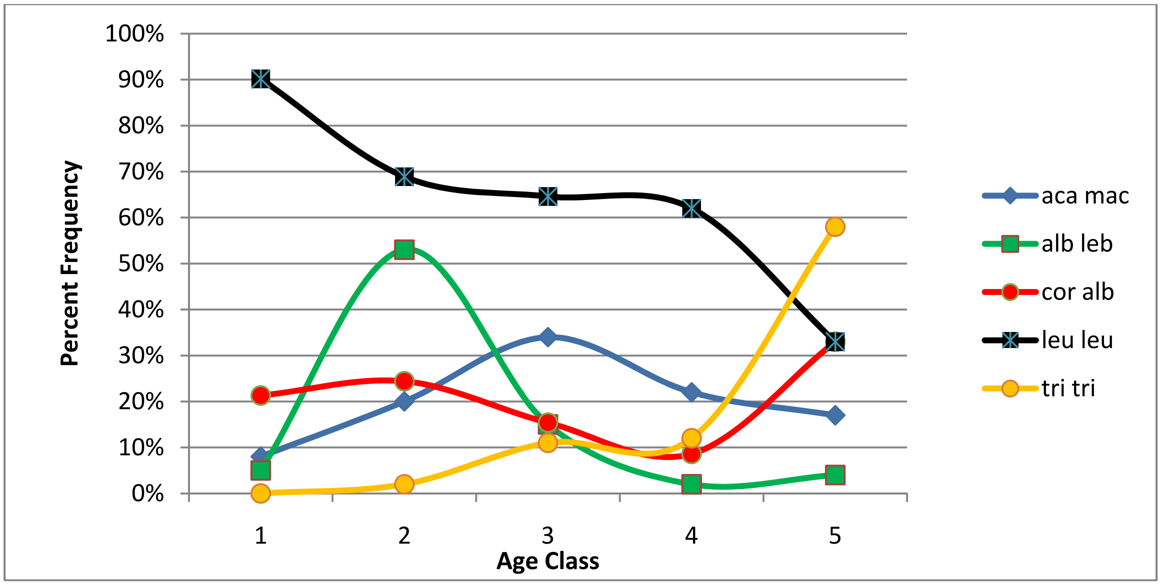


B

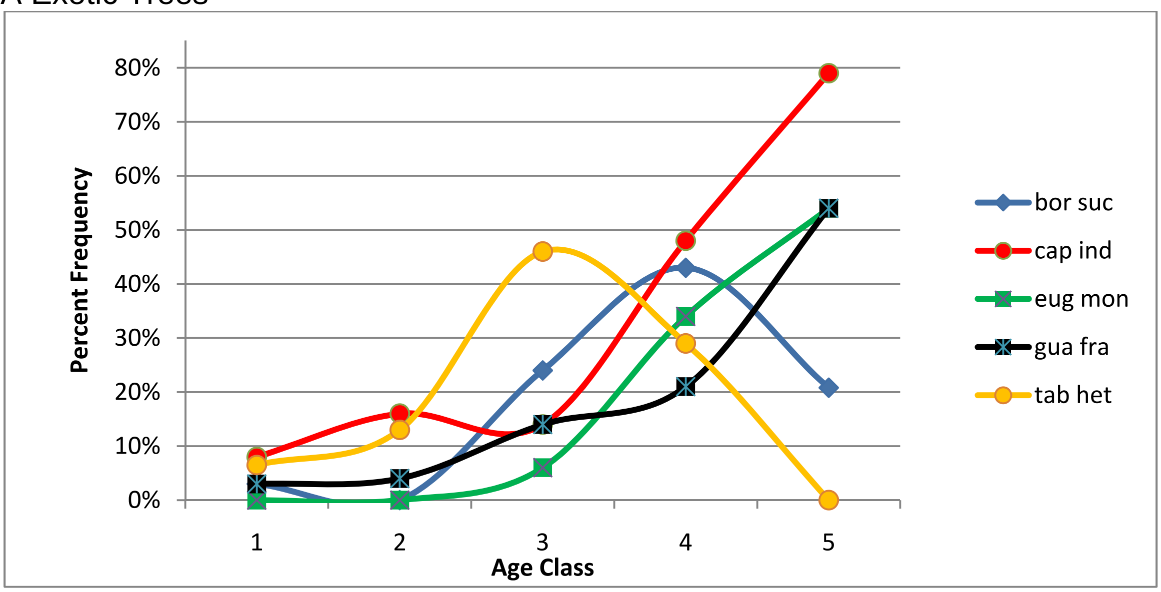
Figure 3-1. A) St. Croix, US Virgin Islands and the distribution of 50 vegetation sampling transects in secondary forests from 5 age classes ranging from 3 to <50 years and B) an idealized pair of parallel vegetation sampling transects, divided into 10m segments

A B

Figure 3-2. Recording canopy structure and composition data along 50m long transects in A) a three year old regenerating pasture comprised primarily of the exotic legume *Leucaena leucocephala* in the thin overstory and the exotic grass, *Panicum maximum* below and B) sampling vegetation in a patchy, 25 year-old secondary forest with downed woody debris from *Cordia alba* growing on a site previously used for agriculture.

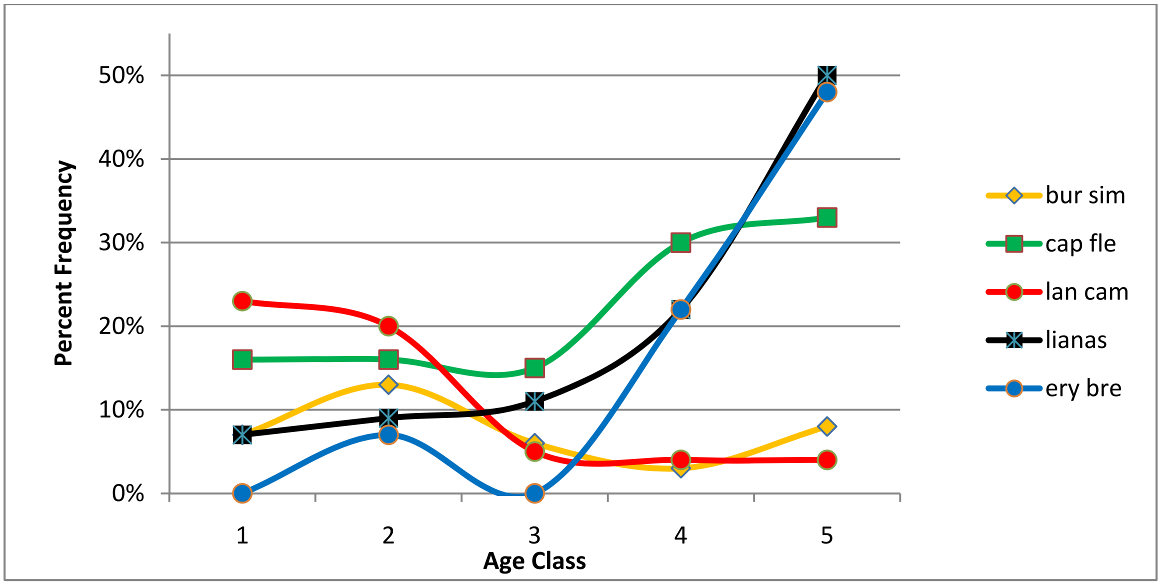


A Exotic Trees



B Native Trees

Figure 3-3. Frequency of groups of the most common plants in secondary forests of St Croix. A) Exotic trees and shrubs. Sun loving species such as *L. Leucocephala* demonstrate decreasing frequency with increasing stand age, while share tolerant exotics such as *T. trifolia* tend to increase in frequency. B) Native trees show a trend of increasing frequency as stand age and species diversity increase. C) Frequency of lianas and shade tolerant shrubs (*E. brevipes*) increases with stand age while the pioneer shrub species *L. camara* decreases.



C Other Plants

Figure 3-3. Continued

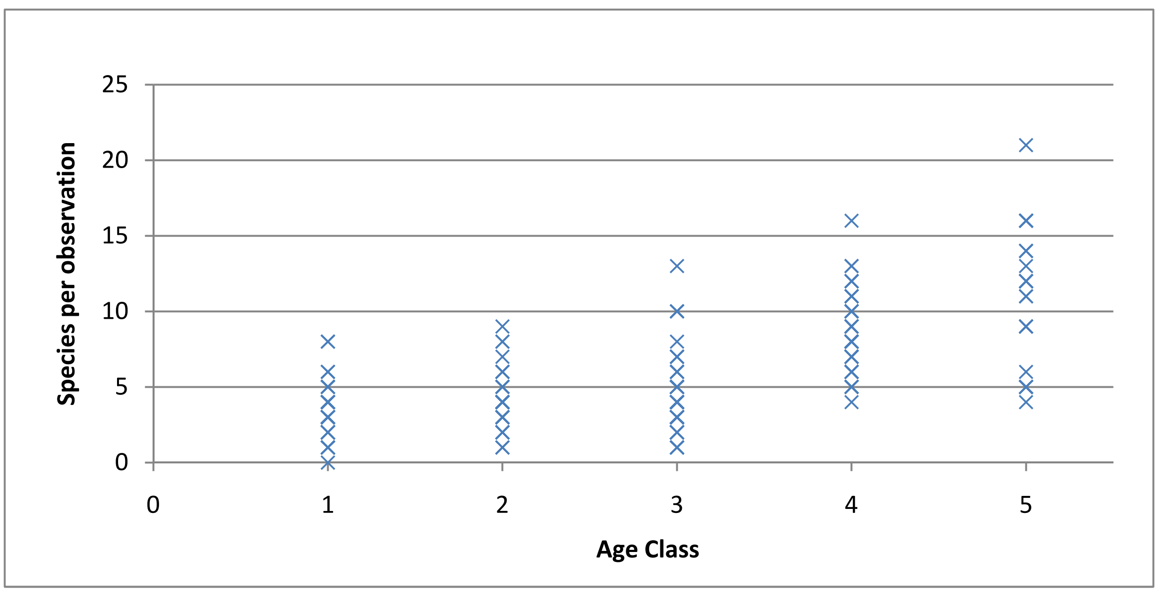


Figure 3-4. he mean number of species recorded per observation for each of 5 age classes of secondary forest in St. Croix, U.S. Virgin Islands.

CHAPTER 4
ENRICHING DEGRADED CARIBBEAN DRY FOREST WITH RARE NATIVE SPECIES

Introduction

Secondary forests are the most extensive forest cover type in the tropics, accounting for over 40% of total forest area (Brown & Lugo, 1990). In the Caribbean, secondary dry forest is the fastest expanding forest vegetation type. They have a simpler structure than intact native forests, with lower species diversity and greater degree of dominance by a few, often alien species. Secondary forests in the Caribbean tend to emerge on 'old fields' that are characterized by soil degradation, more frequent fires, depleted soil seed banks, harsh climatic conditions and high competition with grasses and other pioneer species. The legacy of previous land-use influences the ecosystem function and structure for decades, centuries and longer (Foster et al., 2003). In cases where the duration and intensity of the disturbance is not severe, secondary forests in the Caribbean have proven resilient and can regenerate naturally and recover much of their structure and ecological function (Pascarella et al., 2000). It has been suggested that alien tree species function in the recovery process to stabilize local microclimate and facilitate natural regeneration though recovery may take over 80 years (Vieira et al., 2003). Novel ecosystems are increasing recognized as the likely result when forest regenerates after large-scale anthropogenic disturbance (Hobbs et al., 2009). Lugo & Helmer (2004) have used the term "new forests" to label the unique structure and species composition. Novel ecosystems tend to have native and introduced species living together under new environmental conditions and disturbance regimes and introduced tree species tend to dominate, especially during the first few decades of regeneration. These novel ecosystems offer unique conservation opportunities but may also requite novel management and restoration approaches (Seastedt et al., 2008; Hobbs et al., 2009). These systems are well documented in the Caribbean, including Puerto Rico and the Virgin Islands (Lugo & Helmer, 2004; Brandeis et al., 2009).

Abandoned pastures and agricultural sites present unique environmental conditions that favor the establishment of fast growing exotic species. Lack of seed dispersal is a primary barrier to native forest regeneration (Holl et al., 2000), and is especially important on sites where frequent burning has eliminated the soil seed bank . Even where nearby seed sources provide adequate seed rain other barriers to seedling establishment may be present (Zimmerman et al. 2000). Seed predation, low germination, and early seedling mortality are common in old fields and can significantly influence successional processes. Light and soil moisture also influence seedling survival and the response varies significantly among species (Augspurger, 1984; Loik & Holl, 1999; McLaren & McDonald, 2003).

Seedling competition with grasses, agricultural weeds and invasive woody species can also inhibit successful establishment (Nepstad et al., 1991; Aide et al., 1995; Vieira et al., 2003). For example, in the U.S. Virgin Islands, thirty five year old secondary forests adjacent to native stands were found to have sparse canopies dominated by thorny vines and a single exotic species, *Leucaena leucocephala* (tan-tan), accounted for 58% of the species importance and 95% of the understory seedlings (Ray & Brown, 1995a). The term ‘disclimax’ forest has been used to describe the common condition of Antillean dry forests with a canopy and understory dominated by two or three aggressive exotic species and no recruitment of native species in the under story (Roth, 1999). Such forests do not develop increasingly complex assemblages and structures and species compositions and are said to demonstrate ‘arrested succession’. The causes can range from any combination of; depleted *in situ* seed banks, seeds arriving from outside sources being unable to establish and compete, and increased disturbance frequency that ultimately results in a steady state.

Disclimax forests are distinguishable from novel ecosystems by the rate at which they develop structure and species diversity. The novel systems or ‘new forests’ are initially dominated by a few exotic species when human activity ceases on the site. The exotic species stabilize the site microclimate and facilitate native species establishment in the understory. Mature forest species eventually replace pioneer species. After 40 years the forest structure and biomass are similar to native forests, but exotic species play a more prominent role and reflect the legacy of human use of the site. Neotropical forests can quickly recover their structure, ecological function and diversity if there are nearby propagule sources and the extent and the intensity of the land use was not too severe (Guariguata & Ostertag, 2001). When this is not the case and barriers impede succession, the result is a disclimax forest. Arrested succession, when successional sequences are interrupted or even halted, has been documented in a number of systems (Lugo, 1997; Chapman et al., 1999). The cause is frequently the establishment of recalcitrant vegetation (including grasses and lianas) that prevents mature forest species from establishing (Sarmiento, 1997; Schnitzer et al., 2000). Arrested forests in the Caribbean are dominated by a few species of woody vegetation forming a single low, uniform canopy and have an understory comprised of the same canopy species (Ray & Brown, 1995a; Roth, 1999). Unlike the new forests, they are not a refugia for native species, have low species diversity and provide poor wildlife habitat.

Disclimax forests with arrested succession require some form of intervention to restart succession and restore native diversity. Species selection for restoration projects is an important consideration and there are several approaches. Exotic species can be justified in the most extreme circumstances such as in mining restoration (Parrotta & Knowles, 1999), and plantations have been suggested as a way of stabilizing site conditions and promoting establishment of native species (Lugo, 1997). If the project goal is ecological restoration of native forest habitat, exotics species should only be considered a last resort. Some foresters have tended to rely on the few commercial species for which data and seeds are readily available instead of looking toward native trees that can fill the role and generating baseline data for these species. Rehabilitation in harsh conditions such as recently abandoned pastures with strong competition from exotic grasses and full-sun conditions, rapid growing pioneer species may be appropriate to initiate the succession process (Zimmerman et al., 2000).

Dry forest restoration studies have found planting seedlings is more successful than direct seeding (Ray & Brown, 1995b; McLaren & McDonald, 2003; Bonilla-Moheno & Holl, 2009), that pioneer species generally perform better than mature forest species (Holl et al., 2000; Hau & Corlett, 2003) and using many species is preferable to using few (Van der Putten et al., 2000). An additional intervention at a later successional stage can also be made to introduce a larger number and broader range of species to enhance diversity (Lamb et al., 2005). Establishing fast growing shrubs has also been shown to increase tree seedling survival (Holl, 2002). Using fruit bearing trees and bird perches in restoration is considered promising, but a more complex management practice and difficult to evaluate (Wunderle, 1997; Galindo-Gonzalez et al., 1998; Toh et al., 1999; Shiels & Walker, 2003). Unfortunately, there are no universally applicable rules and understanding the unique site conditions is essential to selecting the appropriate restoration method and species for a given site.

In this study I examined the efficacy of planting native tree seedlings in artificial gaps created in a disclimax forest canopy currently dominated by invasive plants, primarily *L. leucocephala*. The objective of the project was to determine the efficacy of the treatments and performance of the species selected. The goal of the research was to develop an effective method for establishing native plants in abandoned old fields to reinitiate forest succession and restore ecological function and native diversity to this forest type.

Methods

Artificial gaps were created in the secondary forest to give seedlings a temporary competitive advantage over the surrounding canopy during the establishment phase. Mortality, seedling height and gap closure were measured over the course of two dry seasons. The relative performance of four native tree species and the effect of a mulch treatment on growth and survival were analyzed. The covariates rainfall and gap canopy closure were also analyzed for their effect on growth.

The Site

This study was conducted in St. Croix, U.S Virgin Islands on Estate Little Princess (ELP), a property owned and maintained by The Nature Conservancy (lon. 64.0689º N, lat. 17.4050º W). ELP is a coastal site with gently sloping (0-10%) topography under 50 m elevation. The soil types on site are Sion clay and very stony Arawak gravely loam, which derive from volcanic and marine parent material and are molisols typical to St. Croix (Davis, 2000). The soils are white in color with a pH. of >8.0 and are locally referred to as 'caliche' and considered poor for farming. ELP receives an average of 75 cm/yr rainfall, but is highly variable between years. Trade winds blow from the east all year, with increased intensity in the winter months. Daily temperature fluctuations approximate annual change.

The Estate was purchased by the first governor of St. Croix from the Danish West India Company in 1743 and had already been cleared for agriculture by the French. In 1750 a great house, windmill, sugarcane processing plant and as many as 36 row houses for enslaved African workers were built. Records indicate that most of the tropical forest cover was hand cleared for crops and remaining pockets of vegetation were periodically burned. The largest area of ELP was reserved for sugar cane production and was cultivated for over 200 years (Burgel & Scopinich, 2002). Cotton and tobacco were planted in the 1800's, but with short-lived success. Low productivity led to conversion to cattle pasture during most of the 20th century, until 1961 when formal agriculture ceased in 1955. Apart from minor landscape plantings, the land has not been cultivated since that time.

The 24 acre property is mostly fenced, but remains accessible along the eastern Long Reef Beach side. Prevailing trade winds from the east travel over open water for many kilometers before reaching ELP and there are no substantial forest fragments within three kilometers, both limiting factors to secondary forest succession. The closest weather station to the site is the University of the Virgin Islands Agriculture

Experiment Station, which measured approximately 150 cm of rainfall per year during the time of this study.

The agricultural land-use history of ELP is typical for St. Croix. After 54 years of abandonment ELP possesses the type of alien-dominated secondary forest that has become ubiquitous on old fields in St. Croix - a low, semi-open canopy with low species diversity, dominated by a few fast growing exotic plant species. The dominant species is *L. leucocephala* and the forest type is locally referred to as 'tan-tan bush'.

Before planting, data were collected within ELP along three randomly distributed vegetation transects, measuring 50 m long by 2 m wide. Transects were sub-divided into 10 m segments to determine species frequency, composition and forest structure. The forest canopy was a patchy, semi-open single layer, 3-4 m in height, with low species diversity and dominated by a few mostly exotic species. *L. leucocephala* was found in high density in 13 of 15 segments. The weedy *Cordia dentata* (white manjack) and *Acacia macracantha* (stink casha) appeared as single plants with spreading crowns and were found in 13 and eight segments, respectively. Dense thickets of the exotic, thorny bush *Triphasia tripholia* (sweet lime) grew in 8 segments, wherever the canopy was most open. Single individuals of the native trees, *Bourreria succulanta* (pigeonberry), *Capparis indica* (white caper) and *Guapira fragrens* (black mampoo) were found in several segments. These seven species accounted for all of the tree diversity in 14 of the 15 segments. These data are consistent with findings of other studies in the region (Ray and Brown, 1995), and are consistent with the disclimax condition described by Roth (1999).

Species Selection

Previous work evaluated growth and survival of native tree species planted in full-sun in grassy field instead of using artificial gaps. Research indicated that 30 cm tall seedlings of 12 native dry forest tree species can be successfully established (90% survival) in regularly maintained plots without supplemental water (Daley and Zimmerman, 2002). In this experiment, I selected species that could either quickly exploit the gap more rapidly than competitors, or subsist in the shaded canopy understory. I gave preference to rare or under-utilized tree species with these attributes (Table 4-1).

Seeds

Fruits of the four tree species were collected at maturity and weighed. Their seeds were removed, cleaned, counted, treated and sown in soil-free Promix in germination trays within 48 hours of collection. The four pregerminative seed treatments were; water (24 hour soak in distilled water), boil, (30 second dip in 100 C water), GA_3 (one hour soak in 2,000 ppm Gibberellic acid solution), and control (Vozzo, 2002). There were 20 seeds per treatment with a minimum of four replications for each species. Trays were maintained in a screened shade-house, the potting media was kept moist and germination was recorded over a 90 day period. Time to germination of the first seed was recorded and germination was considered complete when there was no new germination in a replication for two weeks. Successful seedlings were transplanted to promix filled polybags when they produced their third true leaf and a slow-release, pelletized 20-20-20 fertilizer was mixed into the media. Seedling were grown in the shade house for between 3-6 months and then hardened off for one month in bright sunlight prior to planting. Germination results were inverse sine transformed and a GLM was used to run an analysis of variance (ANOVA) test for differences between treatment means.

Planting

A backhoe was used to clear a 120 m long by 3 m wide transect to facilitate creation of, and access to, 26 artificial gaps within the dense secondary forest (Figure 4-1). A total of 26, gaps were hand-cleared with machetes and evenly distributed on either side of the transect. The gaps were 3 m in diameter, with gap centers spaced at least 5 m from each other and 5 m from the edge of the cleared transect. Gap centers were marked with stakes and native tree seedlings were planted in the four cardinal directions at a distance of 1.5 meters from center. Four plants were randomly assigned to each of the gaps for a total of 104 (26x4) plants. Gaps were randomly assigned a treatment of mulch or no-mulch. A 20 cm layer of straw hay was applied around the tree seedlings in the mulched gaps. No supplemental water or fertilizer was given to the seedlings in the field.

Seedlings were planted in December, 2006, coinciding with the end of the hurricane season and the peak of the seasonal rains. The data were collected 13 times over an 18 month period that included two complete dry seasons. Plant height was measured from the ground to the base of the highest leaf on the planting day and approximately monthly thereafter. When dead plants were found the likely cause of death was noted.

Canopy gaps were hand-cleared periodically as the surrounding vegetation encroached into the gaps. Canopy closure was measured on the same 13 dates using a spherical densiometer by facing each of the four cardinal directions. Canopy closure was calculated for each gap on each date from these four readings. Plant survival data were analyzed using the SAS statistical package procedure GENMOD which handles binary data. Post hoc comparisons were made using Wald Chi-squares. Plant height data were analyzed using the PROC MIXED (SAS) which is a type of analysis of repeated measures that accounts for both random and fixed effects(Littell et al., 1996). Plant heights were log- transformed to ensure normality of the data. Subject trees varied in their original size and the mixed procedure accounts for this difference. Models accounting for original height difference and use total height over time or absolute growth rate are found to provide the best prediction and clearest interpretation of results (MacFarlane & Kobe, 2006).

When analyzing the factors affecting plant growth, the independent variables species and mulch treatment were considered discreet and rain, rain-lag and canopy closure were continuous covariates. Rain is the total rainfall in the 30 days prior to data collection and rain-lag 31-60 days prior. The gap effect was accounted for with a random statement in the model. Results are reported as significant when p <0.05. Standard deviation and standard error of the means are provided as appropriate and noted.

Results

Seeds

Fruit and seed data, most effective pregerminative treatment, and germination rate are listed in Table 4-2. All of the data provided in the table are based on averages of multiple seed collections and at least four seed germination replications. At least one pregerminative treatment initiated germination in three weeks or less for all four species. At least one treatment significantly (p <0.05) increased the germination rate relative to control for *C. rickseckeri* and *G. officinale* but not for *S. polyphylla* and *S. conocarpum*.

Fruit of *C. rickseckeri* contains a single, hard, woody stone with one to three embryos. Removing the embryos is destructive, so the germination rate provided is per stone and is above 100%. The thin pods of *S. polyphylla* contain highly variable quantities of paper-like seeds that germinate at low rates, but large numbers are easily collected. The 30-second hot water treatment significantly ($p<0.05$) decreased germination rates for all species except for *C. rickseckeri*.

Seedling Survival.

Of the 104 seedlings planted in the 26 gaps a total of 94 (90%) survived at least 18 months. Four of the plants desiccated soon after planting or during the dry season and six were severely browsed by animals, most likely by an introduced deer species (*Odocoileus virginianus)*. Four of the six browsed plants were *S. conocarpum*.

Survivorship data are illustrated in Figure 4-2. Significant differences were found between species ($p<0.05$). A post-hoc analysis using Chi squares found *S. conocarpum* had lower average survivorship than other species, but did not include *C. rickseckeri* because there was 100% survival for that species. There were significant differences ($p=0.015$) between plants in mulched and un-mulched gaps because eight of the ten dead plants were un-mulched. Percent canopy closure did not have a significant effect on survivorship. Interactions between treatments effects (mulch and percent canopy closure) were also non-significant.

Seedling Growth

Figure 4-3 illustrates the overall growth pattern of all four species relative to the mulch treatment, canopy closure and rainfall. For six of the 13 months when measurements were taken, average height change by species was under 1 cm or an actual decrease in height due to drought-induced wilting or die-back. The canopy closure measure follows the rainfall distribution pattern closely. During drought the canopy experienced leaf loss and during periods of higher rainfall there was new growth which closed the canopy gaps somewhat. As expected, plant growth patterns differed between species, but the general trend across species was for increases during high rainfall and flattened curves during drought.

Results of the mixed analysis procedure fixed effects on plant height over time (Table 4-3) indicated highly significant differences ($p < 0.0001$) between species mean heights over time (month*species). The month*mulch treatment was also significant, but less so ($p < 0.034$). Mulch and the interaction between mulch and species were nonsignificant. Mean separation between species using an adjusted Tukey's test places the species in three groups. Figure 4-3 indicates significant differences between species height over the length of the experiment.

All three continuous covariates (rain, rain-lag, canopy closure) had a significant ($p < 0.0001$) effect on seedling height (Table 4-3). Predicted values of LSmeans of log-height were calculated for each species and plotted against the range of rainfall values observed during the experiment. As expected, rain and rain-lag both had positive effects on height. The canopy closure effect was negative and also highly significant ($p<0.0001$) on height when adjusted for rainfall. Canopy effect varied by species, but was negative for three species and had no effect on *S. conocarpum*.

Discussion

As other island in the Lesser Antilles follow similar economic patterns that lead to Forest Transition the patterns of secondary forest succession in St. Croix are likely to be repeated. Puerto Rico, St. Croix's larger and more populace neighbor, has undergone a dramatic transformation from an agricultural-based economy with as little at 6% forest cover in 1940, to an urban industrial economy with over 40% forest cover today (Birdsey & Weaver, 1987; Helmer et al., 2002; Grau et al., 2003). This land cover change resulted from a combination of Puerto Rico's unique relationship with the United States and internal policies that lead to rapid reforestation (Koop & Tole, 1997), although reforestation was not a stated policy goal and the reforestation was unmanaged (Martinuzzi et al., 2007). St. Croix shares a similar economic relationship with the United States that has contributed to rapid post-agricultural changes including industrialization and subsequent increases in tourism, land values, GDP, and secondary forest cover. How the process has differed on the smaller island has not yet been studied, but preliminary work indicates that secondary forests are the most important cover type in St. Croix, but that the island has a larger percentage of land in fluctuation than Puerto Rico. That is, land is still being cleared in some places while secondary forests regenerate in others.

The fruit seed and shade house germination data here is similar to findings in previous work with *G. officinale* (Daley & Zimmerman, 2008). Seeds for this same species germinated at a rate of 5-15% when planted directly in the field in an experiment in St. John, U.S. Virgin Islands (Ray & Brown, 1995b). This may be the first published seed data on *C. ricksekeri* and *S. conocarpum*. . Greenhouse germination rates were high for all species except for *S. polyphylla*. Average *S. polyphylla* seed weight is similar to that reported for Puerto Rico though the germination rate is approximately half (Francis, 1993). No seeds from any species showed any sign of dormancy.

Availability of soil moisture is well known to affect the survival rate of seedlings. While I did not measure soil moisture directly, mulched plants had significantly higher survival than non-mulched plants, and I recommend using any type of mulch possible. The disadvantage, of course, is the increased labor, but there are several benefits including; reduced competition with weeds, improved soil moisture and ease in identifying planted areas in the field.

The dry season began earlier than expected the winter the seedlings were planted. There were two small rain events after planting followed by four months of drought (Figure 4-2). I anticipated a higher mortality rate than observed due to drought, but attribute the success to selecting highly drought-tolerant native plants. I recommend establishing field plants in October in the Virgin Islands to minimize the risk. Shade was not a significant factor on seedling survival in this study.

Rainfall is often the single greatest factor in determining survival and growth in dry forest seedlings. Although growth rates varied significantly between species, the importance of rainfall did not. Predicted values for all four species had the same slope across rainfall gradients for both rain and rain-lag variables. Mulch effect was significant on height, but only temporarily as the mulch broke down over the course of the experiment.

Droughts (Dec-April and May-Aug) were the periods of lowest average height increase and highest mortality. The mulch treatment likely alleviated some of this stress through reduced competition from weeds and from increased soil moisture. Supplemental watering would be impractical in establishing field plants and survivorship in this project was high enough to conclude it unnecessary.

Shade can also significantly affect the survival and growth range of planted seedlings, but shade does not affect species equally (Augspurger, 1984; Hooper et al., 2002). Field studies in the Caribbean have concluded that planting seedlings is the most effective method of establishing plants and that varying amounts of shade have increased growth and survival relative to full sun (Ray & Brown, 1995b; McLaren & McDonald, 2003). In this study the artificially created gaps created varying degrees of heavy shade with canopy closure values for gaps ranging from 55 – 98%. Since canopy closure had a negative effect of growth, it is possible that larger gaps may create conditions suitable for more sun-demanding species. A disadvantage to the gap method is that the canopy thins during the dry season and exposes the seedlings to increased sun when they are the driest. During periods of high rainfall when the seedlings have moisture available, gaps tend to close due to growth of the surrounding canopy.

Four rare endemic species that would not likely have established on their own were selected for planting. Two of the planted species were multi-stemmed shrubs or small trees (*S. polyphylla* and *S. conocarpum*) and two were upright trees (*C. rickseckeri* and *G. officinale*). The two shrubby trees were the best performers as measured by change in height. This measure is a conservative indicator of their relative productivity compared to the single-stemmed species because these plants were multi-stemmed and grew in a spreading V-shaped canopy. Both *S. polyphylla* and *S. conocarpum* rapidly filled the space created by the gap. *G. officinale* also has a somewhat spreading canopy architecture, though less so. This species achieved the lowest overall height, but plants appeared in very good health and grew consistently in rain, drought and shade. Individuals of this dense hardwood species are known to live for hundreds of years (Little & Wadsworth, 1964) and begin producing flowers after one year and viable seeds after two years (Daley & Zimmerman, 2004).

The most surprising result for the height variable was the performance of *C. rickseckeri*. This species was selected primarily due to its rapid height increase in a preliminary study. In a full-sun, regularly mowed planting, 50 cm *C. rickseckeri* saplings grew to an average of over 400 cm in a 30 month period without any supplemental watering (Daley and Zimmerman, 2004). That same growth rate would have resulted in a 200 cm average height increase by the end of this study instead of the average height of 20 cm average increase recorded here. The species has not previously been described as a pioneer, but appears to require full sun for its characteristic rapid growth.

Conclusion

Disclimax forests experiencing stalled or arrested succession require intervention to restart the natural regeneration process. The secondary forest used in this project was typical of old-field succession in St. Croix, U.S. Virgin Islands. Fifty four years after agricultural abandonment the canopy remained dominated by three pioneer species (*L. leucocephala*, *A. macracantha* and *C. alba*).

The seasonally dry secondary forest presented multiple barriers to native seedling establishment and the goal of the project was to test a method of establishing rare native plants under these conditions. This project successfully established four endemic species in artificial gaps in a disclimax forest dominated by exotic species. Seedlings were established in the wet season and required no supplemental water. Seedling survivorship was improved 15% by using hay mulch.

Table 4-1. Botanical and common names of the 4 native tree species grown for this study and a brief description.

Family, Genus species (common)	Description
Boraginacaea *Cordia rickseckeri* Millsp. (orange manjack)	Fast growing pioneer species with animal dispersed seeds and an upright, single-stemmed habit to 12-15 m tall. Highly drought tolerant and endemic to the dry forest of Puerto Rico and St. Croix.
Zygophyllacaea G*uaiacum officinale* Linn. (lignum vitae)	Relatively slow growing, long-lived, hard wood tree with animal dispersed seeds and an upright but spreading habit. It is highly drought tolerant and grows well in both the understory and full sun. This plant appears on the U.S. Virgin Islands Endangered Species List
Fabacaea *Senna polyphylla* Jacq. (desert cassia)	Medium growth rate, shade-intolerant, multi-stemmed shrub or small tree (3 m) has small seeds reported to be dispersed by cattle. Native to lowland dry forest of Hispaniola, Puerto Rico and the Virgin Islands, it is both salt and drought tolerant.
Solanacaea *Solanum conocarpum* Dunal (purple maron bacuba)	Medium growth rate, multi-stemmed bush or small tree (3 m), seeds are likely animal dispersed. Known only in the U.S. Virgin Islands, only 200 plants are believed to remain in the wild. The petition for U.S. endangered species status was rejected in 2006 due to lack of information. Little is known about the ecology of the species.

Table 4-2. Fruit and seed data summary for four native species. Standard error of the means is provided. Seed germination treatments tested were; 24 hour water soak, 1 hr soak in 2,000 ppm Gibarellic acid (Ga_3), hot water and control.

	Cordia rickseckeri	*Guaiacum officinale*	*Senna polyphylla*	*Solanum conocarpum*
Fruit weight (g)	5.19 ± 0.49	0.72 ± 0.054	0.275 ± .028	12.02 ± 2.4
Fruit/kg	193 ± 18	1,389 ± 104	3,672 ± 418	86 ± 7
Seed/fruit	1.00 ± 0.01	1.68 ± 0.49	12.93 ± 4	81.3 ± 10.7
Seed weight (g)	1.89 ± 0.20	0.31 ± 0.03	.049 ± .004	.0496 ± .007
Seed/kg	530 ± 60	3,219 ± 251	22,350 ± 1,960	20,550 ± 2,950
Germination begins (days)	15	15	18	8
Germination ends (days)	30	45	40	18
Most effective treatment	Water	Ga_3	Control	Control
Germination rate	140%*	71%	27%	95%

[* Multiple embryos are contained in a single stone for this species. Germination rate is given as the number of seedlings per stone.]

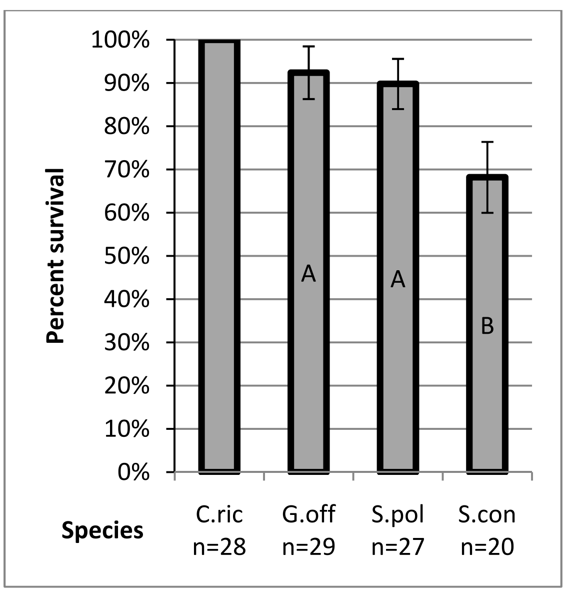
Table 4-3. Results from PROCMIXED analysis of fixed effects on plant height over time indicate significant differences between species. Results also indicate the effect of the mulch treatment and the interaction had no significant effect on height. Month and the interactions with month indicate that height increases were not constant over time. The effects of the three covariates (rain, rain_lag and canopy closure) were highly significant.

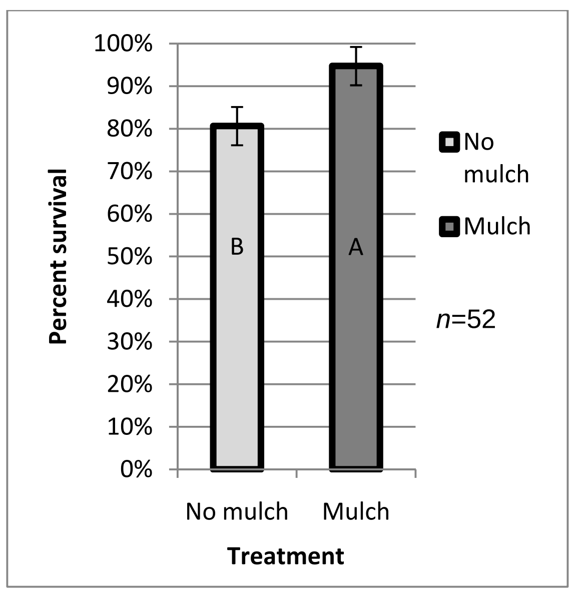
Effect	Num DF	Den DF	F -Value	Pr > F
Species	3	193	5.54	0.0011
mulch	1	32.3	0.46	0.503
mulch*species	3	157	2.54	0.0583
month	1	244	262.64	<.0001
month*species	3	231	8.28	<.0001
month*mulch	1	233	4.55	0.034
rain	1	706	156.44	<.0001
rain_lag	1	919	299.07	<.0001
canopy	1	691	340.37	<.0001


A

B

Figure 4-1. Field data collection at the planting site. A) 3m by 100m transect is cut in a dense, low secondary forest. B) student research assistant collects seedling height data in an artificial gap



A


B

Figure 4-2. east Square Means of percent survival after 18 months for four tree species and for mulched and unmulched plants A) mean survivorship by species appears on the left and B) averages by mulch treatment are on the right. Error is expressed as SE. Significant differences are noted with different letters.

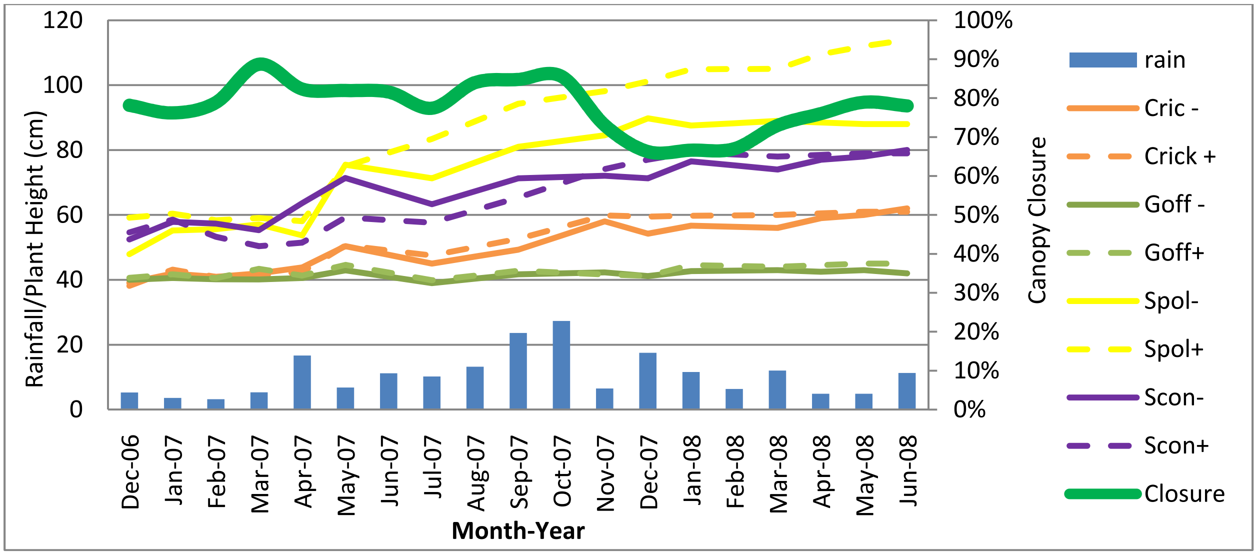


Figure 4-3. Growth patterns of four trees species plotted along with monthly rainfall (cm). Canopy closure is plotted on a separate Y-axis on the right. Species averages for the mulch treatment (+) are shown with dashed lines and averages for no-mulch treatment (-) have solid lines.

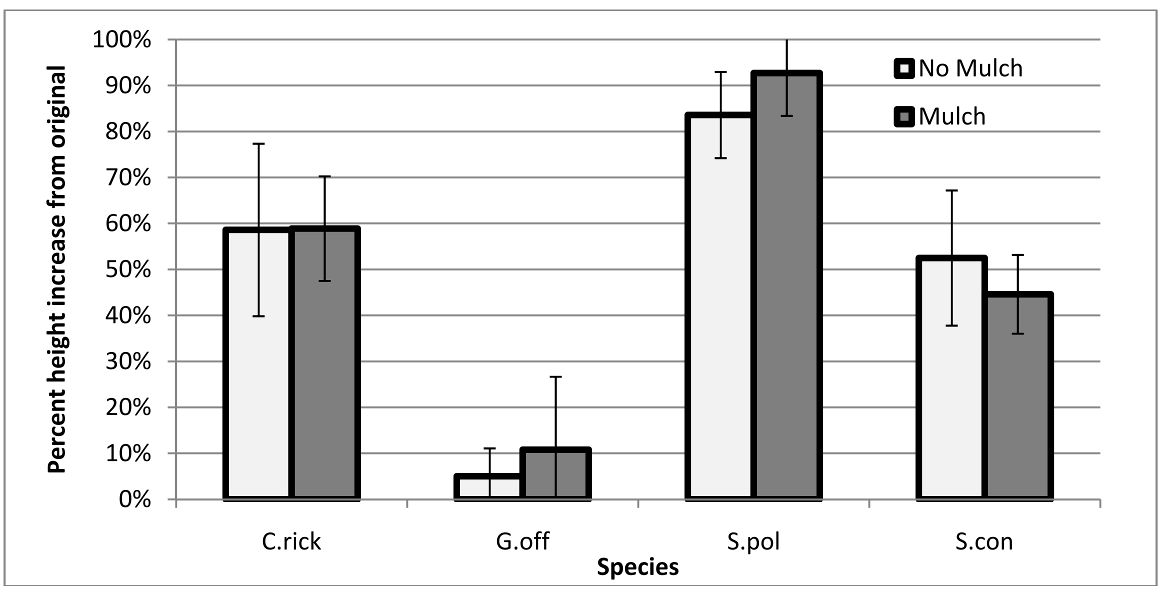


Figure 4-4. Final heights by species after 18 months, with and without mulch treatment, expressed as a percentage of original height. Error terms are SE.

CHAPTER 5
CONCLUSION

The results of this research provide the reader with detailed, spatially explicit descriptions of land-cover distribution on St. Croix for two distinct points in time (1992, 2002). A second study resulted in species-specific descriptions of the composition and structure of secondary forests of St. Croix with a focus on the influence of exotic invasive plants in succession. A final study tested rehabilitation methods for forests experiencing arrested succession through the introduction of rare native tree species. Together the projects identify landscape level trends, describe stand level problems with the succession process in highly impacted sites on the island and test methods or addressing the problem by stimulating succession. St. Croix is used a model system to describe Forest Transition problems on small Caribbean island such as those in the Lesser Antilles. I project that the forest transition problems currently being experienced in St. Croix will be repeated as other small islands in the Windward and Leeward chains go through the same economic and social changes.

More specifically the change analysis describes a forest dominated landscape (56%) experiencing a high degree of change. There was no net change in forest area, but there was substantial change within the forest class and a strong trend toward younger secondary forest and increased forest fragmentation. Approximately 1,500 ha of forest were lost, with the majority converted to development and 1,500 ha of forest were gained, the majority coming from regenerating grassland.

The largest transition between classes resulted in over 5% of the island changing from grassland to development during the 10 year time span. The loss of grassland was corroborated by independent non-spatial data collected by the Virgin Islands

Department of Agriculture. These findings indicate St. Croix is still experiencing Forest Transition and economic realities favor increased urbanization at the expense of grassland while net area of forest remained stable. Tax incentives likely exert a strong influence on the process by rewarding low-quality, low-production pasture. Secondary forest growth would likely increase sharply if these agricultural tax incentives were removed or alternative incentives for protection of secondary forests were supported.

I tested the hypothesis that changes in forest cover decrease with increased distance to roads and concluded that forest change area only varies at the greatest distance values. The pattern is not as pronounced as in other studies and occurs over a smaller spatial scale. Also, patches of both forest gain and forest loss are spatially (patch size, location and distribution) similar and are two parts of the same process where small patches of land are irregularly cleared and then left fallow. The process is driven by macroeconomic changes (increasing worker wages, population density and real estate prices) and re-enforced by the property tax exemption for land that is registered as agriculturally productive in name only.

During the entire field data collection process for this study not a single site was found where St. Croix's dry forest was regenerating without the heavy influence of exotic species. The current reality is that, young secondary forests are completely dominated by exotic species, regardless of location, previous land use or any biotic or abiotic factors. After 50 years without disturbance other aggressive exotic plant species are still present, but no longer dominate forest canopies in some sites. Other sites are totally dominated by only two or three invasive exotics and show no signs or successional progression. These results indicate that secondary forests of St. Croix tend to recover species diversity and canopy structure over time. However, multiple sites in this study exhibited strong signs of arrested succession, including undeveloped canopies, low species diversity and dominance by exotic species. An additional confounding factor is that 60-70 yr old secondary forests began regeneration under conditions that did not include island-wide domination of *Leucaena leucocephala* and the this has had on successional pathways cannot be easily determined.

Stand age accounted for only a portion of the variability in species diversity in this study. Land use history can play an important role in the rate of forest recovery, but quantifying severity of previous land-use is challenging, even with detailed information from land owner interviews. Attempts to correlate slope, aspect and elevation to stand age were inconclusive. The secondary forests arising from abandoned agricultural sites on St. Croix are novel ecosystems with unique species compositions where exotic species play a major role even half a century after abandonment. The most likely explanation is the small spatial scale of the island has caused the forests to reach some type cross some threshold of resilience from where they are no longer able to recover unassisted. St Croix is likely on the leading edge of this phenomenon as dozens of small islands in the Lesser Antilles are transitioning out of agricultural and into manufacturing and tourism-based economies that will likely lead to forest transitions under similar circumstance to St Croix.

Secondary forest suffereing arrested succession require intervention to restart the natural regeneration process. The field site in the third experiment in this project was typical of old-field succession in St. Croix, U.S. Virgin Islands. Fifty four years after agricultural abandonment the canopy remained dominated by three pioneer species (*L. leucocephala*, *A. macracantha* and *C. alba*).

The seasonally dry secondary forest presented multiple barriers to native seedling establishment and the goal of the project was to test a method of establishing rare native plants under these conditions. This project successfully established four endemic species in artificial gaps in a disclimax forest dominated by exotic species. Seedlings were established in the wet season and required no supplemental water. Seedling survivorship was improved 15% by using hay mulch. Compared to other methods such as direct seeding or large scale clearing and planting, this gap-planting method offers the opportunity to successfully establish native plants across large areas at relatively low cost. Such a method is required in St. Croix today as an estimated 150 ha of new secondary forests begin regenerating on abandoned agriculture every year.

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BIOGRAPHICAL SKETCH

Brian Daley graduated from St. Johns Preparatory School in Danvers in 1987 and obtained a Bachelor of Science degree in sociology from Salem State College in 1992. He served as a Peace Corps volunteer in Costa Rica from1994-1996 and was awarded a Master of Science in Natural Resource Management from the School of Forestry at the University of Montana in 1999. In that same year he began work at the University of the Virgin Islands, Agriculture Experiment Station as an Agroforestry Research Specialist. Since 2010 he has been a Natural Resources Specialist and Partner at the private firm, Geographic Consulting LLC. Brian Daley was awarded a Doctor of Philosophy from the University of Florida, School of Forest Resources and Conservation in 2010.