Gap dynamic modeling of a subtropical dry forest: effects of hurricanes on forest change and productivity in climate change scenarios

Jennifer Allison Holm
Atlanta, GA

M.S., University of Florida, 2007
B.S., Emory University, 2004

A Dissertation presented to the Graduate Faculty
of the University of Virginia in Candidacy for the Degree of
Doctor of Philosophy

Environmental Sciences Department

University of Virginia
May, 2012

Abstract

Because of human pressures, the need to understand and predict the long-term dynamics and development of subtropical dry forests is urgent. The new gap model ZELIG-TROP was developed, parameterized, and successfully modeled the forest dynamics of the Puerto Rico subtropical dry forest. Along with new forest parameterization, additions to ZELIG-TROP increased the level of detail in gap models by including a new natural disturbance routine and by tracking litterfall, leaf production, coarse woody debris, and carbon components at the individual tree level. This research developed a valuable tool to understand the process of rehabilitating dry tropical forests, understand the unique aspects and predict the future direction of subtropical dry forests. In addition to validating a new model, simulating the succession of secondary forests on abandoned fields was achieved, showing that secondary forests have a delayed response to recover and reach a mature forest status (100+ years).

Realistic hurricane simulations were implemented within the modeled Puerto Rican subtropical dry forest from ZELIG-TROP, for the first time. A major gap in the literature is to compare storm effects on vegetation from storms varying in intensity, duration, and frequency that are forecasted in climate change scenarios. Increasing hurricane intensity of severe storms did not create a large shift in the average aboveground biomass, net primary productivity (NPP), annual litterfall, leaf production, coarse woody debris, or annual autotrophic live carbon accumulation (AALCA) from that of historical hurricane regime (control). During both control and increased hurricane intensity scenarios, AALCA was negative indicating a carbon transfer from the live forest to the surrounding ecosystem. Increasing the frequency of hurricanes had a much stronger effect on forest dynamics. In comparison to the control scenario, increased hurricane frequency decreased the aboveground biomass by 5%-40%, increased NPP by 32%-50%, increased leaf production, decreased litterfall and coarse woody debris, and AALCA became positive indicating a carbon sink into the forest over 600 years. Overall community composition does not substantially change from the control treatment when there is an increase in hurricane intensity or frequency, but species diversity was the highest during all treatments which increased the frequency of hurricanes.

TABLE OF CONTENTS

ACKNOWLEDGMENTS

I gratefully thank my supervisory committee, Dr. Howard Epstein, Dr. Bob Davis, Dr. Gerard Learmonth, Dr. Guy Larocque, and most importantly my committee chair and advisor, Dr. Herman H. Shugart for their time and effort. I owe a large amount of gratitude to Dr. Hank Shugart who picked me up as a graduate student and graciously gave me much assistance, guidance, and support while completing my research. This work was made possible by the Environmental Sciences Department at University of Virginia (Charlottesville, USA) through funding and support, and in part by US National Aeronautics and Space Administration Experimental Project to Stimulate Competitive Research (NASA EPSCoR, Grant No. NNX09AV03A). A special thank you goes to the Environmental Sciences staff/faculty and in particular to Jerry Stenger for providing weather data, Cindy Allen, Pam Hoover, and Dr. Dave Smith.

I would like to give a strong thank you to my collaborators in Puerto Rico, mainly Dr. Skip J. Van Bloem and his wife Stephanie. Dr. Bloem contributed long-term data records from Puerto Rico forest plots, logistical assistance while in Puerto Rico, and valuable time spent editing papers. Acknowledgments also go to Ricardo Santiago, Freddie O. Perez Martinez, and Dr. Jesus Danilo Chinea for their help during field measurements. Additional guidance and support came from Dr. Ariel Lugo, Dr. Peter Murphy, the International Institute of Tropical Forestry for assistance with data, and Dr. Miguel Velez Reyes for guidance while working in Puerto Rico

I am also extremely grateful to my friends and family members who have stood by me through-out my graduate school career. My fellow graduate students have provided long hours of laughter and comfort. I would like to thank Elizabeth Whitman, Dana Oster, Amy Grady, Stacy Lynn, Dr. Jackie Shuman, Dr. Dave Lutz, and Dr. Katie Tully for their help during the completion of this research, and a special thanks to Matt O'Connell for programming assistance. I have been extremely lucky to have a wonderful family and boyfriend who have stood by my side, and have encouraged me immensely along the way. It is my family and friends who I owe a large thank you, and I am honored to have your support and words of wisdom.

LIST OF FIGURES

LIST OF TABLES

LIST OF PICTURES

LIST OF APPENDICES

Chapter 1 Introduction to the Dissertation and Background

1.1 Introduction

Tropical and subtropical forests are vastly important in the terrestrial world. Tropical forests provide functional and structural diversity value which can help manage against environmental uncertainty (Naeem et al. 2009) and increase flow of genetic diversity (Chase et al. 1996). Tropical forests provide economic value in non-destructive forms through resources such as environmental services (Peters et al. 1989, Costanza et al. 1997, Ferraro and Simpson 2002), indigenous knowledge (Begossi et al. 2000), non-timber forest products (Myers 1988, De Beer and McDermott 1989), medical plants (Balick et al. 1996), and economic incentives to maintain and conserve tropical forests for wildlife sanctuaries or eco-tourism (Tobias and Mendelsohn 1991). Tropical forests host many biodiversity hot spots that are biologically rich while at the same time threatened by humans (Cincotta et al. 2000, Myers et al. 2000). Tropical forests can mitigate consequences from climate change through absorbing and sequestering carbon due to fast rate of biological growth (Malhi et al. 2001, Canadell and Raupach 2008).

Out of all the tropical forests, dry forests are routinely overlooked and understudied, yet they make-up the largest percent of tropical land mass (Murphy and Lugo 1986a). Studies have shown that dry forests are under serious treat, with 97% of the world's dry forest at risk of eradication (Miles et al. 2006), but only 5% are in protected areas (Van Bloem et al. 2004). There is a trend of failing-to-notice that these regions cover a large extent such as the Cerrado of Brazil expanding 2.5 million km^2 and the

Miombo woodlands of Africa covering 2.7 million km^2, but much of the Cerrado region is being destroyed and replaced by agriculture (Silva et al. 2006).

Furthermore, dry forests which account for 42% of tropical forest (Murphy and Lugo 1986a) are the most inhabited of all tropical locales (Holdridge 1967, Murphy and Lugo 1986a). Tropical dry forests are highly populated all over the world, but dry forests in North and Central America have one of the highest percent of forest area (63.2%) that are occupied by the high population densities (>2500 individuals in 10 km^2) (Miles et al. 2006). The mild and favorable climate creates a choice habitat location for land use conversion in light of high population growth rates. Dry forests are at risk from climate change, fires, forest fragmentation, conversion to agriculture, and human expansion but threats directly related to human activity cause the highest risk to dry forests (Miles et al. 2006).

Dry forests are subject to rapid and extreme cases of human disturbances (Quesada and Staner 2004, Fajardo et al. 2005, Leal-Pinedo & Linares-Palomino 2005). Fuelwood production, which provides large supplies of energy, is constantly in need. Large scale production and extraction of fuelwood is a common practice in tropical dry forests, reducing the intact forested area. Many crops, cultivation practices, and cattle grazing are more suitable in seasonally dry climates over wetter forests, further exasperating human disturbance (Maass 1995). Overall the opportunity for human disturbance in dry forests, either in the forms of clear cuts, cultivation, pasture, or human-related development is more accessible in dry forests due to ease of cutting smaller trees, ease of access, better soils, and seasonal climates.

In addition to growing human disturbances, dry forests of the Caribbean and Central America are routinely hit by hurricane disturbances. Hurricane effects on the unique forest structure of dry forests need to be further quantified. Dry forests have the potential to be both a carbon sink and carbon source with varying patterns of disturbance. Dry forests do not grow as rapidly as wet forests, with tree diameter at breast height (DBH) growth rates ranging from 0.3 – 4.7 mm/yr, averaging 3 mm/yr (Murphy and Lugo 1986b, Dunphy et al. 2000), and litter production rates range from 1.5 to 12.6 Mg ha^{-1} yr^{-1} (Martinez-Yrizar 1995). Disturbances typically open gaps in the canopy or sections of the forest, which lead to nutrient access and increased light availability; increasing growth rates and litter production rates. Likewise, more frequent recovery from increasing forest disturbance can lead to larger carbon sinks.

Even though it is clear that threats and risks to the forests are imminent, until recently dry forests have been under-represented in scientific studies. In a meta-analysis by Van Bloem (2005), since 1970, dry forests have represented 30% of tropical forest literature, while the remaining 70% have focused on moist, wet, and rain forests. The vast size of dry forests and the high population densities within them are not the only traits that make dry tropical forests unique. Dry forests are also unique due to the fact that these forests change with seasonal droughts and moisture stress, are being highly disturbed by natural and anthropogenic means, and dry forests tend to be a mix of deciduous, semi-deciduous, and evergreen canopies, all which contribute to difficulties in understanding accurate carbon dynamics of these systems. A more thorough explanation of the carbon dynamics with successional changes and disturbances is required.

1.1.1 Field Site Description

The field site for the research composed in this dissertation is located in the subtropical dry forest of Puerto Rico. Puerto Rico is located within the tropics; defined as a region surrounding the equator and limited between the Tropic of Cancer (23° 26' N) and the Tropic of Capricorn (23° 16' S). While Puerto Rico is an island located within the tropics the Holdridge (1967) life zone classification was used for the forests in Puerto Rico, which is defined as subtropical. The work for this project was completed in Guanica State Forest, a mature, semi-deciduous subtropical dry forest which is located on the southwestern portion of the island (17° 58' N, 65° 30' S). Pictures of the field site and forest physiognomy can be found in the appendix (Picture 1.1 – 1.3).

Guanica Forest has similar and common climate to many other dry forest regions through-out the world (Murphy and Lugo 1986a). Dry forests can range from 603 – 1800 mm/yr rainfall (Udaipur, India to Costa Rican dry forests), mean temperature ranges from 19.2 – 27.1 °C (Zaire to Venezuela dry forests), temperature to precipitation ratio[1] ranging from 1.4 – 4.1 (Costa Rica to Udaipur, India) and number of dry months consist of 3 to 6-8 (Sri Lanka to Chamela, Mexico). Guanica Forest on average has 860 mm/yr rainfall, 25.1 °C, temperature to precipitation ratio of 2.9, and 6 dry months through-out the year (Murphy and Lugo 1986a). The average maximum, minimum, and total precipitation (mm) can be seen in Figure 1.1. Two wet seasons occur; the first from April

---

[1] Temperature to precipitation ratio = (mean annual temperature (T), C° / mean annual precipitation (P), mm) x 100. The T/P ratio is used in forest ecology as a descriptor to help classify forest types, and determine dry forests vs. wet forests. Preferably the ratio of potential evapotranspiration (PET) to precipitation (P) is a more accurate classification for dry forests (if PET/P exceeds unity, then study site is a dry forest), but data necessary to calculate PET/P ratios are unknown. Therefore T/P ratios are used.

to May and the main wet season from August to November corresponding with the hurricane season. Average high and low monthly temperatures (°C) from a nearby weather station in Ensenada, Puerto Rico can be seen in Figure 1.2.

Guanica Forest has a unique physiognomy with short, thin trees that are shrubby in form and have a high tendency to sprout. Despite the fact that the climate in Puerto Rico is comparable to other dry forests (except for the annual precipitation being on the low end); the high stem density is extreme. Many stems (>40 %) are multi-stemmed causing the forest to be highly dense (Murphy and Lugo 1986a, Van Bloem et al. 2003). In general, stem densities are higher in the Caribbean forests, but the high density seen in Guanica, Puerto Rico is among the highest (>10,000 stems ha^{-1}, and sometimes reaching 12,000 stems ha^{-1}).

The species composition and community assemblage has been studied in detail by Little and Wadsworth (1964) and Murphy and Lugo (1986b) over the years (Farnsworth 1993, Gentry 1995, Van Bloem et al. 2007 to name a few). Three major plant associations, that are not distinct in boundaries, are found in the mature forested section of Guanica. They are scrub forests occurring mostly on heavy limestone beds, deciduous forests, and semi-evergreen forests. Outside the area comprised as solely forest there are 3 other plant community associations in Guanica: mangrove swamps, salt flats, and beach associations. Research for this dissertation only focused on the 3 non-mangrove tree dominated plant associations. Thirty-seven species have been found in Guanica Forest, with the dominant species changing over time but usually found to be *Gymnanthes lucida*

(Murphy and Lugo 1986b, Van Bloem 2005). However, 169 tree species are known to occur in the three plant associations located in Guanica (Little and Wadsworth 1964).

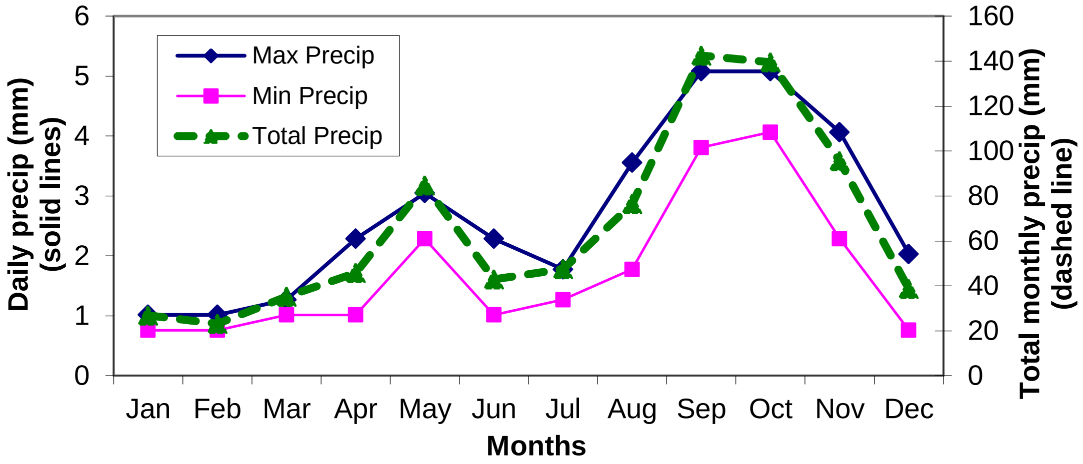


Figure 1.1. Daily (mm) and total monthly precipitation values (mm) for Ensenada, PR weather station (close to Guanica) reported for each month. Solid lines are maximum and minimum precipitation events that occurred in one day during each month. Dashed line is average total precipitation for each month.

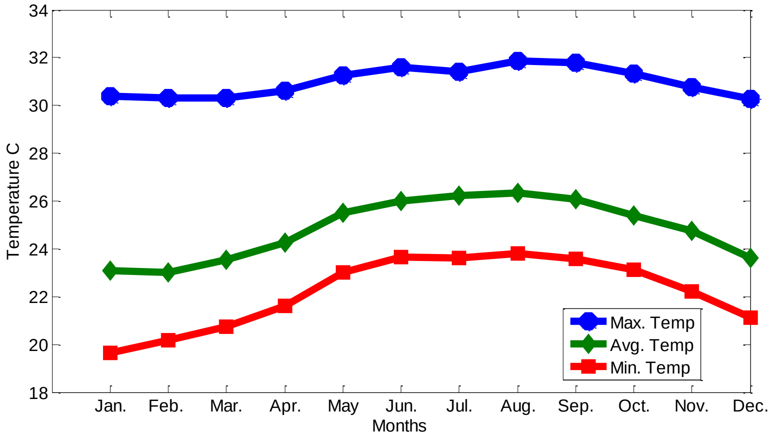


Figure 1.2. Average temperature (°C) for Ensenada, PR weather station (close to Guanica) reported for each month. Average high and low temperatures and record maximum and minimum temperature during each month.

1.1.2 Guanica Forest History

Guanica Forest was originally protected by the U.S. Government in 1917, with further areas set under protection in the 1930's and 2000 by Puerto Rico's Department of Natural Resources and the U.S. Forest Service. The study site for this dissertation now covers 4500 ha of intact forest in southwestern Puerto Rico (Figure 1.3). Prior to the 1930's expansion of protection the previous land use on those areas were maize and goat production, as well as a small settlement of houses, gardens, and a baseball field (Molina Colon and Lugo 2006). Also prior to 1930 there were extensive forested areas that were selectively cut for charcoal production, and limited amount of charcoal production still occurred until the 1970's (Lugo and Scatena. 1996, Molina Colon 1998). The abandonment of a small village, small agriculture, and charcoal production in 1930 leads to a unique opportunity to study long term of forest succession. It was found that regrowth on abandoned land, which was used for human growth, had lower stem densities, less multiple-stemmed trees, and more exotic species (Molina Colon 1998).

Outside of the protected Guanica State Forest much of the land has historically been used for agriculture, grazing, and city/residential development. Economic incentives to use the land for human needs generated widespread deforestation. Around the 1940-1950's due to deforestation only 5% of intact forest remained on the island (Dietz 1986, Birdsey and Weaver 1987). Deforestation can have very negative consequences in drier tropical locations which typically have low resistance to disturbance (compared to wetter tropical areas). Deforestation of dry forests in Puerto Rico can lead to reduced biodiversity, degraded soils, and alter the regional hydrological cycle by creating a cycle more vulnerable to fluctuations (Lugo et al. 1981). But there has been a recent trend of abandonment of old fields, due to the switch to manufacturing and industry. Thus many old agricultural and grazing lands are being reclaimed as secondary forests, and large recovery is taking place. Depending on the previous land use, i.e. agriculture, pasture, plantation, or residential will result in different secondary forest regeneration (Rivera and Aide 1998).

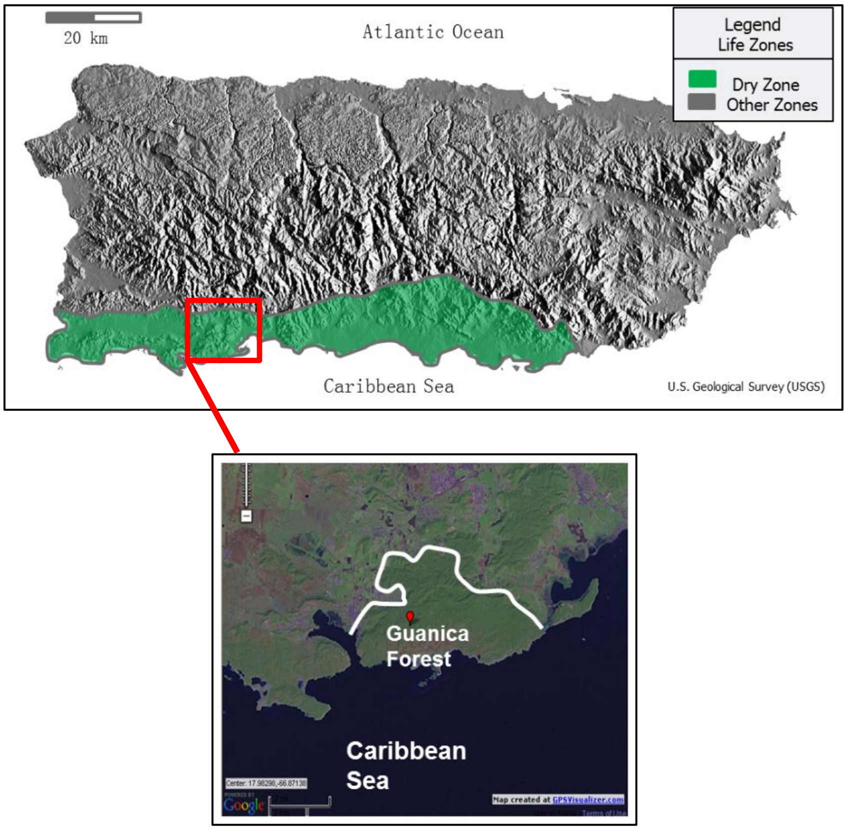


Figure 1.3. Map of Puerto Rico (provided by the U.S. Geological Survey), indicating the dry forest zone and the field site, Guanica State Forest, located on the southwestern portion of Puerto Rico (image provided by Google Earth).

1.1.3 Field Data Collection

Long-term forest-ecology data, and over large spatial areas, were needed to complete the research needed for this dissertation. Out of the 37 tree species present in Guanica, this research limited the species specific data collection to the top 18 most common species, due to higher availability of data on these species. A combination of gathering data from past field studies was used, as well as collecting my own species data from Puerto Rico. The majority of the data were used to parameterize an individual based gap model (discussed in proceeding chapter), while the remaining data were used to validate the model, or as a baseline for comparison to model outputs. Field data was also used to gain an overall understanding of forest and environmental dynamics in the subtropical dry forest of Puerto Rico.

Permanent plots with tagged individual trees have been set up in Guanica Forest since 1981 and have been repeatedly measured almost annually from 1981 until present (Lugo and Murphy 1986, Murphy and Lugo 1986b). The main measurements that were obtained from these repeated censuses were abundance of stems per species and average size in diameter at breast height (DBH, cm), thus being able to track mortality, regeneration, and growth rates (Murphy and Lugo 1986b, Van Bloem 2003, 2005, 2007). Literature searches provided details on the successional status, seedling and germination traits, general crown shape, leaf traits, and tolerances to stress (sources discussed in later sections). A field campaign was conducted in Guanica Forest to “fill in” gaps in the literature data for the data needed to complete this dissertation.

Detailed tree and crown characteristics, which are important for model parameterization and validation, for each of the 18 common species, can be found in this section. After collecting data from the field in 2010, specific leaf area (SLA: ratio of leaf area to dry weight, cm^2 g^{-1}) was calculated from repeated measurements of measuring leaf area (cm^2) on graph paper, divided by dry leaf weight (mg) (Table 1.1). SLA ranged from 0.03 to 0.12, with an average of 0.06 cm^2 g^{-1}. The pioneer species, *Bursera simaruba,* had the highest SLA: 0.12 (possibly due to its realtively low dry leaf weight). As average canopy coverage increased, SLA slightly decreased, but not showing a strong trend. Average canopy coverage was the percentage of leaves present in the canopy of an individual tree (estimated at 0%, 25%, 50%, 75%, or 100% at the time period of viewing), averaged from ~50 trees per species, over 10 years. Average canopy coverage (%), successional status (pioneer, intermediate, or late), leaf trait (evergreen vs. deciduous), and wood density (g cm^{-3}) for each species can be found in Table 1.1 and 1.2 (Little and Wadsworth 1964, Molina Colon 1998, Santiago-Garcia et al. 2008).

The field research conducted here added additional data to the existing knowledge on these Puerto Rican tropical tree species, and also confirmed similar results. For example, leaf area index (LAI) for Guanica Forest from earlier records, as well as results from this research showed that LAI had seasonal and species variation (Figure 1.4). Changes to LAI provided insight into changing patterns of forest functioning. Leaf area accounts for a large amount of carbon gained during the year. Forested systems with high LAI generally have high carbon gain and productivity.

Leaf area index is generally low in dry forests (1.6 to 3.4) compared to wet tropical systems (5 to 8) (Murphy and Lugo 1986a). In Guanica Forest there was an increase in LAI during the wet season, a time when there was adequate water to support larger leaf area (Figure 1.4). In the LAI estimate from Lugo et al. (1978) and Murphy and Lugo (1986b) all species present in the 1.4 ha permanent plot in Guanica Forest were included. During the 2010 field season LAI was reported from two groups; one group including all species recorded in the permanent plot and another group including the smaller subset of common species used in the model (Figure 1.4). Out of the common species *Pisonia albida, Krugiodendron ferreum*, and *Coccoloba diversifolia* had the highest LAI values (Figure 1.5 and Table 1.3). These species were seen in high frequency in the forest, with the exception of *Krugiodendron ferreum*. Alternatively, another abundant species, *Exostema caribaeum,* was seen to have smaller LAI values. Compared to wetter tropical sites, Guanica Forest mainly consists of tree species with smaller LAI, due to the lack of annual rainfall (~860-900 mm/yr).

Another important tree characteristic to measure for the purpose of this research was variations in species-specific photosynthesis. Photosynthesis, and likewise carbon gain, is related to leaf area. Net photosynthesis for each species has been calculated from field measurements during the dry season of 2010 (Appendix 1.1, 1.2). Measurements rate of photosynthesis (μmol CO_2 m^{-2} s^{-1}), as well as stomatal conductance (g_s) and transpiration (mol), were collected using a LICOR-6400 gas exchange system (Lincoln, NE, USA) during January and February of 2010. To determine these variables, carbon dioxide and water vapor inside a reference chamber and sample chamber were measured using the closed-path infrared gas analyzers of the LICOR. Measurements were taken from living leaves, at the top of the canopy in full sun (unless there was a little shading from clouds at the sampling period) for a period of 3 minutes per leaf. Measurements were auto-logged every 10 seconds with a matching of the closed-path infrared gas analyzers every 1 minute. If needed, supplemental photosynthesis data on Puerto Rico dry forest species can also be used from Lerdau and Keller (1997). The tree species with the highest average LAI (*Pisonia albida)* was also recorded with the highest average photosynthesis (Appendix 1.1), and ability to utilize carbon dioxide from the atmosphere.

Table 1.1. Canopy and leaf measurements for 18 common tree species found in Guanica Forest. Canopy coverage (%) averaged from field data over 10 years; average leaf area (cm^2) and average dry weights (mg) taken from individual leaves in 2010.

Species	Avg. Canopy Coverage (%) [§]	Avg. Leaf Area (cm^2)	Avg. Leaf Dry Weight (mg)	Specific Leaf Area (cm^2/g)
Amyris elemifera	91.85	6.63	0.14	0.05
Bourreria succulent	80.54	7.62	0.2	0.04
Bucida bucerus	77.5	7.38	0.1	0.07
Bursera simaruba	61.57	7.05	0.06	0.12
Cassine xylocarpa	90	2.54	0.07	0.04
Coccoloba diversifolia	75	20.54	0.34	0.06
Coccoloba microstachya	66.5	7.2	0.13	0.06
Crossopetalum rhacoma	67.31	7.354	0.16	0.05
Erithalis fruticosa	87.5	11.94	0.34	0.04
Erithroxylon rotundifolium	89.06	0.72	0.01	0.07
Eugenia foetida	76.84	1.22	0.04	0.03
Exostema caribaeum	70.51	3.97	0.08	0.05
Guettarda krugii	77.94	12.99	0.21	0.06
Gymnanthes lucida	93.67	5.95	0.14	0.04
Jacquinia berteroi	95	1.77	0.04	0.04
Krugiodendron ferreum	97.92	4.79	0.05	0.10
Pictetia aculeate	53.11	16.38	0.26	0.06
Pisonia albida	87.5	11.2	0.13	0.09

[§] Van Bloem Tree Growth Data 1998-2009 (unpublished)

Table 1.2. Successional status, leaf trait, and average wood density for 18 common species in Guanica Forest.

Species	Successional Status*,+	Leaf Trait±	Wood Density (g/cm^3)*
Amyris elemifera	Mature	Evergreen	1.10
Bourreria succulent	Pioneer	Evergreen	1.48
Bucida bucerus	Mature	Both	0.93
Bursera simaruba	Pioneer	Deciduous	0.32
Cassine xylocarpa	Mature	Evergreen	NA
Coccoloba diversifolia	Mature	Evergreen	0.80
Coccoloba microstachya	Mature	Both	0.66
Crossopetalum rhacoma	Mature	Both	NA
Erithalis fruticosa	Unknown	Evergreen	NA
Erithroxylon rotundifolium	Mature	Deciduous	0.97
Eugenia foetida	Mature	Evergreen	0.65
Exostema caribaeum	Pioneer	Evergreen	1.00
Guettarda krugii	Mature	Evergreen	0.79
Gymnanthes lucida	Mature	Evergreen	1.10
Jacquinia berteroi	Unknown	Evergreen	NA
Krugiodendron ferreum	Mature	Evergreen	1.4
Pictetia aculeate	Pioneer	Deciduous	0.8
Pisonia albida	Pioneer	Deciduous	0.42

* Molina Colon (1998)
\+ Santiago-Garcia et al. (2008)
± Little and Wadsworth (1964)

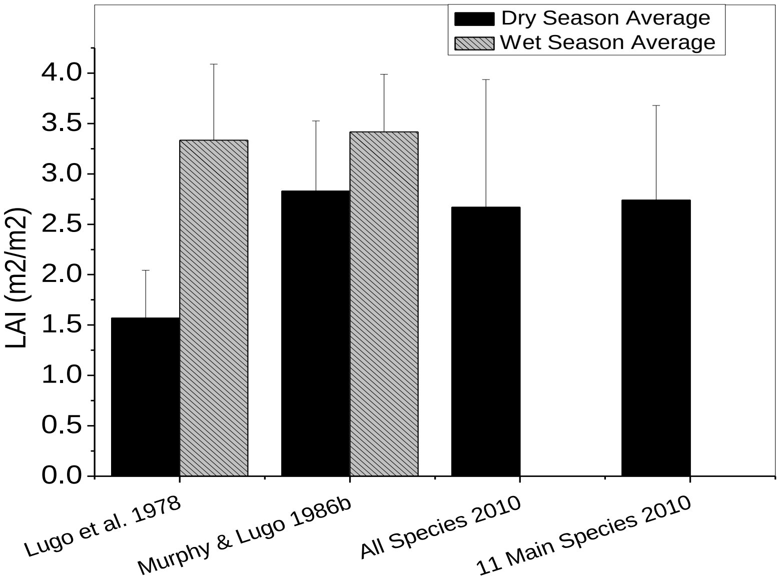


Figure 1.4. Seasonal difference in LAI; dry season and wet season, for Guanica Forest. Data taken from 3 different sources.

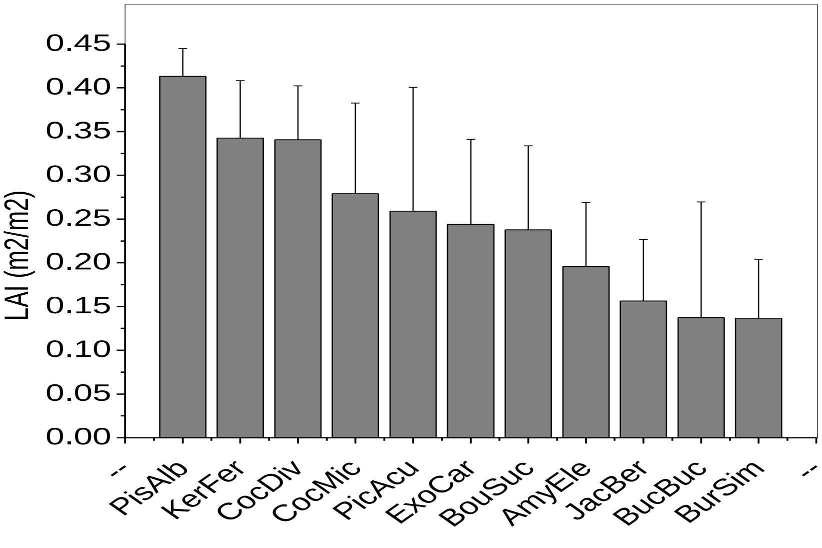


Figure 1.5. Average LAI per species. Data only collected for 11 out of the 18 common species, using a LICOR 2000.

1.1.4 Background and Introduction to Hurricane Disturbances

Reoccurring disturbances, such as hurricanes, can change the level of forest productivity in otherwise productive tropical forests. Tropical forests typically have a longer growing season than other forests thus potentially accumulating more carbon. Carbon accumulation and balance in carbon cycling is critical for primary production and ecosystem processes. Furthermore, carbon entering the ecosystem is essential for vegetation growth, and ultimately the energy that sustains all organisms. Quantifying the changes to carbon flux and storage is critical to understanding the productivity of the terrestrial world.

In tropical ecosystems most of the carbon is stored in the aboveground components. The belowground storage is low (especially compared to tundra and boreal systems), partially (but not only) due to high levels of leaching and fast decomposition rates. Since the majority of carbon is aboveground, the changes in outgoing fluxes from land use/land cover change, harvesting, deforestation, or disturbance could have a strong effect on depleting the carbon in the ecosystem. Disturbance is a critical flux in the tropics and can also remove much of the above ground vegetation.

A doubling of destructiveness and intensity of storms in the Atlantic Basin over the past 30 years has been reported (Emanuel 2005, Webster 2005) as well as projected by the end of the 21st century by Bender et al. (2010). While there are multi-decadal fluctuations over time, Goldenberg et al. (2001) reported a 2.5 fold increase in overall activity of storms in the Atlantic and fivefold increase in the Caribbean over a 6 year period from 1995-2000, and that this high level of hurricane activity could continue for

10-40 years. Terrestrial forest studies which have incorporated hurricane simulations tend to follow these storm predictions. For example a study which simulated the effects of various hurricane treatments on soil organic matter and forest production in the wet forest of Puerto Rico, choose to model a scenario which increased all storms over the simulation period to a higher level (category 4) and disregarded weaker storms (Sanford et al. 1991).

1.2 Model Background

In this dissertation research a forest gap model was used to help answer my research questions. Forest gap models are computer simulations that simulate the forest dynamics by tracking the fate of each individual tree over its lifetime. Therefore the gap model used here is a type of individual based model. Individual based models are powerful because they reject some old assumptions that would limit the power of model prediction. These old assumptions that were typically upheld in early ecological models are 1) that the individuals are assumed to be identical and the unique features are unimportant, and 2) that are no local interactions and the population is perfectly mixed so that local interactions do not occur (Shugart 2002). It is recognized that both of these assumptions are false in real-world settings and long-lived individual trees are very different from each other, landscapes are heterogeneous, and local environmental variations can lead to highly irregular populations.

Forest gap models operate by simultaneously incorporating tree operations such as birth of individual trees, growth of tree components, competition among individuals, mortality, and regeneration on small patches in a highly detailed manner. Gap models also integrate environmental and climate conditions common to the area and location being modeled. With the inclusion of environmental variables the response of individual trees to prevailing environmental conditions, and allowing individual trees to modify these existing environmental conditions is allowed. The death of a large, dominant tree will allow for light to reach suppressed individuals and potential new growth and regeneration (thus coining the title gap models). Detailed equations and descriptions of how trees are modeled, interact, compete for light, nutrients, and moisture, die over time, and other model factors are described in the appendix of this chapter. In this research the gap model ZELIG (Urban 1990) and subsequent newer descendants (Urban et al. 1991, until Larocque et al. 2011) was modified, parameterized, and built-on to model the dry forest ecosystem in Puerto Rico.

The original forest gap models (Botkin 1972, Shugart and West 1977, Shugart 1984) were complex in nature, making them applicable to assess large scale complex systems for forest ecosystems. Each descendant of the original forest gap models is becoming more complex and detailed (as done in this dissertation), making each one more powerful. Gap models have been applied to a diverse set of applications, making them capable of addressing a plethora of ecosystem questions. For example, gap models have been used to address climate change effects in boreal forests using predictions from general circulation models (Bonan et al. 1990, Smith et al. 1995, Shuman and Shugart 2009). The full span of gap models that have addressed climate change issues cannot be covered here, but the applicable use of these models for predicting forest dynamics and forest growth in reponse to climate and environmental change is strong and well tested (Prentice et al. 1993, Dale and Rauscher 1994, Smith et al. 1995, Shugart 1998).

The majority of gap models have been applied to temperate and boreal forests (100+), and only a few have been applied to tropical forests (Shugart et al. 1980, Van Daalen and Shugart 1989, Huth et al. 1998, Kohler and Huth 1998), and a couple specifically in Puerto Rico (Doyle 1981, O’Brien et al. 1992). The transition to modeling tropical forests has been limited due to the high diversity, complexity, and limited long term datasets from tropical locations. Tropical forests can contain hundreds of tree species in limited space and have contrasting climates compared to temperate and boreal systems, (where gap models have historically been applied) thus requiring new species, site, and environmental parameterization. This dissertation answers the needed demand for predicting the future of tropical forests in response to climate change and increasing disturbances in tropical locales.

1.3 Dissertation Objectives and Questions

This research re-created the observed forest succession for a Puerto Rican subtropical dry forest using an individual based modeling approach, which entailed developing a new gap model, ZELIG-TROP. After model creation and parameterization the new gap model was validated by reporting the forest dynamics and successional changes of species over time and tested against observed mature forest preserved in the Puerto Rico region. After model validation, ZELIG-TROP measured the response of individual trees and species to multiple hurricane disturbances (both increased and decreased levels of hurricane disturbances) in predicted climate change scenarios. This project played a critical role in estimating long-term carbon dynamics and emissions from tropical forests undergoing natural disturbances in climate change predictions. Forest response to simulated changing environmental conditions, and monitoring the recovery of secondary forests from abandoned fields was tested. These results can help predict future states of tropical forests and will aid in many useful applications, such as developing new forest management approaches or developing predictions of forests response to climate change.

1.3.1 Overall Project Questions

1) Can the subtropical dry forest with its unique physiognomy be simulated in an individual-based, gap model approach and validated against real-world data?

2) What is the future forest successional pattern for the current subtropical dry forest in Puerto Rico?

3) What is the recovery pattern of secondary forests on abandoned fields with decreased soil moisture in Puerto Rico?

4) How does carbon cycling change in response to various hurricane disturbances in climate change scenarios?

5) How does aboveground biomass, net primary productivity, coarse woody debris, annual litterfall, and annual leaf production change in response to various hurricane disturbances in climate change scenarios?

6) How does species diversity for a subtropical dry forest change in response to various hurricane disturbances in climate change scenarios?

1.3.2 Specific Objectives

1) Accurately re-create the observed forest succession for a Puerto Rican subtropical dry forest using an individual based modeling approach.

2) Create the following forest features and demographic traits from a simulation model that are accurate to observed/inventory data.

    a. Stem density, stand basal area, leaf area, stand height, total biomass

3) Predict the recovery of abandoned fields, with decreased soil moisture, at different ages into secondary forests.

4) Generate and implement a new hurricane disturbance routine within the newly modified ZELIG-TROP gap model.

    a. Use historical hurricane return intervals and species specific damage probabilities from field observations.

5) Report the changes to carbon levels (and other forest components) in the subtropical dry forest after increasing and decreasing hurricane intensity and frequency in predicted climate change scenarios.

    a. Report the total forest biomass (Mg ha^{-1}) with various hurricane disturbances.

    b. Report the changes to Net Primary Production (NPP), the net carbon gained by the vegetation (Mg C ha^{-1} yr^{-1}).

    c. Report the changes to annual litterfall and leaf production (g C m^{-2} yr^{-1}).

   d. Report components to the annual autotrophic live carbon accumulation (AALCA) model: leaf production, diameter increment, sprouting, regeneration, coarse woody debris, and litterfall (g C m^{-2} yr^{-1}).

   e. Analyze coarse woody debris to litterfall ratio and relationship.

6) Monitor the level and changes to species composition and diversity with various hurricane regimes.

1.3.3 Composition of Dissertation

The above research questions were addressed and answered in four distinct dissertation chapters. Each of the four chapters was written in journal manuscript style with separate introductions, methods, results, figures and tables, and discussions. Each chapter builds off of the previous chapter, and chapters three, four, and five could not have been possible without the work and results in the second chapter.

Chapter 2. Gap model development, validation, and application to succession of secondary subtropical dry forests in Puerto Rico.

In chapter 2, the new gap model ZELIG-TROP was developed, parameterized, and accurately modeled the forest dynamics of the Puerto Rico subtropical dry forest. The main goal of chapter two was to develop a valuable tool (computer forest model) to understand the critical process of rehabilitating dry tropical forests, address the problem of understanding unique aspects of dry tropical forests, and predict the future direction of subtropical dry forests. As a second goal, this chapter tested the robustness and realism of the new ZELIG-TROP model, by evaluating its effectiveness at simulating the succession of abandoned agriculture fields that are being reclaimed as secondary forests.

Chapter 2 Abstract:

Because of human pressures, the need to understand and predict the long-term dynamics and development of subtropical dry forests is urgent. Through modifications to the ZELIG simulation model, including the development of species- and site-specific parameters and internal modifications to the model, the capability to model and predict forest change within the 4500-ha Guanica State Forest in Puerto Rico can now be accomplished. Published datasets and additional data from the U.S. Forest Service Forest Inventory Analysis were used to parameterize the new gap model, ZELIG-TROP. Data was used from permanent plots (1500m^2) located inside the Guanica State Forest in Puerto Rico to test the model.

The first objective was to accurately re-create the observed forest succession for a Puerto Rican subtropical dry forest using ZELIG-TROP. For this objective, the model testing was successful. Simulated total basal area, species composition, total stem density, and biomass all closely resembled the observed Puerto Rican forest (r: 0.59-0.96). Leaf area index was the variable predicted least accurately (r = 0.59).

The second objective was to test the capability of ZELIG-TROP to predict successional patterns of secondary forests across a gradient of abandoned fields currently being reclaimed as forests. Abandoned fields that are on degraded lands have a delayed response to fully recover and reach a mature forest status during the simulated time

period for this objective, 200 years. The forest recovery trends matched predictions published in other studies; attributes involving early resource acquisition (canopy height, canopy coverage, density) were the fastest to recover, but attributes used for structural development (biomass, basal area) were relatively slow in recovery. Recovery of abandoned fields, especially degraded systems, may take longer time periods, as simulated here. Biomass and basal area, two attributes that tend to increase during later successional stages in some studies, are significantly lower during the first 80-100 years of recovery than in a mature forest, suggesting that the time scale of resilience in subtropical dry forests needs to be partially redefined.

Chapter 3. Simulating varying hurricane disturbances in climate change scenarios: biomass and net primary productivity changes for a subtropical dry forest.

One of the primary goals of this chapter was to develop and implement hurricane simulations that interact with the modeled Puerto Rican subtropical dry forest from ZELIG-TROP. A major gap in the literature is to compare storm effects on vegetation (such as changes in biomass) from different storm occurrences. The time and resources have not been available to compare differences in storm intensity, duration, and frequency. Simulation modeling can achieve this goal. Furthermore, there is a need to understand carbon levels in terms of aboveground forest biomass and net primary productivity (NPP) across longer time scales. This would involve reporting long term ecosystem level changes, and from varying damage levels and frequencies. There is still on-going research and debate about the history, current forecast, and future predictions of hurricanes with respect to human induced climate change. This chapter addressed and estimated the long term changes to aboveground biomass and NPP from natural disturbances, under climate change scenarios.

Chapter 3 Abstract:

Caribbean and Central American tropical forests are subject to varying levels of hurricane disturbances; from large but infrequent storms, to more recurrent and smaller storms. In addition to storm incongruity, climate change can alter the formation, duration, frequency, and intensity of these storms. The question of storm disturbance effects on tropical forests over longer time periods such as decades and centuries is not easily answered through field studies, given the temporal and spatial scales required. Through model based investigations, this chapter assessed the impacts of multiple storms ranging in intensity and event frequency on forest dynamics in Puerto Rico.

The development of a new hurricane damage routine in the previously validated individual-based gap model ZELIG-TROP with a parameterization for site- and species-specific damage was completed. With this model, the long-term forest dynamics in Puerto Rico in response to simulated hurricane disturbances using 800 year simulations was assessed. A base-line case with the historical hurricane regime was developed; and built upon by subsequently adding ten treatments that manipulated the hurricane return time and hurricane intensity (nine treatments increasing intensity, frequency, and both intensity and frequency by 25%, 50%, and 100% and one treatment decreasing by 50%). This chapter reported the treatment-related change in the overall forest structure over time (both basal area and density), the changes in aboveground forest biomass (Mg ha^{-1}), and the net primary production (NPP) or forest productivity (Mg C ha^{-1} yr^{-1}).

Increasing hurricane intensity of severe storms (even up to 100%) did not create a large shift in the aboveground biomass or productivity (NPP) from that of historical hurricane regimes. It did, however, cause large fluctuations between high and low biomass values. Increasing the frequency of hurricanes, (shortening the return intervals) had a stronger effect on forest dynamics. Increased hurricane frequency decreased the aboveground biomass by 5%-40% and increased the NPP by 32%-50% (depending on hurricane treatment). The fluctuations between biomass loss and gain were attenuated relative to the base case. The hurricane treatment that produced a forest with the highest values of biomass and NPP was the scenario which decreased both the hurricane intensity and frequency by 50%.

There was a dynamic relationship between NPP and biomass. In each of the ten treatments net primary productivity always increased above the control values. When biomass was low due to damage, then NPP was high due to recovery (an inverse relationship). With increasing biomass levels, NPP increased (positive linear relationship between biomass and NPP). NPP was lowest during the control setting. Forest pre- and post-damage can be used by many audiences as a tool for programs like REDD (Reducing Emissions from Deforestation and Degradation) for estimating carbon-sequestration expected under natural disturbances. In the long term, carbon emissions from natural disturbances, even under climate change scenarios, will be mitigated due to the capability of this forest system to recover and sequester higher amounts of carbon.

Forest regeneration and stand development after a disturbance produces a level of carbon sequestration that was higher than the loss of carbon during the damage phase.

Chapter 4. Annual carbon production and functionality of a subtropical dry forest after hurricane disturbances.

Quantifying the changes to the flux, storage, and balance of carbon is very important for understanding the productivity of the terrestrial world, and was also a main goal of this section. This chapter estimated the long term carbon emissions from natural disturbances, under climate change scenarios, and the ability for this forest system to recover and sequester higher amounts of carbon.

Chapter 4 Abstract:

Tropical forests can be a large source of carbon to the atmosphere due to land cover change and disturbances, but can also be carbon sinks due to forest recovery and growth. This chapter evaluated how natural disturbances (hurricanes) affect carbon fluxes, carbon storage, and functionality of a subtropical dry forest in Puerto Rico. A simulation model approach has been used to evaluate changes to annual autotrophic live carbon accumulation (AALCA). The previously validated ZELIG-TROP for the Puerto Rican forest, which also successfully simulates hurricane disturbances, was used for the objectives of this study. A base-line disturbance scenario, using the historical hurricane regimes and modeled forest dynamics for 800 years was modeled. Three additional hurricane treatments were implemented: increasing the hurricane intensity by 50%,

increasing hurricane frequency by 50%, and decreasing both hurricane intensity and frequency by 50%. Changes to the following functionality traits were reported: litterfall, leaf production, diameter increment, basal-sprouting, regeneration, woody loss (labeled as coarse woody debris), and annual carbon production, (all in units of g C m^{-2} yr^{-1}).

It was found that annual litterfall, leaf production, and coarse woody debris contribute a large amount to annual autotrophic live carbon accumulation (AALCA). Litterfall was highest when hurricanes are decreased in intensity and frequency by 50%. Leaf production was significantly increased during treatments that increase the frequency of hurricanes and also the decreased hurricane treatment, but leaf production remained low, and near the control levels, when intensity of storms was increased. Coarse woody debris was higher during the control treatment and when hurricane intensity was increased, but lower during increased frequency of storms and decreasing storm treatments. This difference in functional components led to a significant difference in AALCA with each of the hurricane treatments. During control scenarios as well as increased hurricane intensity, AALCA was negative indicating a carbon loss from the aboveground live system, and a carbon source to the ecosystem, during the 600 years of simulation. However during treatments that increased the frequency of storms and decreased the intensity and frequency of storms, AALCA was positive indicating a carbon sink into the forest components over 600 years.

Through the additions to ZELIG-TROP, this report has increased the quantitative and detailed nature of ZELIG-TROP by including new methods to track litterfall, leaf production, and carbon components at the individual tree level, a new addition to gap models. Evaluating long term changes in carbon fluxes, litterfall, CWD, and other forest functioning parameters with various hurricane scenarios is important for initiatives like REDD+ (Reducing Emissions from Deforestation and Degradation). Quantifying the changes to carbon was achieved, an area in REDD+ that needs further research and monitoring.

Chapter 5. Species diversity response to increasing and decreasing hurricane disturbances in Puerto Rico.

Biodiversity in tropical forested ecosystems is very important in order for organisms to adapt to continually changing environmental conditions, maintain vital ecosystem functions, increase gene flow, and provide an array of ecosystem services. Disturbance is also a natural occurrence in tropical locations. The growth of disturbance ecology has been developed over the years, and it is generally accepted that disturbance deters competitive exclusion and is a strong contributor to shaping community structure. Despite this knowledge, the effect of disturbance size (e.g. very large disturbances) and frequency of large disturbances (i.e. increased occurrences) on species diversity in additional forest types (i.e. dry tropical forests) still needs to be further examined. This chapter quantified how long-term increases in hurricane disturbances affect tropical forest diversity, and whether the Intermediate Disturbance Hypothesis holds true.

Chapter 5 Abstract:

Tropical forests are known to have high vascular diversity, due to mechanisms that limit the competitive exclusion principle: such as gap dynamics, niche specializations, seedling survival based on spatial distance from parent, and sharing of pollination/seed dispersers. But high biodiversity in tropical forests is being reduced due to land-use change and increased disturbances. The previously validated ZELIG-TROP individual based gap model for the dry tropical forest in Puerto Rico, and simulated repeated hurricane disturbances for 800 years was used to evaluate long-term changes in species diversity and community composition. It was tested whether the Intermediate Disturbance Hypothesis (IDH) holds true for a subtropical dry forest; a location where disturbance has been known to play a role in shaping community structure.

The historical hurricane regime was set as a base-line disturbance scenario (control) and forest dynamics were modeled for 800 years. Six hurricane treatments of separately increasing hurricane intensity or hurricane frequency by 25%, 50%, and 100% over the historical hurricane regime (control) were modeled. A relative importance value (RIV, %) and Shannon's Diversity Index were used to assess community composition and species diversity. The RIV calculation combines both species dominance (basal area, m^2 ha^{-1}) and species abundance (stem density, stems ha^{-1}).

Overall species diversity and community composition does not substantially change from the control treatment when there is an increase in hurricane intensity or frequency by 25%, 50%, or even 100%, but there are some shifts in individual species RIV. In all seven hurricane treatments *Gymnanthes lucida* and *Coccoloba diversifolia* remained the first and second highest ranked species. The following species were most sensitive to increases in hurricane intensity in terms of changes in RIV from the control: *Bucida bucerus* decreased 24% to 57%, *Bursera simaruba* decreased 31% to 49%, *Coccoloba microstachya* increased 8% to 17%, and *Eugenia foetida* increased 22% and 39%. The following species were most sensitive to increase in hurricane frequency in terms of changes in RIV from the control: *Bursera simaruba* decreased 16% to 34%, *Erythroxylon rotundifolium* decreased 8% to 32%, and *Coccoloba diversifolia* decreased 7% to 24%. The majority of species (12 out of 18) showed an increase in RIV from the control during the three treatments which increased hurricane frequency. This was not observed during scenarios which increased hurricane intensity.

Shifts in community composition in terms of early successional vs. late successional species were weak, but present. During scenarios when hurricane intensity was increased, late successional species were favored and early successional species decreased. A different result was found during scenarios in which hurricane frequency increased. ZELIG-TROP showed a small increase in both late successional species and early successional species. Species diversity was found to be the highest, and greater than the control scenario, during all treatments which increased the frequency of hurricanes, as determined by the Shannon Diversity Index. The treatment which produced the largest Shannon Index (2.54 out of 2.89) was the treatment which increased frequency by 100%, possibly suggesting that the IDH does not necessarily hold true for the dry forests of Puerto Rico and that highest diversity is found at higher occurrences of disturbance.

1.4 Literature Cited

Balick, M. J., E. Elisabetsky, S.A. Laird. Medicinal resources of the tropical forest: biodiversity and its importance to human health (Biology and Resource Management Series). Columbia University Press, New York.

Begossi, A., N. Hanazaki, N. Peroni. 2000. Knowledge and use of biodiversity in Brazilian hot spots. Environment, Development, and Sustainability, 2: 177-193.

Bender, M.A., T.R. Knutson, R.E. Tuleya, J.J. Sirutis, G.A. Vecchi, S.T. Garner, I.A. Held. 2010. Modeled impact of anthropogenic warming on the frequency of intense Atlantic hurricanes. Science. 327: 454.

Birdsey, R. A., and P. L. Weaver. 1982. The forest resources of Puerto Rico. Resource Bull. SO-85. USDA Forest Service, South. For. Exp. Stn, New Orleans, Louisiana.

Bonan, G B, Shugart, H H, and Urban, D L. 1990. The Sensitivity of Some High Latitude Boreal Forests to Climatic Parameters, Clim. Change, 16: 9–31.

Botkin, D. B., J. F. Janak, and J. R. Wallis. 1972. Some Ecological Consequences of a Computer Model of Forest Growth. J. of Ecology. 60, 849-872.

Canadell, J. G. and M. R. Raupach. 2008. Managing forests for climate change mitigation. Science. 320, 1456-1457.

Castilleja, G. 1991. Seed germination and early establishment in a subtropical dry forest. Ph.D. Dissertation. Yale University. 209 pp.

Chase, M.R., C. Moller, R. Kesseli & K. S. Bawa. 1996. Distant gene flow in tropical trees. Nature. 383: 398-399.

Cincotta, R.P., J. Wisnewski, R. Engelman. 2000. Human populations in the biodiversity hotspots. Nature. 404: 990-992.

Costanza, R., R. d’Arge, R. De Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R.V. O’Neill, J. Paruelo, R.G. Raskin, P. Sutton, M.Van Den Belt. 1997. The value of the world’s ecosystem services and natural capital. Nature. 387: 253-260.

Dale, V. H. and Rauscher, H. M. 1994. Assessing Impacts of Climate Change on Forests: The State of Biological Modeling, Clim. Change 28: 65–90.

De Beer, J.H., McDermott, M.J., 1989. The Economic Value of Non-Timber Forest Products in Southeast Asia. Netherlands Committee for IUCN, Amsterdam, The Netherlands.

Dietz, J.L. 1986. Economic history of Puerto Rico. Princeton University Press, Princeton, New Jersey.

Doyle, T. W. 1981. The Role of Disturbance in the Gap Dynamics of a Montane Rain Forest: An Application of a Tropical Forest Succession Model, *In* West, D. C., Shugart, H. H., and Botkin, D. B. (eds.), Forest Succession: Concepts and Application, Springer, New York a.o., pp. 56–73.

Dunphy, B. K., P. G. Murphy, and A. E. Lugo. 2000. The tendency for trees to be multi-stemmed in tropical and subtropical dry forests: Studies of Guanica Forest, Puerto Rico. Tropic. Ecol. 41, 1-7.

Emanuel, K. 2005. Increasing destructiveness of tropical cyclones over the past 30 years. Nature 436:686-688.

Fajardo, L., V. Gonzalez, J. Nassar, P. Lacabana, C. Portillo, F. Carrasquel, J. Rodriquez. 2005. Tropical dry forests of Venezuela: Characterization and current conservation status. Biotropica 37: 531–546.

Farnsworth, E.J. 1993. Ecology of semi-evergreen plant assemblages in the Guanica dry forest, Puerto Rico. Caribbean Journal of Science. 29:106-123.

Ferraro, P., and R. Simpson. 2002. The cost-effectiveness of conservation payments. Land Economics 78:339–353.

Gentry, A.H. 1995. Diversity and floristic composition of neotropical dry forests. *In* Seasonally Dry Tropical Forests Eds. S.H. Bullock, H.A. Mooney and E. Medina. Cambridge University Press, New York.

Goldenberg, S.B., C.W. Landsea, A.M. Mestas-Nunez, W.M. Gray. 2001. The recent increase in Atlantic hurricane activity: causes and implications. Science. 293: 474.

Holdridge, L.R. 1967. Life Zone Ecology. San Jose, Costa Rica: Tropical Science Center.

Huth, A., Ditzer, T., Bossel, H., 1998. The rain forest growth model FORMIX3D Model description and analysis of forest growth and logging scenarios for the Deramakot forest reserve (Malaysia). GoÈttinger BeitraÈge zur Land- und Forstwirtschaft in den Tropen und Subtropen 124 (ISBN 3±88452±385±6). Erich Goltze, GoÈttingen, pp. 182.

Kohler, P. and A. Huth. 1998. The effects of tree species grouping in tropical rainforest modelling: simulations with the individual-based model FORMIND. Ecol. Modell. 109, 301-321.

Larocque, G. R., L. Archambault, and C. Delisle. 2011. Development of the gap model ZELIG-CFS to predict the dynamics of North American mixed forest types with complex structures. Ecol. Model. 222: 2570-2583.

Leal-Pinedo, J., and R. Linares-Palomino. 2005. The dry forests of the biosphere reserve of Northwestern (Peru): Tree diversity and conservation status. Caldasia 27: 195–201.

Lerdau, M. and M. Keller 1997. Controls on isoprene emission from trees in a subtropical dry forest. Plant Cell and Environment. 20:569-578.

Little, E.L. and F.H. Wadsworth 1964. Common Trees of Puerto Rico and the Virgin Islands. US Department of Agriculture Forest Service, Washington, DC. 556 p.

Lugo, A. E., J. A. Gonzalez-Liboy, G. Cintron, and K. Dugger. 1978. Structure, productivity and transpiration of a subtropical dry forest in Puerto Rico. Biotropica 10, 278-291.

Lugo, A.E, G. Cintron, C. Goenaga. 1981. Mangrove ecosystems under stress. In G. W. Barret and R. Rosenberg (Eds.). Stress effects on natural ecosystems, pp. 129-153. John Wiley & Sons, Ltd. 305 pp.

Lugo, A.E. and P.G. Murphy 1986. Nutrient dynamics in a subtropical dry forest. Journal of Tropical Ecology. 2:55-72.

Lugo, A. E. and F. N. Scatena. 1996. Background and Catastrophic Tree Mortality in Tropical Moist, Wet, and Rain Forests. *Biotropica*. 28, 585-599.

Malhi, Y., O. Phillips, B. Kruijt, et al. 2001. The magnitude of the carbon sink in intact tropical forests: results from recent field studies. In: Sixth International Carbon Dioxide Conference, Extended Abstracts. Tohoku University, Sendai, Japan. pp. 360-363.

Martinez-Yrizar, A. 1995. Biomass distribution and primary productivity of tropical dry forests. As Bullock, S. H., Mooney H. A., & Medina, A. Seasonally dry tropical forests. Cambridge University Press, Cambridge, UK. pp. 326–345.

Maass, J. M. 1995. Conversion of tropical dry forest to pasture and agriculture. In S. H. Bullock, H. A. Mooney, and E. Medina (Eds.). Seasonally dry tropical forests, pp. 399–422. Cambridge University Press, Cambridge, UK.

Mitchell, H.L., and R.F. Chandler. 1939. The nitrogen nutrition and growth of certain deciduous trees of the northern United States. Black Rock For. Bull. 11.

Molina Colón, S. 1998. Long-term recovery of a Caribbean dry forest after abandonment of different land uses in Guánica, Puerto Rico. PhD Dissertation. University of Puerto Rico, Rio Piedras.

Molina Colón, S. and A. E. Lugo. 2006. Recovery of a Subtropical Dry Forest After Abandonment of Different Land Uses. Biotropica 38, 354-364.

Monsi, M. & Saeki, T. 1953. Uber den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung fu¨r die Stoffproduktion. Japanese Journal of Botany. 14: 22–52.

Miles L., A. C. Newton, R. S. DeFries, C. Ravilious, I. May, S. Blyth, V. Kapos , and J. E. Gordon. 2006. A global overview of the conservation status of tropical dry forests. J. of Biogeo. 33, 491-505.

Murphy, P. G. and A. E. Lugo. 1986a. Ecology of tropical dry forest. Annual Review of Ecology and Systematics 17, 67-88.

Murphy, P. G. and A. E. Lugo. 1986b. Structure and Biomass of a Subtropical Dry Forest in Puerto Rico. Biotropica. Vol. 18: 89-96.

Myers, N., 1988. Tropical forests: much more than stocks of wood. Journal of Tropical Ecology 4, 209–221.

Myers, N. R.A. Mittermeier, C.G. MIttermeier, G.A.B. da Fonseca, J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature. 403: 853-858.

Naeem, S., D. Bunker, A. Hector, M. Loreau and Perrings C. (eds). 2009. Biodiversity, Ecosystem Functioning, and Human Wellbeing: An Ecological and Economic Perspective, Oxford, Oxford University Press.

O'Brien, S.T., B.P. Hayden, H.H. Shugart. 1992. Global change, hurricanes and a tropical Forest. *Climatic Change* 22, 175-190.

Peters, C.M, Gentry, A, Mendelsohn, G. 1989. Valuation of an Amazonian rainforest, *Nature*, 339: 655-656.

Prentice, C., M.T. Sykes, W. Cramer. 1993. A simulation model for the transient effects of climate change on forest landscapes. Ecol. Model. 65: 51-70.

Quesada, M. and K.E. Staner 2004. Threats to the conservation of tropical dry forest in Coosta Rica. In: Biodiversity conservation in Costa Rica: learning the lessons in a seasonal dry forest. Ed: G.W. Frankie, A. Mata, S.B. Vinson. University of California Press, Berkeley and Los Angeles, California.

Rivera, L.W., and T. M. Aide. 1998. Forest recovery in the karst region of Puerto Rico. Forest Ecology and Management 108:63-75.

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

Santiago-García, R. J., S. Molina Colón, P. Sollins, and S. J. Van Bloem. 2008. The role of nurse trees in mitigating fire effects on tropical dry forest restoration: A case study. Ambio. 37:604-608.

Shinozaki, K., Yoda, K., Hozumi, K. & Kira, T. 1964. A quantitative analysis of plant form – the pipe model theory. Basic analysis. Japanese Journal of Ecology, 14: 97–105.

Shugart, H. H. and D. C. West. 1977. Development of an Appalachian Deciduous Forest Succession Model and its Application to Assessment of the Impact of the Chestnut Blight. J. of Environ. Manage. 5, 161-179.

Shugart, H. H., M.S. Hopkins, I. P. Burgess, and A. T. Mortlock. 1980. The development of a succession model for subtropical rain forest and its application to assess the effects of timber harvest at Wiangaree State Forest, New South Wales. J. Environ. Manage. 11: 243-265.

Shugart, H.H. 1984. A theory of forest dynamics. Springer-Verlag, New York.

Shugart, H H. 1998. *Terrestrial Ecosystems in Changing Environments*, Cambridge University Press, Cambridge.

Shugart, H. H. 2002. Forest Gap Models. Vol. 2, The Earth system: biological and ecological dimensions of global environmental change. Eds. H. A. Mooney and J. C. Canadell in Encyclopedia of Global Environmental Change. John Wiley & Sons. pp. 316-323.

Shuman, J.K., and H.H. Shugart. 2009. Evaluating the sensitivity of Eurasian forest biomass to climate change using a dynamic vegetation model. Environ. Res. Lett. 4: 045024, 7pp.

Silva, J.F., M.R. Farinas, J.M. Felfili, C.A. Klink. 2006. Spatial heterogeneity, land use and conservation in the cerrado region of Brazil. J. of Biogeogr. 33: 536-548.

Smith, T M, Halpin, P N, Shugart, H H, and Secrett, C M. 1995. Global Forests, in *If Climate Changes: International Impacts of Climate Change*, eds K M Strzepek and J B Smith, Cambridge University Press, Cambridge, 146–179.

Tobias, D. and R. Mendelsohn. 1991. Valuing ecotourism in a tropical rain forest reserve. Ambio. 20: 91-93.

Urban, D.L., 1990. A Versatile Model to Simulate Forest Pattern: A User's Guide to ZELIG Version 1. 0. University of Virginia, Charlottesville, Virginia.

Urban, D.L., Bonan, G.B., Smith, T.M., Shugart, H.H., 1991. Spatial applications of gap models. Forest Ecol. Manage. 42, 95–110.

Van Bloem, S.J., P.G. Murphy and A.E. Lugo 2003. Subtropical dry forest trees with no apparent damage sprout following a hurricane. Tropical Ecology. 44, 137-145.

Van Bloem, S. J. 2004. Multiple scale patterns in growth and structure of subtropical dry forests: soils, trees, and hurricanes. PhD. Dissertation. Michigan State University.

Van Bloem, S. J., P. G. Murphy, A. E. Lugo, R. Ostertag, R. Rivera Costa, I. Ruiz Bernard, S. Molina Colon, M. Canals Mora. 2005. The influence of hurricane winds on Caribbean dry forest structure and nutrient pools. Biotropica. 37: 571-583.

Van Bloem. S. J., P. G. Murphy, A. E. Lugo. 2007. A link between hurricane-induced tree sprouting, high stem density and short canopy in tropical dry forest. Tree Physiology. 27: 475-480.

Van Daalen, J. C. and H. H. Shugart. 1989. OUTENIQUA – A computer model to simulate succession in the mixed evergreen forests of southern Cape, South Africa. Landscape Ecology. 2, 255-267.

Webster, P.J., G.J. Holland, J.A. Curry, H.-R. Chang. 2005. Changes in tropical cyclone number, duration, and intensity in a warming environmental. Science. 309: 1844.

1.5 Appendix

Picture 1.1. Canopy and leaf data collection in Guanica Forest, Puerto Rico.

Picture 1.2. Main path going through the mature, semi-deciduous Guanica Forest.

Picture 1.3. Measuring trees located inside Guanica Forest (dense, smaller sized physiognomy).

1.5.1 ZELIG-TROP Model Background and Methods

Growth Sub-routine:

The GROWTH sub-routine simulated the growth of each individual tree by increasing the annual increment of the tree's diameter (cm) at breast height (130 cm) during each annual time step. The optimal diameter increment formula to create optimal tree growth (before constrained by environmental factors) was originally seen in Botkin (1972):

$$\delta(D^2H) = R * LA * \left(1 - \frac{DH}{D_{\max} H_{\max}}\right) \qquad \text{(Equation 1.1)}$$

Where D is the diameter at breast height (DBH) of the tree, H is the height of the tree, D_{max} and H_{max} are the maximum quantities for the species, LA is leaf area, and R is a constant. Botkin (1972) further derives the optimal growth increment (cm) into the following equation:

$$\delta D = \frac{GD\left[1 - DH / D_{\max} H_{\max}\right]}{\left[274 + 3b_2 D - 4b_3 D^2\right]} \qquad \text{(Equation 1.2)}$$

where the G is the growth rate of each species, and b_2 and b_3 equal:

$$b_2 = 2(H_{\max} - 137) / D_{\max}; b_3 = (H_{\max} - 137) / D_{\max}^2 \qquad \text{(Equation 1.3)}$$

The detailed integration for finding G, or the Growth equation was listed in the appendix of Botkin et al. (1972), using the maximum age (AGEMX) of the known tree species:

(Equation 1.4)

$$\mathrm{G} = \frac{4H_\mathrm{m}}{\mathrm{AGEMX}}\left\{\ln(2(2D_\mathrm{m}-1)) + \frac{a}{2}\ln\left(\frac{\frac{9}{4}+\frac{a}{2}}{4D_\mathrm{m}^2+2aD_\mathrm{m}-a}\right) - \frac{a+a^2/2}{\sqrt{a^2+4a}}\ln\left[\frac{(3+a-\sqrt{a^2+4a})(4D_\mathrm{m}+a+\sqrt{a^2+4a})}{(3+a+\sqrt{a^2+4a})(4D_\mathrm{m}+a-\sqrt{a^2+4a})}\right]\right\}$$

For this research, limited amount of biological information was known for the Puerto Rican tree species, due to a lack of inventory censuses. The maximum age (AGEMAX) of these species were poorly known, therefore making the G parameter difficult to obtain. Without the G parameter, the diameter increment equation (equation 1.1) cannot perform in the growth sub-routine.

Two methods have been used to determine G for this project. The first method was to solve for AGEMAX using a probability of mortality equation (equation 1.5), then plug the AGEMAX value into the growth equation (equation 1.4) to find G. For this first method the average probability of mortality was calculated from the Forest Inventory Analysis (FIA) data and from a continually monitored dataset set up in Guanica Forest by Lugo et al. (1978). This species specific average probability of mortality (P) was plugged into the following formula from Botkin et al. (1972) and Van Daalen and Shugart (1989) to solve for AGEMAX:

$$P = 1 - \exp(-4.605 / AGEMAX) \qquad \text{(Equation 1.5)}$$

Rearranged to: $$AGEMAX = \frac{4.605}{\ln(P+1)}$$

The second method to determine G was to find the maximum diameter increment from observed individuals. Field data from Van Bloem et al. (2007), was used to calculate the maximum diameter increment, which was plugged into the following equation 1.6 from Botkin et al. (1972) to solve for G:

$$\delta D_{\max} \cong 0.2 G D_m / H_m \qquad \text{(Equation 1.6)}$$

Rearranged to: $$G \cong \frac{\delta D_{\max}}{0.2} * \frac{H_m}{D_m}$$

Where $\delta D_{\max}$ is the maximum diameter increment from field observations. This second value of G was also used to determine a second AGEMAX. Due to a limited amount of knowledge on AGEMAX and growth rates of the Puerto Rican subtropical dry species, the average of the AGEMAX and G from the two methods (averaged two values) was used.

Two other important variables in the GROWTH sub-routine were the determination of leaf area and height of each tree. The leaf area is calculated based on the theory of the pipe model (Shinozaki et al. 1964). Height (m) is found using the polynomial function of diameter from Botkin (1972):

$$H = 137 + b_2 DBH - b_3 DBH^2 \qquad \text{(Equation 1.7)}$$

The model increased the growth of each tree by increasing the diameter increment over time, but this is limited by a function of environment variables. In the GROWTH sub-routine DBH (diameter at breast height), H, and overall growth was limited as a function of light, climate, soil, and competition factors. The amount of light to hit an individual tree was greatest at the exposed top of the tree and decreases with depth into the canopy as light attenuation increases. To determine the light available to each tree, and to represent competition from shading, the decreasing light transmission through-out the canopy was found by the Lambert-Beer Law (Monsi & Saeki 1953):

$$I(Z) = I(0)e^{-kLAI(Z)} \qquad \text{(Equation 1.8)}$$

Where I(Z) equals the available light at a certain height of Z, LAI(Z) was the leaf area index above any height of Z, k was the light extinction coefficient, which in ZELIG was currently set at 0.4.

The function DEGD (growing degree days) takes into account temperature during the growth of individuals (equation 1.9). The amount of growing degree days (DEGD) can also limit the optimal time for growth of a species. It was assumed that there was an optimum temperature for photosynthesis to occur, and either below a minimum or above a maximum temperature photosynthesis will become ineffective, or doesn’t occur. In the sub-tropics there is almost a constant temperature through-out the year and a constant growing season, but there are some extreme temperatures that limit growth. Originally used in Botkin et al. (1972) and the JABOWA model, the following function takes into account temperature and the number of growing degree days:

$$f_T(DEGD) = \frac{4(DEGD_{\max} - DEGD)(DEGD - DEGD_{\min})}{(DEGD_{\max} - DEGD_{\min})^2} \qquad \text{(Equation 1.9)}$$

where $DEGD_{max}$ and $DEGD_{min}$ were the species’ maximum and minimum growing degree days from observed natural rates.

This model took into account other environmental variables that can lead to stress and limit growth. These environmental variables were temperature, drought, poor nutrients in the soil, and shading or limited available light. Depending on each species tolerance level to these variables, each of these inhibitors had the ability to decrease optimal growth. The model began by assuming an optimal nutrient availability for each species, but that level of nutrient maximum requirement was limited by the polynomial equation relating tree growth to nutrient availability (Mitchell and Chandler 1939):

$$f_N(F) = c_1 + c_2 * F - c_3 * F^2 \qquad \text{(Equation 1.10)}$$

where c1, c2, and c3 were species specific parameters that were based off of species tolerances ranking to nutrient limitation, and F was soil fertility based on aboveground biomass and equals 1.0 in non-limiting conditions.

1.5.2. Regeneration Sub-routine

The REGENERATION sub-routine simulated and grew the first tree species on the bare ground in the initial run, then also computed the establishment of new seedlings for each species, and determined the seedling size and growth of those new trees on an annual time step. The model that I manipulated for my research has an established routine to determine the regeneration candidate in each time step. This establishment methodology was slightly altered to match Puerto Rican species life history traits and phenology. Data was collected on the seed bank survival rate, seedling survival rate, sprouting probability, seed size, shape, and the quantity and distance of seed dispersal for Puerto Rican tree species (See appendix 1.3 and 1.4). This sub-routine updated the species' establishment rate (xs), as a function of environmental conditions:

$$xs = RSER * f_L * (f_W f_N) * f_T \qquad \text{(Equation 1.11)}$$

where RSER was relative sapling establishment rate provided as an input value for the Puerto Rico species (%), f_L was available light, f_w was available soil moisture, f_N was soil nutrients, and f_T was temperature. The actual number of seedlings was determined by the total number available and the total number of seedlings possible.

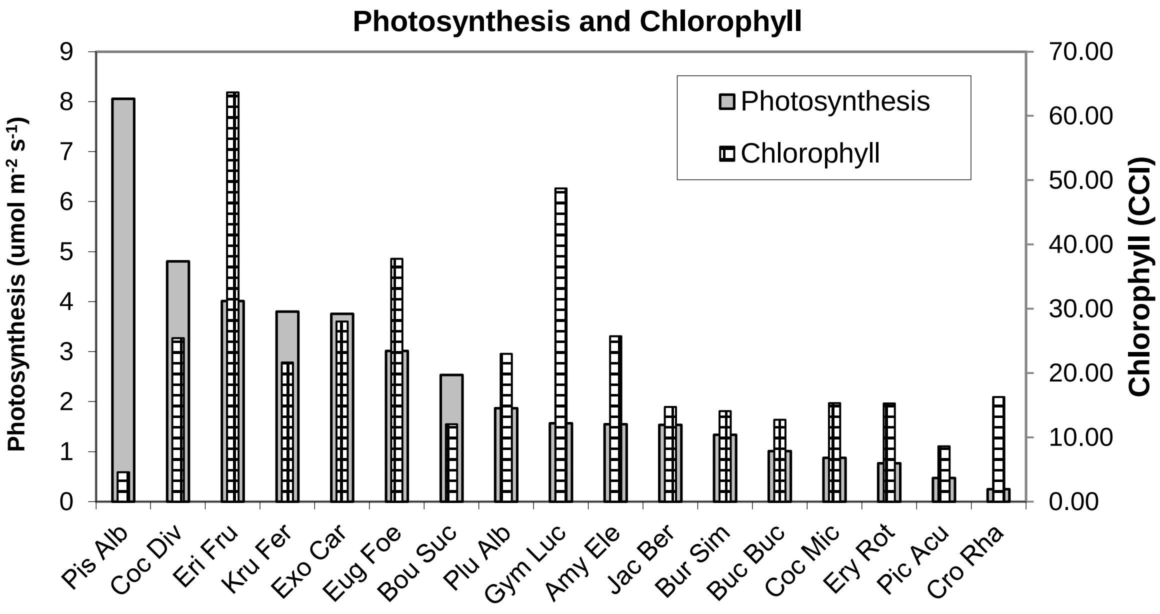
1.4.3. Mortality Sub-routine

Mortality was stochastic and can arise from two separate factors, either age-related (natural) death or stress related due to environmental factors or tree suppression over time. Natural death had two assumptions: 1) that 1% of individuals reaches their species specific maximum age (AGEMAX), and 2) mortality was constant with respect to age. Therefore natural death can be found by (Botkin et al 1972, Shugart 1984):

$$m_n = \left(\frac{4.605}{AGEMAX} \right) \qquad \text{(Equation 1.12)}$$

where 4.605 is the natural log of 1%. The second method for mortality to occur was when stressed individuals were failing to grow 10% of their potential growth increment for 2 or more years. Therefore, this sub-routine included mortality for suppressed trees or environmentally stressed trees that have a slow growth rate and a low diameter increment. Of these suppressed, slow growing trees, the model predicted that 1% will live 10 years. Shugart (1984) and Van Daalen and Shugart (1989) described this additional probability of death (P_s) as:

$$P_s = 0.368$$



Appendix 1.1. Photosynthesis data (umol m^{-2} s^{-1}) and corresponding chlorophyll (CCI) for 17 Puerto Rican species from the dry season in 2010. Cholophyll was measured using a CCM-200 (Apogee Inc.) measured in Chlorophyll Concentration Index (CCI).

Appendix 1.2. Photosynthesis, LAI, and chlorophyll values 17 common Puerto Rico species.

Species	Photosynthesis (μmol m^{-2} s^{-1})	LAI	Chlorophyll (CCI)
Pis Alb	8.06	0.41	4.55
Coc Div	4.80	0.34	25.44
Eri Fru	4.01	NA	63.64
Kru Fer	3.80	0.34	21.64
Exo Car	3.75	0.24	28.03
Eug Foe	3.01	NA	37.75
Bou Suc	2.53	0.24	12.02
Plu Alb	1.87	NA	22.99
Gym Luc	1.57	NA	48.72
Amy Ele	1.55	0.20	25.72
Jac Ber	1.53	0.16	14.71
Bur Sim	1.34	0.14	14.06
Buc Buc	1.01	0.14	12.73
Coc Mic	0.88	0.28	15.31
Ery Rot	0.77	NA	15.27
Pic Acu	0.47	0.26	8.61
Cro Rha	0.25	NA	16.25

Appendix 1.3 Seedling data: germination rate (%), mean germination (days), seed coat type, fruit type, dispersal agent for seeds (Castilleja 1991). This data is available for 14 of the 19 species included in the model, and some species only have partial data included.

Species	Germin-ation %	Mean Germination Time (days)	Seed Coat Type	Fruit Type	Dispersal Agent
Amyris elemifera	80	12	Hard	Drupe	Bird
Bourreria succulent	45	8	Hard	Drupe	Bird
Bucida bucerus	95	3	Soft	Capsule	Unknowm
Bursera simaruba	NA	NA	Hard	Drupe	Vertebrate
Coccoloba diversifolia	NA	NA	Hard	Drupe	Bird
Coccoloba microstachya	15	9	Hard	Drupe	Bird
Erithalis fruticosa	65	15	Soft	Drupe	Bird
Exostema caribaeum	70	9	Soft	Pod	Wind
Guettarda krugii	NA	NA	Hard	Capsule	Vertebrate
Gymnanthes lucida	65	3	Soft	Capsule	Auto
Krugiodendron ferreum	90	5	Soft	Drupe	Bird
Pictetia aculeate	10	3	Hard	Pod	Auto
Pisonia albida	85	4	Soft	Capsule	Unknowm

Appendix 1.4 Continued seedling data: dry weight (mg) of seeds, seed volume (mm^3), seed area (mm^2) and the months observed for fruiting (Castilleja 1991).

Species	Dry Weight (mg)	Seed Volume (mm^3)	Seed Area (mm^2)	Month # of Fruiting (at least one tree)
Amyris elemifera	8.2	17.1	32.1	7,8,11 (rainy)
Bourreria succulenta	31.5	68.5	166.2	All months (dry/rainy)
Bucida bucerus	2.9	2.3	8.3	All months (dry/rainy)
Bursera simaruba	62.4	78.6	85.8	All months (dry/rainy)
Coccoloba diversifolia	182.6	152.2	128.5	3,6,7,8,11
Coccoloba microstachya	1.9	3.3	10.2	3,5,6,7,8,11 (rainy)
Erithalis fruticosa	0.7	0.4	6.7	All months (dry/rainy)
Eugenia xerophytica	45.2	73.4	84.9	NA
Exostema caribaeum	7.5	16.2	31	3,8,11 (rainy)
Guettarda krugii	8	4.7	17.3	NA
Gymnanthes lucida	26.6	38.5	55	7,8,11 (rainy)
Krugiodendron ferreum	46.4	91.6	81.4	7,8,11 (rainy)
Pictetia aculeata	7.7	15.9	44.3	8 (rainy)
Pisonia albida	4.1	5.5	20	3,7,8,11

Chapter 2 Gap model development, validation, and application to succession of secondary subtropical dry forests in Puerto Rico.

2.1 Introduction

For decades subtropical dry forests (SDFs) have been considered the most threatened of all tropical forests, yet lacking in studies compared to wet and moist systems (Bullock et al. 1995, DeFries et al. 2002, FAO 2007, Janzen 1988). There has been a large worldwide decline in the extent of subtropical dry forests due to forest loss and forest degradation, and 97% of remaining forests are at risk from threats such as habitat fragmentation, increasing fire and hurricane frequency, climate change, agricultural conversion, and higher population densities (Brandeis et al. 2003, FAO 2001, 2007, Miles et al. 2006, Pares-Ramos et al. 2008). Dry forests cover the largest portion of the Earth’s tropical and subtropical lands (42%), while 33% is moist forest, and 25% is wet or rain forest (Holdridge 1967). Over such a large area, research is needed on how subtropical dry forest succession might ameliorate carbon emissions from deforestation and degradation.

Due to the global extent of dry forests and the number of countries that contain them, their dynamics and management are important to the REDD+ scheme (Reduced Emissions from Deforestation and Degradation), a significant policy issue (Grainger 2010, Laurance 2007, Miles and Kapos 2008, Mollicone et al. 2007). In the Caribbean, some dry forests are experiencing deforestation while others are recovering from agriculture abandonment and shifting back to forest. Predicting this recovery process is important for economic initiatives such as REDD+. This study will develop and validate a forest simulator that utilizes the detailed nature of an individual-based model (IBM), which tracks individual trees over time, thus providing the future capability of predicting forest succession for such applications.

Three IBMs have been used for the *wet* montane forest located in Luquillo, Puerto Rico (Doyle et. al. 1981, O'Brien et al. 1992, Uriarte et al. 2009). Up to now, no IBMs have been created for subtropical dry forests in the Caribbean, a threatened ecosystem fluctuating in biomass/carbon levels (Brandeis et al. 2006, Brown and Lugo 1982), but could play a major role in reducing atmospheric carbon emissions (Canadell and Raupach 2008). The existing gap dynamics model ZELIG (Cumming and Burton 1993, Urban 1990, 2000; Urban et al. 1991, 1993) was modified for the SDFs of Puerto Rico (model description and justification for choosing ZELIG in Methods).

The typical gap model paradigm consists of multiple assumptions, one being that the forest is a composite of many small patches that can be different ages or successional stages, interspersed with gaps, where regeneration generally, but not always, occurs in the open gap. Subtropical dry forests are unique in that they challenge this modeling paradigm due to high stem density and a majority of vegetation reproduction through sprouting. Therefore, the forest gap dynamics may be masked by higher frequency of sprouting saplings filling gaps. This paper develops and parameterizes the forest model (ZELIG-TROP) to simulate and examine the critical process of regenerating dry tropical forests, address the problem of understanding unique aspects of dry tropical forests, and predicts the future direction of SDFs. ZELIG-TROP's simulation outputs were validated using field data from Puerto Rico.

While modeling dry tropical forests is lacking, computer simulation models have recently modeled and found applications in other tropical forests. With the exceptions of the Shugart et al. (1980) KIAMBRAM model of Australian montane rain forest and the Van Daalen and Shugart (1989) OUTENQUA model of South African montane rain forest, many of the other tropical forest models have used groups of species (i.e. functional types), largely due to the shortage of species-level growth data and complexity of tropical forest ecosystems. These include FORMIX3, and the later developed FORREG and FORMIND. FORMIX3 (Ditzer et al. 2000, Huth et al. 1998) has the strength of being simple in nature for ease of use, thus has been employed to study the complex forests of Malaysia. FORMIND (Kohler and Huth 1998) is an individual based model and has been applied to more locations and disturbed forests, such as Malaysia, Venezuela, Mexico, and French Guiana due to its grouping of species into 10-20 plant functional types (Huth et al. 2004, 2005, Kammesheidt et al. 2001, Kohler et al. 2001, 2003; Kohler and Huth 2004, Tietjen and Huth 2006). These models went through a rigorous parameterization process in order to be easily applicable and required a few parameters to run, therefore providing an aggregated approach to modeling diverse tropical forests with large number of species. This approach can be useful in tropical locations where long-term data needed for parameterization are not always available. An advantage in Puerto Rico is that the subtropical dry forest contains lower number of species (37 species) compared to rainforests (500+ species), and research in forest dynamics has a history of >50 years, providing long term data. As opposed to previous models ZELIG-TROP also has the advantage of being highly detailed for a tropical forest model using site and species specific parameters instead of general functional types.

As a second goal, the robustness and realism of ZELIG-TROP was tested by evaluating its effectiveness at simulating the succession of abandoned agricultural fields that are being reclaimed as secondary forests. During the first half of the 20th century, major population increases, sugarcane cultivation, extraction of wood, and grazing nearly eliminated the dry forests of Puerto Rico, leaving only 5% intact forest by the 1940s remaining (Birdsey and Weaver 1982, Scarano 2000, Wadsworth 1950). The switch from agriculture to manufacturing in the 1950s and 60s, has allowed forest cover in much of southern Puerto Rico to regenerate on old fields (Aide et al. 1996, Molina Colon and Lugo 2006, Pares-Ramos et al. 2008). The final forest composition at these locales and time frame of transition is not known. This needs to be quantified. A variety of factors in forest patches can influence successional patterns and eventually produce different mature forest communities. The model used here will evaluate forest transitions on abandoned agricultural fields, driven by land-use change and economic development that shifts agriculture to manufacturing (Aide et al. 2000, Grau et al. 2003, Pares-Ramos et al. 2008).

The unique nature of SDFs and difficultly in simulating these systems is the driver of the main goal: creating and validating a new model (ZELIG-TROP) that overcomes modeling challenges. Such as very high stem density, the possibility of no gap dynamics, heavy reliance on vegetation reproduction by basal-sprouting, soil conditions where evaporation annually exceeds precipitation, and the need for detailed silvicultural data of tropical species. The purpose of this research is to develop a new forest successional model and validating the model by comparing outputs to known forest stands. Upon completion of this task, model outcomes reported in this paper can thus be used to understand and monitor Caribbean SDFs. For example, simulation modeling is designed to predict how a forest will respond to various disturbances and can lead to better management and conservation practices of threatened, hurricane-prone, and biologically diverse SDFs.

2.2 Methods

2.2.1 Description of ZELIG-TROP

ZELIG-TROP (derived from ZELIG) is a gap model based on the original principles of the JABOWA (Botkin et al. 1972a, 1972b) and FORET gap models (Shugart and West 1977). ZELIG is an individual-based model and follows the growth and development of each individual tree (Urban 1990, 2000; Urban et al. 1991, 1993). As in many gap dynamic and individual-based models, the main routines of the model include growth, mortality, regeneration, and tracking environmental conditions. These four sub-routines in the model simulate forest stands by tracking all trees as they grow, die, and regenerate across many plots ($400m^2$ plots, replicated 100 times). ZELIG-TROP began with maximum potential behavior for forest processes (seedling establishment rate, diameter increment, survival rate), and then reduced these optimal behaviors depending on the resources available. Potential tree regeneration, growth, and survival are decreased depending on the following environmental constraints: light conditions, soil moisture, level of soil fertility resources, and temperature. Specific details on methodical approaches used in the model can be found in Urban (1990, 2000), Urban et al. (1991, 1993), and Cumming and Burton (1993). The expansion of this model over many large-scale and diverse landscapes (Busing and Solomon 2004, Coffin and Urban 1993, Cumming and Burton 1994, 1996, Larocque et al. 2006, 2011, Laurence et al. 2001, Nakayama 2008, Pabst et al. 2008, Yaussy 2000), as well as the on-going validation of this expansion suggests that the model is robust in its ability to represent forest dynamics. Due to the combination of versatility among forest types and detailed nature of the model, ZELIG is a good choice to be applied to unique tropical regions that challenge the model paradigm.

2.2.2 Site Description

The site for this research has been in the Guanica State Forest (protected since 1917), a mature semi-deciduous subtropical dry forest located in southwestern Puerto Rico (17° 58′ N, 65° 30′ W). The mean height of the forest ranges from 5-7m, with the basal area ranging from 17-21 m^2 ha^{-1}. Stem density can range from 6,000 -10,000 stems ha^{-1}, but locations can have densities reaching 12,000 stems ha^{-1} due to high rates of sprouting (Van Bloem et al. 2003, 2004, Murphy and Lugo 1986a). Elevation ranges from 125-185m. The annual precipitation is 860mm with a minor wet season occurring in

April-May, and the main wet season occurring from September to November, corresponding with the hurricane season (Murphy and Lugo 1986a, Van Bloem et al. 2003). The mean annual temperature is 25.2 °C, and the yearly evaportranspiration is 722mm (Lugo et al. 1978, Murphy and Lugo 1986a).

An additional area within Guanica Forest was protected in 1930, which required the abandonment of a small village, allowing for 60+ years of monitoring successional and land use changes (Molina Colon 1998) at the time of data collection. The opportunity for data collection on such a large area of mature forested land has been unique in Puerto Rico (a somewhat rare occurrence in tropical locations compared to temperate regions) and is useful for long-term forest studies, and needed for modeling parameterization required in this study. This background and additionally early experiments of forest succession (Dunevitz 1985, Ewel 1977, Wadsworth 1950), makes Puerto Rico a good candidate for this research.

2.2.3 Data Collection/Model Parameterization

Data have been collected from fifteen permanent 10 x 10 m plots ($1500m^2$) set up in 1981, inside the mature Guanica State Forest (Lugo et al. 1978, Murphy and Lugo 1986a), over three census periods; 1981, 1999, and 2009. The permanent plots consist of approximately 37 native tree species (the top 18 dominant species are used in ZELIG-TROP). This data ($1500m^2$) has been reserved and only used to validate the model. The majority of data used to parameterize the model has come from *separate* transects

(~600m^2) established in 1998 located near the 1500m^2 permanent plots in Guanica Forest (Van Bloem et al. 2005, 2007), with a slight amount of data provided by the US Forest Service Forest Inventory Analysis (FIA) from plots located in southwestern Puerto Rico, near Guanica Forest (Brandeis 2003, USDA 2006). Forest Inventory Data came from the 2003 and 2008 censuses (4.0 ha). Similar to the Guanica Forest data collection, FIA tracked individual tree growth, mortality, and regeneration from 2003 to 2008. Outside Guanica Forest and throughout the Caribbean, the majority of the areas that were once dry forests have been converted to agriculture, grazing, or returning to secondary forests. In order to validate the second goal of this paper, data have also been gathered from secondary forests in areas of varying land uses and lengths of time since abandonment, throughout southwestern Puerto Rico and outside the mature Guanica Forest. These data have been provided by the US Forest Service FIA (1.0 ha).

ZELIG-TROP requires silvicultural parameters specific to each tree species, making it a detailed tropical model (Table 2.1). The maximum age of the species (AGEMAX) was not available in published literature or field data, so it was estimated. To determine AGEMAX, the average annual mortality equation from Botkin et al. (1972b) and Van Daalen and Shugart (1989) (Equation 2.1) was used and re-arranged to solve for AGEMAX. The species specific average probability of mortality (P) was taken from mortality field data located within the study site.

$$P = 1 - \exp(-4.605 / AGEMAX) \qquad \text{Equation 2.1}$$

To determine the growth rate G (cm/year), the maximum diameter increment ($\delta D_{\max}$) was determined using the 95th percentile of increments recorded from the dataset collection, and used in the diameter increment growth equation from Botkin et al. (1972b) to solve for G (Equation 2.2).

$$G \cong \frac{\delta D_{\max}}{0.2} * \frac{H_m}{D_m} \qquad \text{Equation 2.2}$$

Growth rate equation (Equation 2.2) derived from the diameter increment equation (Botkin 1972b) to solve for G, where $\delta D_{\max}$ is the maximum diameter increment, H_m is maximum height, and D_m is maximum diameter. The growth rate (G) was required for calculating the new diameter growth of each individual within ZELIG-TROP and similar methods have been investigated for other gap models (Fyllas et al. 2010, Risch et al. 2005). Additional parameters required for ZELIG-TROP were species specific values for relative seedling establishment rate (FIA, Brandeis 2003, USDA 2006), regeneration stocking (%), and other seedling descriptors such as germination percent and rate, dry weight (mg) of seeds, seed volume (mm^3), seed area (mm^2) (Castilleja 1991, Little et al. 1974, Wolfe 2009). The environmental parameters used in ZELIG-TROP, and the plot area (400 m^2) can be found in Table 2.2.

Table 2.1. Species specific allometric and ecological parameters used in the ZELIG-TROP model. All species were assigned a probability factor of stress mortality of 0.369, probability factor of natural mortality of 4.199, and zone of seed influence of 200.

Species	Age max	DBH max	HT max	Shape Adj.	G	DegD Min	DegD Max	L.	D.	N.	Crown Shape	RSER	Stock	Sprout
Amyris elemifera	58	11.3	580	1.3	94	5500	9630	2	4	3	1	0.68	0.3	2
Bourreria succulent	188	14.5	830	0.75	44	6139	9630	3	4	3	2	0.79	0.2	1
Bucida bucerus	450	45.0	1590	0.9	32	5800	9630	4	4	3	2	0.08	0.3	2
Bursera simaruba	65	35.0	1070	1.5	154	5000	9630	3	5	1	1	0.37	0.2	1
Cassine xylocarpa	244	14.4	760	1.6	29	6139	9630	4	5	2	1	0.73	0.15	1
Coccoloba diversifolia	158	23.0	1100	2	102	5500	9800	1	4	3	1	0.33	0.2	1
Coccoloba microstachya	174	15.0	880	1.9	46	6139	9630	4	5	2	3	0.82	0.2	1
Crossopetalum rhacoma	105	6.8	480	0.9	41	5500	9800	4	5	2	4	0.57	0.2	1
Erithalis fruticosa	105	9.0	800	1.8	68	6139	9630	4	4	2	2	0.5	0.2	2
Erythroxylon rotundifolium	132	8.3	600	1	63	6139	9630	2	3	2	4	0.29	0.3	1
Eugenia foetida	46	7.7	610	2	118	5500	9800	2	4	2	2	0.11	0.2	1
Exostema caribaeum	45	9.6	720	1.2	141	5500	9630	3	5	3	3	0.49	0.8	1
Guettarda krugii	236	10.0	750	1.9	37	6139	9630	3	2	1	2	0.5	0.3	2
Gymnanthes lucida	140	11.4	740	1.8	71	5500	9630	2	4	3	1	0.7	0.4	1
Jacquinia berteroi	140	14.0	700	1.9	46	6139	9630	3	4	2	1	0.5	0.2	1
Krugiodendron ferreum	144	12.0	500	1.1	43	5500	9800	1	4	3	2	0.54	0.2	1
Pictetia aculeate	248	15.0	740	0.5	54	6139	9630	3	4	2	4	0.19	0.2	1
Pisonia albida	152	22.0	700	1.7	80	6139	9630	4	4	2	4	0.6	0.4	2

Key: Agemax, maximum age for the species; DBHmax, maximum diameter at breast height (cm); HTmax, maximum height (m); G, growth rate scaling coefficient; DegDMin and DegDMax, minimum and maximum growing degree days; Light (L), Drought (D), Nutrient (N), light/shade tolerance class, maximum drought tolerance class, and soil fertility tolerance class; Crown Shape, crown form associations; RSER, relative seedling establishment rate; Stock, regeneration stocking; Sprout, basal sprouting ability, 1=stronger re-sprouter, 2=intermediate re-sprouter (full parameter explanation found in original ZELIG paper: Urban 1990).

Table 2.2. Environmental parameters used in the ZELIG-TROP model for Puerto Rico.

Lat./ Long./Alt. (m)	Plot Area (m^2)	Mean Monthly Temperature (C°)	Mean Monthly Precipitation (cm)	Soil Field Capacity (cm)
17.97/66.93/129	400	25.4-28.1	2.31-14.25	20
Soil Wilting Point (cm)	Mean Monthly Radiation (W m^{-2}) (PET Eq.)	Mean Monthly Rel. Humidity (%) (PET eq.)	Relative Direct and Diffuse Solar Radiation (%)	
10	166.0-231.2	0.776-0.893	0.6/0.4	

2.2.4 ZELIG-TROP model modifications

Modifications include re-parameterizing the model for climate, environmental site conditions, and species common to southwestern Puerto Rico. Modifications also include re-coding parts of the existing model to forest characteristics specific to a tropical forest site. These major changes include improving ZELIG-TROP’s ability to calculate accurate heights for SDFs trees, the application of a new crown interaction algorithm based on the mean available light growing factor developed in ZELIG-CFS (Larocque et al. 2011), a new equation for potential evaporation, and addition of a re-sprouting subroutine. The minor changes include the following: changes to the stress and natural mortality functions, decreasing the initial DBH size (cm) of new seedlings, and updating the aboveground biomass equation for the Puerto Rico region (Brandeis et al. 2006). Additional changes, included updating the leaf allometric equation (Sollins et al. 1973) and modifying the way in which canopy architecture was determined within the model.

2.2.4.1. Height-Diameter relationship and PET modifications

To calculate accurate heights of subtropical dry trees, new values for the shape adjustment factor (S) were determined specifically for Puerto Rico trees. ZELIG-TROP uses a polynomial equation to determine height from the stem diameter. The shape adjustment factor (S) was computationally determined for each of the Puerto Rican species, by comparing observed height vs. DBH data to simulated ZELIG-TROP results, and iteratively adjusted the shape adjustment factor until there was a strong agreement between the two curves. A similar method to determine S was used by Risch et al. (2005).

Originally potential evapotranspiration (PET) was found using the methods of Thornthwaite and Mather, with regressions for Northern Hemisphere latitudes which are further north than tropical latitudes, and not appropriate. Initial simulations of the Puerto Rican SDF showed that using the Thornthwaite and Mather equations resulted in an over-estimation of the PET. For this study the methods of Priestly-Taylor (1972), later modified by Yan and Shugart (2010) were used to estimate PET (Equation 2.3).

$$\mathrm{ET}_{(\lambda E+H)} = 1.45\mathrm{RH}\frac{\mathit{\Delta}}{\mathit{\Delta}+\gamma}(\lambda E+H) \qquad \text{Equation 2.3}$$

where ET is the evapotranspiration (W m^{-2}), RH is relative humidity (%), λE is the latent heat flux, H the sensible heat flux, $\mathit{\Delta}$ is the gradient of the saturated vapor pressure to the air temperature (Ta, °C), and γ is the psychrometric constant. The λE equation equals net radiation (Rn, W m^{-2}) minus ground heat flux (G, W m^{-2}) minus sensible heat flux (H), which along with RH, were calculated and averaged from weather stations in southwestern Puerto Rico (Table 2.2).

2.2.4.2. Basal-sprouting

The addition of a basal-resprouting subroutine was very important for simulating this forest system, since studies show that 46% of all trees in Guanica are multi-stemmed as a result of resprouting, creating high stem density (>10,000 stems ha^{-1}) (Murphy and Lugo 1986a, Van Bloem et al. 2003). Re-sprouting is common in areas where cutting or damage to trees has occurred, but it also occurs naturally in uncut locations or undamaged trees, with new sprouts off of roots (Dunphy et al. 2000, Molina Colón 1998, Murphy et al. 1995, Van Bloem et al. 2003). The method of calculating re-sprouting on individual trees was adapted from the OUTENIQUA gap model (Van Daalen and Shugart 1989) and from notes in the original user guide of ZELIG (Urban 1990). Re-sprouting ability for each species was assigned one of the following: strong re-sprouter, intermediate re-sprouter, or does not tend to resprout based on field data. Studies have showed that allowing species to have individualized sprouting probabilities and inclusion of specific life histories improved model capabilities (Fyllas et al. 2007, Pausas 1999, Vesk & Westoby 2004). Only trees with a DBH greater than 3.0cm at time of death were evaluated for resprouting, with the understanding that these were established trees capable of re-sprouting, given that in the Puerto Rican dry forest the average DBH is 5.0 cm. In the regeneration subroutine, resprouts from dead trees were grown in the same manner as a new sapling from a seed. Since sprouts grew from existing root systems and theoretically should have more vigor and faster growth, sprouts started with an initial DBH of 2.5cm, while seedlings started at 1.5cm.

2.2.4.3. Mortality estimation

Initial simulations of the Puerto Rican SDF showed that the original methods to produce death by *natural mortality* (age-related) were killing the tropical trees too soon, and trees were not reaching their potential age or size. Therefore the natural survivorship was increased from the original value of 1% (Botkin's 1972b and Shugart et al.'s 1980 derivation of the tree mortality function) to 1.5% of trees being able to survive to their maximum age. When using the original methods to produce death by *stress mortality* (Equation 2.4) it was observed in initial simulations that the majority of trees never experienced stress induced mortality. Stress mortality is due to stress from site/environmental factors or suppression. From empirical studies, tree species in Puerto Rico do have the potential to die from stress (Jimenez et al. 1985, Lugo and Scatena 1996, Walker 1995). In the growth subroutine, the code was modified with Equation 2.5 to allow death due to stress:

$$\text{RDI} < 0.10*(D_{max}/\text{AgeMax}) = \text{death due to stress} \qquad \text{Equation 2.4}$$

$$1-((\text{PDI} - \text{RDI})/\text{PDI}) < 0.15 = \text{death due to stress} \qquad \text{Equation 2.5}$$

where RDI is the realized diameter increment (cm), D_{max} is maximum diameter, and PDI is the potential diameter increment also known as the optimal increment based on DBH, observed growth, and height-diameter allometric variables before environmental constraints.

2.2.4.4. Above-ground biomass and crown architecture

Estimated above-ground biomass (Mg ha^{-1}) using DBH (D) cm and stem height (H_T) m has been updated in the model (Equation 2.6) to use the allometric biomass equation specific for Puerto Rican subtropical dry forests found in Brandeis et al. (2006):

$$\ln(AGTB) = b_1 + b_2 \ln(D^2 H_T) \qquad \text{Equation 2.6}$$

where above-ground total biomass (AGTB) is in kg. By using direct measurements of 26 trees (mixed species) from a SDF in Puerto Rico, and using an ordinary least squares procedure model the coefficients b_1 was found to be -1.9437 and b_2 was 0.8413 (r^2 = 0.9175). An error was found within ZELIG concerning the biomass calculator, which has been corrected for ZELIG-TROP, and should be investigated for other versions of ZELIG. Biomass was continually growing over time; caused by each year's annual biomass accumulating on top of the previous biomass level. The error was corrected by setting the total biomass at the beginning of each time step to zero, thus allowing ZELIG-TROP to accurately calculate annual total biomass each year.

New estimations of crown width were estimated by using the average ratio of crown width to total tree height, based on empirical data (FIA). Ratio of crown width to total tree height ranged from 0.24 to 0.67 (average: 0.47). Due to the dense nature of SDFs, crowding, and majority of light absorption limited to the upper canopy, a high density of trees can limit crown length of individual trees. Therefore, crown length was also estimated by using the average ratio of crown length (CR_L) to total tree height ($^{CR_L}/_{Ht}$) but divided by a fraction of the simulated plot density (number of stems on a plot) to account for dense conditions (Equation 2.7).

$$\text{Crown Length} = \frac{\left(^{\mathrm{CR_L}}/_{\mathrm{Ht}}\right) * \text{Tree Height}}{(0.02 * \text{Plot density})} \qquad \text{Equation 2.7}$$

The existing allometric equation within ZELIG to determine total leaf area (m^2, Sollins et al. 1973) was found to overestimate leaf area for subtropical trees, so the allometric equation was adjusted (reduced by 10%) to match observed leaf area index (LAI) results calculated from the field (Equation 2.8).

$$\text{Leaf Area} = 0.16094(D^{2.129}) * 0.9 \qquad \text{Equation 2.8}$$

2.2.5 Validation Methods

All model simulations were run for 800 years and replicated for 100 independent plots. The period when ZELIG-TROP began to reach a stable state (after it had been initiated from bare ground), and coincided with the observed mature forest, was seen around 200 years (total basal area used to determine stable state). All validation results from ZELIG-TROP (i.e. basal area, stem density, biomass) were averaged over 100 years (stand age of 200 to 300 years old), and from an average of 100 plots. The model simulated tree populations on 0.04-ha plots, a plot size typical of other subtropical forest models (Van Daalen and Shugart 1989). The model was validated by two methods. Both methods of validation tests compared ZELIG-TROP results to observed forestry data in Guanica Forest that was set aside for validation (0.15ha) and not used in parameterization. First, forest attributes from ZELIG-TROP such as total basal area, species composition, stem density, and total above-ground biomass were compared to observed forestry data from 1981-2009 (0.15ha area). To test the prediction and validity of the new forest succession model the Pearson correlation coefficient (r) was reported, between the last 10 years of observed forestry data and 10 time periods of ZELIG-TROP data starting at the mature successional phase; year 200.

The second method of model validation reported the magnitude of percent error between observed values and model runs started with two different initialization points; testing the appropriate method to initialize the model for this forest type. First, it was tested how well ZELIG-TROP would simulate the Puerto Rico forest using the last measured forest inventory, which was in 2009, as the initialization point. Therefore, the initial forest in ZELIG-TROP was the same density of trees, composition of species, and DBH values from 2009 inventory data as inputs, and forest growth was simulated for 250 years. The percent error between the simulated results and the 2009 census year were calculated, at 25-year intervals up to year 125 (five percent error calculations in total). These percent error results are termed “vegetation initialized” for the remainder of this paper. The second method compared ZELIG-TROP results from runs that were started from bare ground (un-vegetated), to field results from 2009. By comparing these two percent error tests (vegetation initialized and un-vegetated/bare ground model versions) to field data, model performance was assessed. It was predicted that the ‘vegetation initialized' version should match the observed census well, since the model was replicating the last census, as opposed to the model which started from bare-ground.

2.2.6 Model Testing: Transition of Abandoned Fields to Secondary Forest:

A second goal of this chapter was to report how secondary forests recover on patches of abandoned fields with degraded soils, an application of the validated ZELIG-TROP model. One site parameter in the ZELIG-TROP model was adjusted to simulate abandoned fields in Puerto Rico: field capacity (i.e. the amount of soil moisture or water content held in the soil after excess water has drained away). This helped distinguish the environmental differences between continuous, mature forest and abandoned, open fields that could develop into forest fragments. In forest edges, fragments, or open fields a decrease in soil moisture or water content is generally seen (Kapos 1989), due to increases in light level, air and soil temperature, vapor pressure deficit, and wind levels (Camargo and Kapos 1995, Laurance and Yensen 1991, Ming et al. 2007, Ranney et al. 1977, 1981).

In Puerto Rico the soil is variable throughout the southwestern region of the island (Lugo Camacho 2005), and particularly between locations of old agriculture, scrub/coastal forest, and mature forest (Perez Martinez 2007), thus influencing the vegetation above the soil. One study found that recovery of forests on abandoned fields around Guanica was highly affected by "poor root development and harsh soil conditions" (Molina Colon and Lugo 2006). The authors found that locations which had past history of land use (houses, farms, and baseball fields) within and around Guanica

Forest, were chosen on locales with some of the best soil, but all vegetation and roots had been removed, soil had been compacted, and increased runoff occurred. In scrub/coastal forests in Puerto Rico (which had land-use such as grazing) the field capacity and water content (%) is significantly lower than in the mature forest of Guanica State Forest (Lugo et al. 1978), Table 2.3 (4.9% vs. 23.0% for field capacity and 4% vs. 17.38% for water content). In this study the assumption was made that old fields are similar to scrub/coastal forests only in terms that they both have higher percentages of sand, are well drained, and low water availability. The main difference between old agricultural fields and scrub/coastal forests is the increase of rocks in scrub/coastal land. The mature forest has more organic matter, higher water content, and higher percentages of clay, which retains more water against drainage, falling in the soil series Aguilita stony clay and Guanica (Lugo et al. 1978, USDA 2008, Perez Martinez 2007).

Due to soils in abandoned fields having the combination of being more compacted, and also being similar to scrub/coastal forests (as described in Appendix A), it was hypothesized that soils in abandoned fields like scrub/coastal forests will contain less moisture. The lower field capacity was also assumed to be attributed to differences in soil properties (soil type, soil texture, bulk density) (Molina Colon and Lugo 2006, Lugo et al. 1978). The degraded soil conditions could also be attributed to overuse of land or soil disturbance (Chazdon 2003). Therefore field capacity in the ZELIG-TROP model for old agricultural fields was lowered. To mimic decreased soil moisture conditions in young secondary forests that were previously farmed, the field capacity (cm) was reduced by 25% (multiplied by 0.75), a conservative estimate compared to past studies (Table 2.3).

Old fields that have experienced degraded soils and physical changes over time were compared to simulated mature forests. Plots located in simulated secondary forests of stand age 5, 10, 20, 50, 80, 100, and 200 years were compared to two simulated mature forests (plots in continuous forest, on normal soil conditions, of age 50 and 100). A MANOVA was used examine differences in the nine forest ages and three dependent variables: total basal area, total biomass, and stem density. Canonical distances were compared between the two main canonical variables.

Table 2.3. Soil characteristics and properties between a scrub/coastal forest and old growth, mature forest in southwestern Puerto Rico, near or in Guanica Forest. All measurements taken at a depth of 15cm, unless otherwise specified. Water content for the scrub forest was taken in January; and for the mature forest from January to May, 1976. Molina Colon and Lugo (2006) reported bulk density from old farms at 0.8 g/cm^3 during January and from mature forests at 0.4 g/cm^3 from January to May. (*Lugo et al. 1978, §Lugo and Murphy 1986).

	Scrub/Coastal Forest	Mature Forest
	Very sandy, rocky	More clay like
Field Capacity % *	4.9	23.0
Water Content (5cm) % *	4.0	17.4
Water Content (15cm) % *	14.4	17.7
Bulk Density (g/cc) *	0.9	0.8
% Gravel *	3.1	0.0
% Sand *	89.0	21.7
% Silt *	5.0	18.6
% Clay *	3.0	59.6
Infiltration rate (cm/min) *	1.9	7.5
Organic Matter (5cm) % §	21.1	23.2
Organic Matter (15cm) % §	16.9	18.0-23.0

2.3 Results

2.3.1 Validation Results

The ZELIG-TROP simulation results for the SDF of Puerto Rico were qualitatively similar to the observed field data (Table 2.4), and accurately portrayed forest attributes and characteristics. Three variables were underestimated by ZELIG-TROP (basal area, density, and DBH) while two variables were overestimated (biomass and LAI). LAI was the variable least likely predicted by ZELIG-TROP ($r = 0.59$). All validation results (prior to the percent error tests) were from simulations where species are seeded onto bare ground.

Table 2.4. Averages (and standard deviations) of five forest attributes between the observed values recorded from Guanica Forest, PR during 1981-2009 on a plot scale (0.15ha) and the modeled ZELIG-TROP results. ZELIG-TROP results are averaged for 100 years, after an initial spin up of 200 years. Corresponding correlation coefficient values (r) between the last 10 years of observed data (2000-2009) and simulated values starting at year 200, the percent difference between the observed and simulated values, and the minimum and maximum range of a ZELIG-TROP simulation.

Forest Attributes	Observed 1981-2009	ZELIG-TROP Simulation	r (last 10 years)	% Difference	ZELIG-TROP Plot Level (Min/Max)
Total basal area (m^2 ha^{-1})	20.15 (2.3)	19.17 (1.72)	0.96	-5	14.7/23.9
Stem Density (stems ha^{-1})	9322 (1552.8)	8704 (475.2)	0.77	-7	7515/9877
Biomass (Mg ha^{-1})	64.78 (11.95)	69.90 (5.76)	0.72	+7	55.4/86.2
Leaf Area Index (LAI)	2.77 (0.66)	3.24 (0.39)	0.59*	+17	2.26/4.26
DBH (cm)	5.06 (0.29)	4.35 (0.13)	0.93	-14	3.98/4.71

*Using the last 30 years of observed data

2.3.2 Total Basal Area and Aboveground Biomass.

A close fit was found between the observed total basal area that was recorded from 1981 to 2009, and the simulated total basal area using the ZELIG-TROP model (Table 2.4). The observed Puerto Rico total basal area from the period 1981 to 2009 began around 17 m^2 ha^{-1}, reached 22 m^2 ha^{-1} in 1998, and then dropped to approximately 20 m^2 ha^{-1} in 2009, due to some stem loss from a hurricane in 1998 (Van Bloem et al. 2005). The field basal area is dynamic as a result of drought and hurricane disturbances. The average total basal area from ZELIG-TROP was 19.17 m^2 ha^{-1} ($r = 0.96$), tabulated once the model reached a stable, mature forest occurring at stand age 200-300 years, and from an average of 100 plots. While the average ZELIG-TROP total basal area was below the observed basal area, there was evidence that the model had potential to simulate a higher basal area that was representative of the Puerto Rican forest. This was seen when reviewing the simulation data at the individual plot level; at the plot level, the maximum basal area ranged from 21.73 to 26.75 m^2 ha^{-1}.

In Murphy and Lugo (1986a), the above-ground biomass from direct measurements, based on five 10m x 10m plots was 53 Mg ha^{-1}. In 1998 the biomass increased to 76.9 Mg ha^{-1}, and then decreased to 64.5 Mg ha^{-1} in 2009. This sharp increase in biomass in 1998 and decrease afterwards was also consistent with the trend in basal area and stem density. The Puerto Rico forest is routinely subject to disturbances. A category 3 hurricane, Hurricane George, hit southwestern Puerto Rico in September 1998 (after the sampling period in 1998), causing the sharp decrease in biomass (Van Bloem et al. 2005). ZELIG-TROP does not have disturbance implemented in the routines of the model, leading to the steady state results. The simulated biomass from ZELIG-TROP ranged from 55.4 – 86.2 Mg ha^{-1} for a mature forest, averaging 69.9 Mg ha^{-1}, r = 0.72 (Table 2.4), an overestimation of the observed average 64.8 Mg ha^{-1}. The overestimation is likely due to errors in the allometric equation used, given that the basal area and DBH was underestimated. As a comparison, the biomass for a neotropical wet forest of French Guiana for trees measured at 10cm DBH ranged from 284 to 309 Mg ha^{-1} (Chave et al. 2001). Using the Brandies et al. (2006) allometric equation, the simulated biomass for Puerto Rico was capable of reaching the peak witnessed in 1998.

2.3.3. Species Composition.

The forest simulator, ZELIG-TROP, was able to predict a community composition dominated by pioneer species in the early development of the forest, followed by a more climax community composition once the forest reached a mature status. When the simulated forest was in its early development (first 15 years), the dominant species were wind-dispersed, pioneer species *Pisonia albida* and *Exostema caribaeum* (Figure 2.1, early successional species with an asterisk). As succession progressed from bare ground to mature forest, the contribution of *Exostema caribaeum* to total basal area decreased over time at a quicker rate than *Pisonia albida.* By simulation year 200 (mature forest state) the five known pioneer species accounted for 25% of the total basal area. The seven known late successional species accounted for 63% of the total basal area. The remaining six species whose successional status was unknown, or are likely to be in an intermediate class, accounted for 12% of the total basal area.

To further evaluate how closely the model predicted each species basal area individually, Figure 2.2 compared the three field sampling periods to ZELIG-TROP simulations. Over the 1981-2009 sampling period the three main species were *Gymnanthes lucida*, *Pisonia albida,* and *Coccoloba microstachya,* and varied in basal area over the three sampling periods by a large amount. The model only predicted 1 out of these 3 species (*Gymnanthes lucida*) in the top three. Instead, ZELIG-TROP predicted *Coccoloba diversifolia* as the dominant species with the highest amount of basal area. The model did not display the same variability in changes in species composition as seen in the field, although the modeled species-specific regeneration is based off of characteristics observed in the field. The major difference with respect to successional traits was that the observed forest was approximately half pioneer species, accounting for an average of 51% of the basal area. The known late successional species accounted for 31% of the total basal area (versus 63% by ZELIG-TROP). Most species simulated in ZELIG-TROP (except for three) had basal areas that were below the observed basal area from one of the three sampling periods, but not necessarily all of the sampling periods. In both the modeled results and in the field data *Eugenia foetida*, *Guettarda krugii*, *Erithalis fruticosa*, and *Crossopetalum rhacoma* contributed the least to basal area (summing to 2% and 6% in modeled and field data respectively). In the field *Eugenia foetida* was found not to be rare, but instead only common in juvenile classes, thus usually not obtaining large basal area.

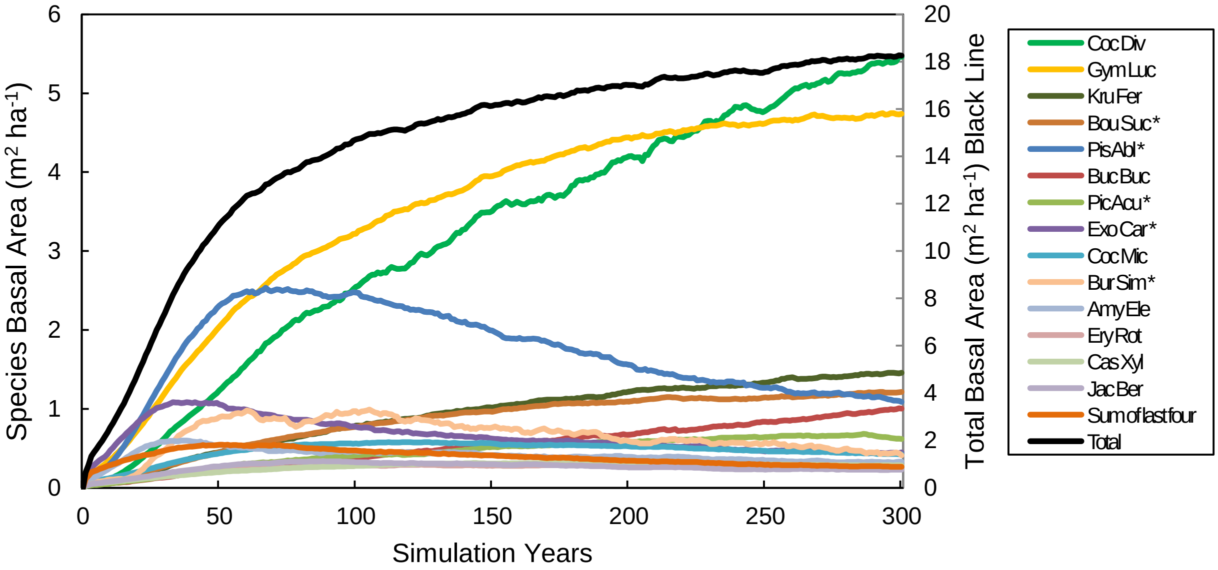


Figure 2.1. ZELIG-TROP simulated successional development by species, initiated from bare ground at year 1 and simulated for 300 years. Species composition reported in basal area (m^2 ha^{-1}) for 18 species seen in Puerto Rico subtropical dry forest. (The early successional species have an asterisks).

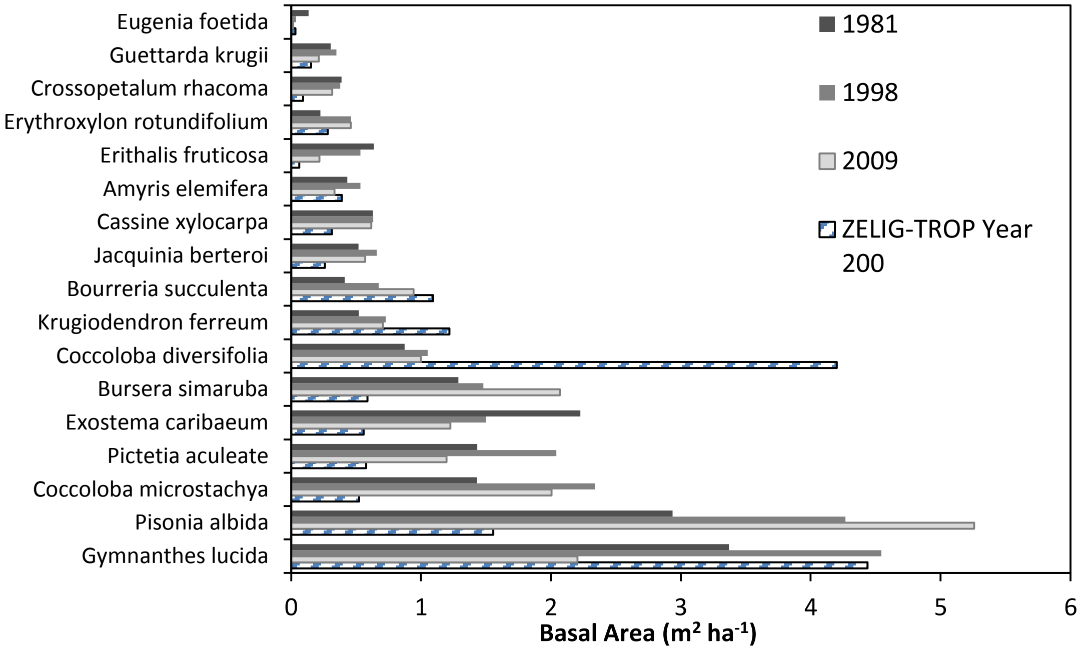


Figure 2.2. Basal area ($m^2 ha^{-1}$) for 18 tree species from Guanica Forest, recorded from the census periods 1981, 1998, and 2009, as well as from the ZELIG-TROP simulation at year 200.

2.3.4. Density Analysis

Guanica forest is a dense forest, due to small DBH of the tree species and prevalence of stem sprouting. Correctly modeling the high stem density is a crucial step needed for model validation. The observed stem density was highly variable, ranging from 7,944 to 11,509 stems ha^{-1} (Average: 9322, SD: 1,553). ZELIG-TROP predicted a narrower, more constant range of stem density ranging from 7,515 to 9,877 stems ha^{-1} over 100 years (Average: 8704, SD: 475.2, r = 0.77). As with the simulated basal area, results were tabulated once the model reached a stable, mature forest occurring at stand age 200-300 years, and from an average of 100 plots. At the individual plot level (0.04 ha), the maximum stem density ranged from 9,525 to 10,475 stem ha^{-1}.

Simulating the frequency of live stems in each DBH (cm) size class is crucial for understanding the structure of the forest. Once the simulation reached a mature, stable population, (at year 200) the size class distribution was a classic reverse-J shape (Figure 2.3a). The size class with the most frequent number of stems was 2-3 cm DBH and decreased in a consistent fashion for each subsequently increasing size class. The only exception was a small increase at the 10-15 cm DBH size class. The modeled mature forest had a consistent number of stems in each size class during each time step, showing that the model was uniform through iterations. The observed size class distribution was more variable than the model predictions and the dominant size class varied from 4-5 cm to 5-6 cm DBH (Figure 2.3b). The observed Puerto Rico forest consisted of stems with larger DBH compared to the simulated forest. This followed the pattern that the observed forest had higher basal area than the simulated forest.

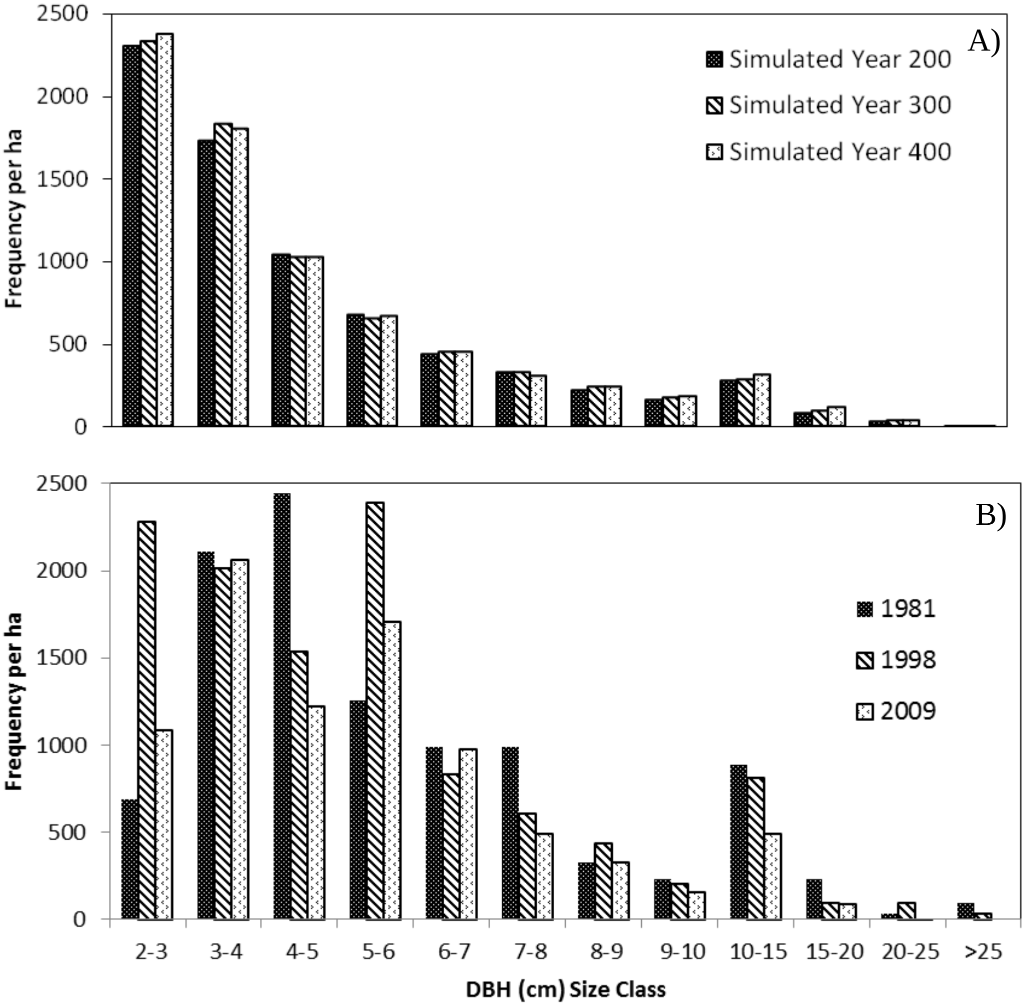


Figure 2.3. A) ZELIG-TROP simulated size class distribution for 12 DBH (cm) size classes. Size class distribution once the model reached steady-state equilibrium, simulated plots from 200-400 years. B) Observed size class distribution (per hectare) of Guanica State Forest measured from three different censuses: 1981, 1998, and 2009, for 12 size classes starting at 2.5cm DBH and going to >25cm DBH.

2.3.5. Percent Error Testing Using Actual Data

The percent errors for the ‘vegetation initialized’ runs after initializing the model with the 2009 replication were high (Table 2.5). Percent error for total basal area was highest, averaging 26.85% for all plots between initiation and 125 years after starting the model. During the first 25 years the smallest percent error for two of the forest attributes was observed, excluding stem density. The average percent errors for stem density and above ground biomass were lower than total basal area (19.2% and 16.7%). The observed Puerto Rico forest data used in the vegetated version and for purposes of accuracy testing can be seen in the middle of Table 2.5.

ZELIG-TROP, which simulated a forest *without* a user-provided initialization point and started from bare ground, had lower percent errors than the ‘vegetation initialized’ version (lower portion of Table 2.5). The model performed well and was in closer agreement with the observed data, after the model was allowed to progress through natural succession based on the parameterization values at year zero. The ‘vegetation initialized’ version also used the same parameterization values (Table 2.2) as the bare-ground version, but the bare ground runs yielded a more homogenous stand over time, and higher values of basal area and biomass (Table 2.5) that were realistic of the observed forest. It was predicted that the results using the mimicked forest conditions would be more accurate, when in fact the model which developed vegetation on its own, without user provided data was more successful.

When starting the simulation from bare ground, total stem density (stems ha^{-1}) was the forest parameter that was most accurately predicted. The average percent error was 1.5% between the model predicted results and the 2009 census period (16.0%, 24.4% for 1981 and 1999 respectively). Second to total stem density was basal area, averaging 5.3% difference between the model results and the observed 2009 forest value (7.7%, 14.4% for 1981 and 1999 respectively). The parameter that was least likely to be predicted by the model was total biomass, averaging 8.5% difference (31.9%, 9.1% for 1986 and 1999 respectively).

Table 2.5 Top portion: ZELIG-TROP results for total basal area (m^2 ha^{-1}), total stem density (stems ha^{-1}), and above ground biomass (Mg ha^{-1}) for 25 year intervals starting from vegetation initialized simulations, using a replication of the observed Puerto Rico forest from 2009 as the initialization point, and percent error values between the simulation results and the 2009 field data (2009 field data found in the middle of the table). Bottom portion: ZELIG-TROP results from un-vegetated simulations (bare-ground at year 0) for 25 year intervals, between the simulated time period 200-300 years, a time period when the forest has reached maturity (thus can be compared to vegetation initialized runs). Percent error values are between the main ZELIG-TROP simulation results and the 2009 census period.

	Vegetation Initialized ZELIG-TROP			Percent Error		
Simulation Year	Total Basal Area (m^2 ha^{-1})	Total Density (stems ha^{-1})	AG Biomass (Mg ha^{-1})	% Error BA	% Error Density	% Error Biomass
25	18.15	7069	67.68	10.33	18.72	5.01
50	13.66	6828	50.24	32.53	21.48	22.04
75	13.8	6959	51.2	31.97	19.98	20.56
100	14.28	7086	52.95	29.44	18.51	17.84
125	14.17	7188	52.87	29.97	17.35	17.97
ZELIG-TROP Average	14.81	7026	54.99	26.85	19.21	16.68
2009 Field Data	20.2	8696	64.5	NA	NA	NA
	Un-Vegetated ZELIG-TROP			Percent Error		
200	18.56	8409	67.34	8.29	3.3	4.48
225	18.89	8608	68.87	6.68	1.01	6.86
250	19.16	8703	69.81	5.35	0.08	8.32
275	19.61	8860	71.47	3.12	1.88	10.9
300	19.88	8932	72.91	1.78	2.71	13.13
ZELIG-TROP Average	19.22	8702.4	70.08	5.28	1.45	8.46

2.3.6 Model Testing: Transition of Abandoned Fields to Secondary Forest

In general, the abandoned fields which were simulated with degraded soil and physical changes can take 100 years to generate a forest structure that resembled plots located in mature forests (Figure 2.4). A multivariate analysis of three dependent variables (stem density, biomass, and basal area) with forest age (six secondary forests and one continuous mature forest) was highly significant (MANOVA, $p<0.001$, df=349, d=3). After running a canonical analysis, the first canonical variable (y-axis = forest age) showed a distinctive separation between the young secondary forests and the mature forest plots (Figure 2.4). Older secondary forests (>50 years) did show some similarities with plots in a mature forest, from overlapping of data points in the canonical analysis.

Simulated succession on abandoned fields are able to resemble a mature forest structure (in terms of basal area, biomass, and stem density), but there was a 50-100 year delay. For example, recovered secondary forests have forest attributes that were similar to plots in a 50 year old mature forest also starting from bare ground, but it took 100 years for the secondary forests after field abandonment to reach this resemblance (therefore a 50 year difference or delay). The similarity between secondary plots at 100 years old and mature plots at 50 years old was seen by overlapping data points between the two forest types in Figure 2.4 and 2.5, as well as from separate ANOVA tests: basal area and biomass between 100 year secondary forest and 50 year cut regenerated mature forest are $p=0.898$ and $p=0.918$ respectively, showing strong similarity, or no significant differences. This showed that secondary forests that were modeled on abandoned fields with decreased soil moisture develop quite differently and at a slower rate than mature forests. With increasing forest age, from young secondary forest (age 5) to old secondary forest (age 200) there was increasing basal area, biomass, and density (Figure 2.5). There was a strong positive linear relationship between basal area and biomass. There was more scatter and variation between total stem density and biomass or basal area, but the relationship still showed a general logarithmic trend for stem density and biomass. For very young secondary forests (age 5-20 years), there was a large increase in stem density, but the biomass and basal area was very low (owing to many small stems). For recovering abandoned field plots that are 50 to 100 years of age, the stem density stayed consistent with young forests (or only slightly increases), but the biomass and basal area increased. Eventually at an old secondary forest age or mature forest status the biomass and basal area leveled out.

Modeled secondary forest plots, starting as early as 20 years old, had simulated forest heights (both average and maximum height, meters) which were similar to the modeled mature forest (Table 2.6). Within 20-50 years secondary forest plots had reached average and maximum height values that are similar to plots in a 50-100 year old mature forest. As a comparison to field data, abandoned fields in the FIA census between 2006 and 2008 had total basal area of 2.38 m^2 ha^{-1}, total biomass of 9.11 Mg ha^{-1}, density of 558 stems ha^{-1}, and average height of 4.5 m (Table 2.6). FIA data were taken from 4 young secondary forest plots in the dry subtropical forest of southwestern Puerto Rico, on private land that was under some form of use. Upon comparison the modeled secondary forest at stand age 10-20 years looked similar to the observed FIA secondary forest data in terms of DBH and biomass.

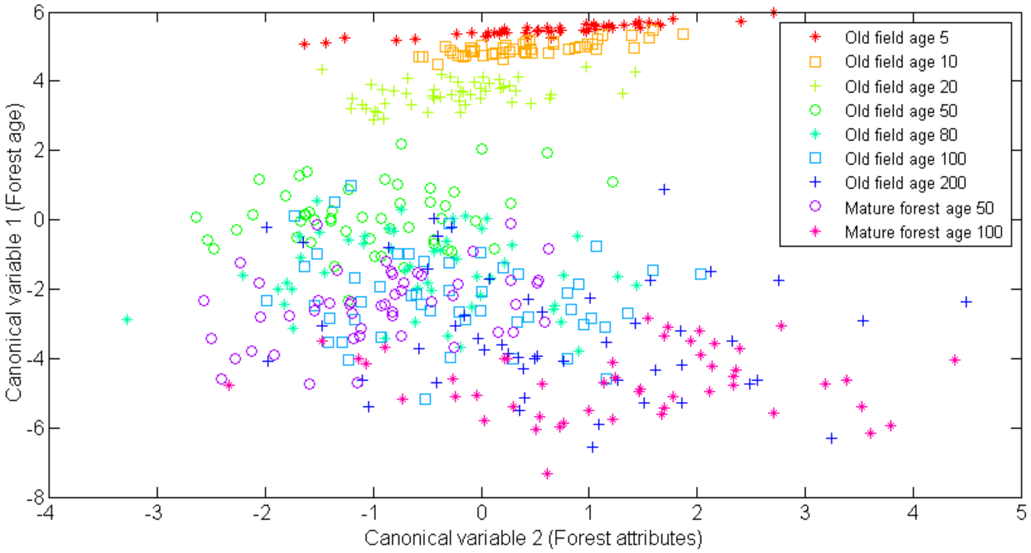


Figure 2.4. Recovery of abandoned fields simulated on degraded soils. Canonical distances between two canonical variables after running a MANOVA. Canonical variable 1 (forest age) roughly separates the mature forests (age 50 and 100 years) from the secondary forests (plots of age 5, 10, 20, 50, 80, 100, and 200 years). Canonical variable 2 separates basal area, biomass, and stem density.

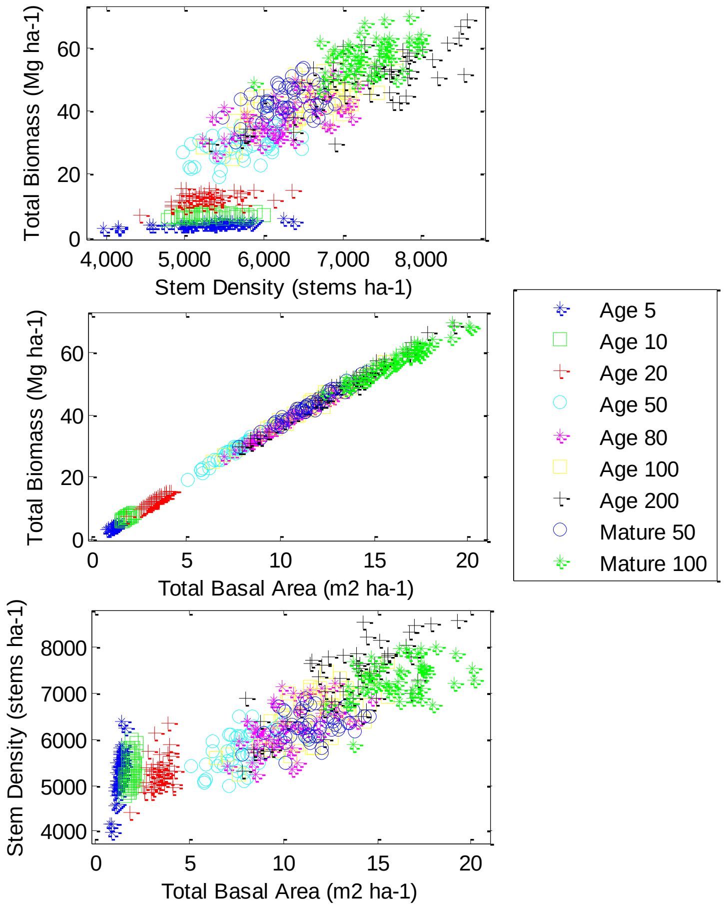


Figure 2.5. Simulated forest recovery on abandoned fields with degraded soil conditions. Scatterplot of 3 forest structure variables: basal area vs. stem density, basal area vs. biomass, and stem density vs. biomass, for all forest ages and forest types (plots in seven modeled secondary forests from age 5 to 200 years old and two mature forests at 50 and 100 years).

Table 2.6. Simulation of forest regeneration on abandoned fields. Average basal area, biomass, stem density, LAI, average height, and maximum height for 7 modeled secondary forests ranging from age 5-200 years, 2 modeled mature forests from age 50-100 years, and from FIA field data from 4 plots in young sapling secondary forest, estimated around 10 years old.

Stand Age (years)	Basal Area (m^2 ha^{-1})	Total Biomass (Mg ha^{-1})	Total Density (stems ha^{-1})	LAI$^+$	Average Height (m)	Max Height (m)
Old field: 5 yrs	1.23	4.53	5284	0.08	2.88	5.0
Old field: 10 yrs	1.88	6.93	5275	0.14	3.39	6.1
Old field: 20 yrs	3.33	12.51	5266	0.35	3.84	7.4
Old field: 50yrs	7.84	29.49	5766	1.18	4.18	8.5
Old field: 80 yrs	10.31	38.26	6278	1.68	4.06	8.6
Old field: 100 yrs	11.53	42.46	6503	1.9	4.11	8.5
Old field: 200 yrs	13.41	49.26	7248	2.21	4.10	8.0
Mature Forest 50	11.49	42.59	6269	1.92	4.12	7.5
Mature Forest 100	16.06	57.49	7304	2.73	3.99	8.7
FIA Data**	2.38*	9.11	558	NA	4.50	13.5

* Seedling/sapling forest: 0.25-1.25 cm DBH

** Young secondary forest, close to current agriculture, private land (1 ha)

LAI (Leaf area index) is similar to canopy coverage in this study

2.4 Discussion

2.4.1 Model Validation

The creation and validation of a new gap model ZELIG-TROP for the dry subtropical forest of Puerto Rico was quite satisfactory. The prediction of four forest attributes, total basal area, basal area by species, total biomass, and total stem density were similar to observed values from Guanica Forest. Overall ZELIG-TROP did well at predicting the unique attributes and structure of a dry forest system: low basal area, low LAI, low biomass, and high density of stems. ZELIG-TROP can be used as a tool to simulate community patterns in relation to the ecological characteristics of the species, as results showed patterns that changed over time that were related to life histories measured in the field. Once ZELIG-TROP reaches a mature, fully developed forest starting around year 200, a late-successional forest is predicted (Figure 2.1). While the model predicted a more late successional forest, there was still a mix of pioneer species.

It was found that the model which begun in an un-vegetated state (which was used as the main procedure for running ZELIG-TROP) performed well, after comparing the percent error values between two different scenarios. It was anticipated that because the vegetation initiation version begun with values that were exact to the observed forest, then the similarity would be high, and percent error between the predicted and observed would be low. In actuality the simulated forest parameters (basal area, biomass, and stem density) fluctuated over time and did not compare to the field data. Contrary to what was expected, the percent error values were lower when comparing the main validation results (runs starting from bare ground) to the three census periods, than when using the vegetation initialized model runs. For a SDF system in Puerto Rico, and in similar locations, starting future gap models from bare ground, and letting the model develop forest succession should be highly considered, but not always preferred.

In the field a high fluctuation in basal area per species from 1981 to 2009 (species ranging from 2% to 56% change in basal area, Figure 2.2) was observed, and up to 4.45 m^2 ha^{-1} in total. The common species were alternating over the 28-year sampling period. For example the common species *Gymnanthes lucida* and *Coccoloba microstachya* were erratic over the sample period, while the pioneer *Pisonia albida* kept increasing (Figure 2.2). The modeled results were very stable over long time periods, possibly due to the model operating at a larger landscape scale (averaging over 100 plots) and also the absence of disturbance. In contrast the field data set aside for validation was at the plot scale (0.15 ha), explaining the lack of model prediction for species composition. The ability to correctly simulate at a single plot level, as opposed to the landscape level, is challenging. Another likely explanation is that the model had an absence of past history and disturbance, and thus estimated a stable, late successional forest.

2.4.2 Need to incorporate disturbance into tropical gap modeling

Natural disturbances are inextricable components of tropical systems and these ecosystems can be dependent on disturbance regimes (Brokaw and Walker 1991, Tanner et al. 1991, Zimmerman et al. 1996). In this report ZELIG-TROP was a disturbance free simulation, but including a disturbance-related mortality and effects from external disturbances has been achieved and will be reported in later studies. The simulated results showed that forest parameters remained very constant over time (average of 100 plots), while the field data had much more variability (Table 2.4, Figure 2.2, Figure 2.3), most likely due to disturbance in the system.

The year 1999 had slightly higher values for all forest variables (records prior to 1981 are not available), and could be due to the forest being in a dynamic equilibrium and the non-equilibrium state of vegetation (Shugart 1984), and all percent errors comparing 1999 observed data and modeled results were high. The increase in forest size (basal area, density, and biomass) in 1999 could have been the lingering effects of recovery (Brokaw and Walker 1991) or sprouting response from previous hurricanes that had effects on Guanica (such as Hurricane Hortense in 1996). But with Hortense only being a category 1 storm, an explanation could be simple growth and accumulated biomass over a disturbance-free period prior to Hortense. The sharp drop in forest variables after 1999 are most likely due to immediate and delayed mortality effects (a phenomenon that is common in tropical systems; Walker 1995) of the category 3 Hurricane Georges that passed directly over Guanica in 1998 (Van Bloem et al. 2005, 2007). To accurately portray forest dynamics, disturbance should be incorporated into the model, a topic that will be evaluated in the following chapter. Once the simulated forest reached an equilibrium state, the number of individuals and forest structure remained fairly uniform. However, implementing disturbance regimes and replacing the stable state produced in the model with a forest mosaic that is dynamic over time seems more realistic for the investigated forest type.

2.4.3 Relation to Previous Gap Models in the Tropics.

This is the first application of ZELIG for a dry subtropical forest. There has been success of other gap models in wet tropical forests of Puerto Rico, such as FORICO (Doyle et al. 1981), an early version of ZELIG (O'Brien et al. 1992), and SORTIE (Uriate et al. 2009). Outside of Puerto Rico, there are a suite of gap models that have been linked over time and applied to tropical forests around the world (described in the introduction; FORMIX3, FORECE, FORMIND, KIAMBRAM, OUTENIQUA).

The FORICO gap model (Doyle et al. 1981) applied a conceptual framework that had originated in temperate regions to a tropical region with high diversity. The FORICO model was able to predict the stand density and compositional characteristics of the wet subtropical forest in Puerto Rico. Simulated leaf area, abundance of trees, and total biomass were consistent with observed data within 1-12%, 3%, and 8%-33% respectively. O’Brien et al. (1992) used a spatially explicit IBM to extend the Doyle et al. (1981) findings over a range of disturbance frequencies, and to inspect the sensitivity of these responses to spatial effects. ZELIG-TROP was able to utilize a more detailed approach to replicate a Puerto Rican dry forest that is not studied as thoroughly as the wet forest in the O’Brien et al. (1992) study, and still replicate the forests well. Allometric equations specific to leaf area, leaf area distribution, crown length and width, and crown shape were all modifications made to ZELIG-TROP to resemble the subtropical dry Puerto Rico forest. The FORICO and SORTIE model were successful at implementing the role of hurricane disturbances into gap models for a wet forest (FORICO at a somewhat basic level, SORTIE more detailed level). But it would still be beneficial to simulate disturbance effects for SDFs, and dynamically include the role of disturbances within ecosystems.

The modifications made to ZELIG-TROP aid in creating a more realistic model for future modeling in SDFs, but additional improvements could be incorporated. The model was successful at incorporating basal-sprouting, which is highly common in this forest and the predominant mode of reproduction (Dunphy et al. 2000, Molina Colón 1998, Murphy and Lugo 1986a, Murphy et al. 1995, Van Bloem 2003). Sprouting model components resulted in the gap model generating realistic stem density. In initial test runs of ZELIG without the sprouting routine, the total density was further below the observed value of total individuals, averaging around 5,000 stems ha^{-1}. This suggests that basal-sprouting is needed in the model framework to increase the number of stems. Estimations of leaf area index were less accurate than the other forest variables. This could be due to inaccurate measurements in the field (challenging canopy) as well as limitations in the model calculations of leaf area per individual that could be improved upon.

2.4.4 Model Testing: Transition of abandoned fields to secondary forests

Results showed that when abandoned fields have soil degradation, then recovery to plots that are typical of mature, continuous forest is possible, but there was a delay (100+ years). ZELIG-TROP showed that old field regeneration and mature forest regeneration were not equal, due to the changes in soil conditions. Other factors to test could also be associated with dispersal limitation of many natives, exotic species invasion, or colonization of ferns and herbaceous species (Aide et al. 1995). Degraded soil conditions could have occurred from multiple possible causes in this study system. Some examples are from over-use of the land through development or agriculture resulting in soil compaction, erosion, reduced organic matter, altered soil microbial communities, and reducing the capabilities to retain water (Chazdon 2003, Pares-Ramos et al. 2008). Second, previous land-use and human occupation happened to occur on locations where the soil had inherently lower field capacity and higher sand content compared to locations with old-growth forests, potentially producing an environment unsuitable for denser forests (Molina Colon and Lugo 2006, Perez Martinez 2007). Ability to restore forest ecosystems strongly depends on the level of soil degradation and disturbance (Chazdon 2008).

How does the modeled results compare with other studies that look at abandoned fields that have gone through different stages of secondary forest succession? ZELIG-TROP showed that abandoned fields transitioning into secondary forests contained a species composition and species richness that resembled a mature forest. Convergence of species composition between old fields and mature forests in SDFs matched the results found by Lebrija-Trejos et al. (2008) and also the expectations of Ewel (1980) and Murphy and Lugo (1986b). While similar species richness was present between secondary and mature plots, there was lower stem density and smaller sized trees per hectare.

In simulations stem density (in a short period of time) was the fastest variable to recover. This abundance in stem density also persisted over the course of the simulation (200 years), and there was no decline due to large scale die-backs or crowding. These same phenomena were also seen in Lebrija-Trejos (2008), as well in dry sites that had temperature/precipitation ratios (T/P) of 2.8-4.0 and 5-6 months of dry season (DeWalt et al. 2003, Gonzalez-Iturbe et al. 2002, Pereira et al. 2003, and predictions by Brown and Lugo 1990), but not in wetter sites with characteristics closer to subtropical wet forests (Aweto 1981, Kennard 2002, Ruiz et al. 2005). While stem density was fastest to recover in abandoned fields, it was still not as high as a mature forest (6503 vs. 7304 stems ha^{-1} for old fields vs. mature).

In Brown and Lugo’s (1990) review of secondary forests in the tropics, they estimated that tree height and crown cover exhibited the fastest growth increments, with basal area and biomass being the slowest to recover. They predicted that this early allocation of resources to the canopy aids in helping with light capture and early survival, with a later shift to other structural developments (Brown and Lugo 1990, Guariguata and Ostertag 2001). Aide et al. (1995) confirmed that above ground woody biomass in transitioning abandoned fields in northeastern Puerto Rico (wetter climate), was slower to recovery (low levels after 35 years), compared to species richness and stem density, and forest recovery on old fields is slower compared to natural disturbances in the tropics. ZELIG-TROP operates similarly with basal area and biomass being the slowest variables to develop. While, average tree height and crown cover were faster to recover (Table 2.6), presumably in an attempt to capture available light.

Subtropical dry forests have been labeled as having higher resilience than wet or rain forests (Ewel 1977, Murphy and Lugo 1986b), where resilience is defined as recovery back to a defined original state after a disturbance or perturbation. This should not be confused with resistance which is characteristically low in SDFs; resistance defined as the ability for a system to remain unchanged during or after a disturbance (but see Van Bloem et al. 2005). In Ewel (1977) and Murphy and Lugo (1986b) it was predicted that a return to original height can occur in 9-14 years, taxonomic recovery rate was high, but overall recovery occurs in 150+ years, or even 80+ years, if soils are not disturbed. This brings to question, should the *time scale* of resilience (or “elasticity”) for some SDFs be reevaluated? This study showed that due to decreased soil moisture, abandoned fields going through secondary forest succession can take 200 years to recover, if soils are degraded. Furthermore, later successional traits such as high basal area and biomass typical of structurally established forests never reach levels comparable to mature forests. However the current models did not include introduced species (ex. *Leucaena leucocephala*) which may facilitate forest regeneration on old fields (Perez

Martinez 2007). The advantage to simulation models is the ability to predict many years into the future, a luxury that cannot be accomplished with field studies. The simulations reported here suggest that forest resilience in certain plots with previous land use might take longer than expected.

2.5 Conclusions

Overall the gap model ZELIG-TROP was successfully used for the first time in a subtropical dry forest ecosystem, in Puerto Rico. The simulated results, which started from bare ground, have a strong resemblance to the observed forest structure measured over the past 30 years. Basal area was the forest variable more accurately predicted. Improvements with future updates could involve including additional species to the 18 modeled in this report. Disturbance, such as hurricane damage and effects, should be included in future studies in this system. However, the addition of new mortality calculations, a new PET equation, a new sprouting routine, new allometric equations, and crown architecture modifications were useful. ZELIG-TROP was an appropriate model to simulate the challenging and unique forest characteristics of a SDF.

Upon successful model validation, applying the model to a real-world application (evaluation of the transition of young secondary forests from abandoned fields to a continuous, mature forest) was achieved. Plots that were found in degraded soil conditions (conditions with decreased soil moisture, due to decrease field capacity) took longer than expected to recover to a mature forest, up to 100-200 years. Apart from forest height, it would take a secondary forest to grow for 100 years to become similar to a mature forest. Longer recovery times created a longer delay, such that secondary forest that grew for 200 years were similar to a 100 year mature forest, displaying a longer time frame of forest resilience. Upon successful modeling of secondary forest succession, ZELIG-TROP can be applied for testing the reduction in carbon emissions from forest recovery in SDFs in Puerto Rico, as well as predicting carbon estimations/carbon credits. Future use of this forest model is encouraged to understand the changing dynamics of threatened tropical forests.

2.6 Literature Cited

Aide, T.M., J. K. Zimmerman, L. Herrera, M. Rosario, and M. Serrano. 1995. Forest recovery in abandoned tropical pastures in Puerto Rico. Biotropica 77, 77-86.

Aide, T.M., J. K. Zimmerman, M. Rosario, and H. Marcano. 1996. Forest recovery in abandoned cattle pastures along an elevational gradient in northeastern Puerto Rico. Biotropica 28, 537–548.

Aide, T. M., J. K. Zimmerman, J. Pascarella, J. Marcano-Vega, and L. Rivera. 2000. Forest regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology. Restoration Ecology 8, 328–338.

Aweto, A. O. 1981. Secondary succession and soil fertility restoration in southwestern Nigeria: I. Succession. J. Ecol. 69, 601–607.

Birdsey, R. A., and P. L. Weaver. 1982. The forest resources of Puerto Rico. Resource Bull. SO-85. USDA Forest Service, South. For. Exp. Stn, New Orleans, Louisiana.

Botkin, D. B., Janak, J. F., and Wallis, J. R.. 1972a. Rationale, Limitations and Assumptions of a Northeastern Forest Growth Simulator, IBM J. Res. Develop. 16, 101–116.

Botkin, D. B., J. F. Janak, and J. R. Wallis. 1972b. Some Ecological Consequences of a Computer Model of Forest Growth. J. of Ecology. 60, 849-872.

Brandeis, T. J., E. H. Helmer, and S. N. Oswalt. 2003. The status of Puerto Rico’s Forests, 2003. United States Department of Agriculture. Forest Service, Southern Research Station, Resource Bulletin SRS-119.

Brandeis, T. J., M. Delaney, B. R. Parresol, and L. Royer. 2006. Development of equations for predicting Puerto Rican subtropical dry forest biomass and volume. For. Ecol. and Mang. 233, 133-142.

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

Brown, S. and A. E. Lugo. 1982. The Storage and Production of Organic Matter in Tropical Forests and Their Role in the Global Carbon Cycle. Biotropica, 14, 161-187.

Brown, S. and A. E. Lugo. 1990. Tropical secondary forests. J. Trop. Ecol. 6, 1–32.

Bullock, S. H., H. A. Mooney, E. Medina. 1995. Seasonally dry tropical forests. Cambridge University Press. Cambridge, Massachusetts, USA.

Busing, R. T. and A. M. Solomon. 2004. A Comparison of Forest Survey Data with Forest Dynamics Simulators FORCLIM and ZELIG along Climatic Gradients in the Pacific Northwest. U.S. Geological Survey Scientific Investigation Report 2004-5078.

Camargo J. L. C., and Kapos V. 1995. Complete edge effects on soil moisture and microclimate in central Amazonia forest. J. of Tropical Ecology. 11, 205–221.

Canadell, J. G. and M. R. Raupach. 2008. Managing forests for climate change mitigation. Science. 320, 1456-1457.

Castilleja, G. 1991. Seed germination and early establishment in a subtropical dry forest. Ph.D. Dissertation. Yale University, pp. 209.

Chave, J., B. Riera, M. Dubois. 2001. Estimation of biomass in a neotropical forest of French Guiana: spatial and temporal variability. J. of Tropical Ecology. 17, 79-96.

Chazdon, R. L. 2003. Tropical forest recovery: legacies of human impact and natural disturbances. Perspectives in Plant Ecology, Evolution and Systematics. 6, 51-71.

Chazdon, R. L. 2008. Beyond deforestation: restoring forests and ecosystem services on degraded lands. Science. 320, 1458-1460.

Coffin, D.P., Urban, D.L., 1993. Implications of natural history traits to system-level dynamics: comparisons of a grassland and a forest. Ecol. Model. 67, 147–178.

Cumming, S. G. and Burton, P. J. 1993. A Programmable Shell and Graphics System for Forest Stand Simulation, Environ. Software. 8, 219-230.

Cumming, S. G. and Burton, P. J. 1994. 'Zelig ++ v0.9 Documentation, User Notes and Installation Guide', Technical report, Department of Forest Sciences, University of British Columbia.

Cumming, S. G. and Burton, P. J. 1996. Phenology-mediated effects of climate change on some simulated Britich Columbia forest. Climatic Change. 34, 213-222.

DeFries, R. S., R. A. Houghton, M. C. Hansen, C. B. Field, D. Skole, J. Townshend. 2002. Carbon emissions from tropical deforestation and regrowth based on satellite observations for the 1980s and 1990s. PNAS. 99, 14256-14261.

Dewalt, S. J., S. K. Maliakal, and J. S. Denslow. 2003. Changes in vegetation structure and composition along a tropical forest chronosequence: Implications for wildlife. For. Ecol. Manage. 182, 139–151.

Ditzer, T., R. Glauner, M. Forster, P. Kohler, and A. Huth. 2000. The process-based stand growth model Formix 3-Q applied in a GIS environment for growth and yield analysis in a tropical rain forest. Tree Physiol. 20, 367–381.

Doyle, T. W. 1981. The Role of Disturbance in the Gap Dynamics of a Montane Rain Forest: An Application of a Tropical Forest Succession Model, *In* West, D. C., Shugart, H. H., and Botkin, D. B. (eds.), Forest Succession: Concepts and Application, Springer, New York a.o., pp. 56–73.

Dunevitz, V. L. 1985. Regrowth of clearcut subtropical dry forests: Mechanisms of recovery and quantification of resilience. Thesis, Michigan State University, East Lansing, Michigan.

Dunphy, B. K., P. G. Murphy, and A. E. Lugo. 2000. The tendency for trees to be multi-stemmed in tropical and subtropical dry forests: Studies of Guanica Forest, Puerto Rico. Tropic. Ecol. 41, 1-7.

Ewel, J. J. 1977. Differences between wet and dry successional tropical ecosystems. Geo. Eco. Trop. 1, 103-117.

Ewel, J. J. 1980. Tropical succession: manifold routes to maturity. Biotropica 12, 2-7.

FAO. 2001. Global forest resources assessment. Main report. FAO Forestry paper 140. Food and Agriculture Organization of the United Nations, Rome Italy.

FAO. 2007. State of the world’s forest. Food and Agriculture Organization of the United Nations, Rome Italy.

Fyllas, N.M., Phillips, O.L., Kunin, W.E., Matsinos, Y.G., Troumbis, A.Y. 2007. Development and parameterization of a general forest gap dynamics simulator for the North-eastern Mediterranean Basin (GREek FOrest Species). Ecol. Model. 204, 439–456.

Fyllas, N.M., Politi, P.I., Galanidis, A., Dimitrakopoulos, P.G., Arianoutsou, M. 2010. Simulating regeneration and vegetation dynamics in Mediterranean coniferous forests. Ecol Model. 221, 1494-1504.

Gonzalez-Iturbe, J. A., I. Olmsted, and F. Tun-Dzul. 2002. Tropical dry forest recovery after long term Henequen (sisal, *Agave fourcroydes* Lem.) plantation in northern Yucatan,Mexico. For. Ecol.Manage. 167, 67–82.

Grainger, A. 2010. Uncertainty in the construction of global knowledge of tropical forests. Progress in Physical Geography. 34, 811-844.

Grau, H. R., T. M. Aide, J. K. Zimmerman, J. R. Thomlinson, E. Helmer, and X. Zou. 2003. The ecological consequences of socioeconomic and land-use changes in postagriculture Puerto Rico. *Bioscience* 53, 1159–1168.

Guariguata, M. R., and R. Ostertag. 2001. Neotropical secondary forest succession: Changes in structural and functional characteristics. For. Ecol. Manage. 148, 185–206.

Holdridge, L.R. 1967. Life Zone Ecology. San Jose, Costa Rica: Tropical Science Center.

Huth, A., Ditzer, T., Bossel, H., 1998. The rain forest growth model FORMIX3D Model description and analysis of forest growth and logging scenarios for the Deramakot forest reserve (Malaysia). GoÈttinger BeitraÈge zur Land- und Forstwirtschaft in den Tropen und Subtropen 124 (ISBN 3±88452±385±6). Erich Goltze, GoÈttingen, pp. 182.

Huth, A., Drechsler, M., Kohler, P., 2004. Multicriteria evaluation of simulated logging scenarios in a tropical rain forest. J. Environ. Manage. 71, 321–333.

Huth, A., Drechsler, M., Kohler, P., 2005. Evaluation of reduced impact logging using multicriteria decision analysis. For. Ecol. Manage. 207, 215–232.

Janzen, D. 1988. Tropical dry forests. The most endangered major tropical ecosystem. Biodiversity (ed. By E.O. Wilson), pp. 13-137. National Academy of Sciences/Smithsonian Institution, Washington DC.

Jimenez, J. A., A. E. Lugo, and G. Cintron. 1985.Tree Mortality in Mangrove Forests. *Biotropica*. 17, 177-185

Kammesheidt, L., P. Kohler, and A. Huth. 2001. Sustainable Timber Harvesting in Venezuela: A Modelling Approach. Journal of Applied Ecology 38, 756-770.

Kapos, V. 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. J. of Trop. Ecol. 5, 173-185.

Kennard, D. K. 2002. Secondary forest succession in a tropical dry forest: patterns of development across a 50-year chronosequence in lowland Bolivia. J. Trop. Ecol. 18, 53–66.

Kohler, P. and A. Huth. 1998. The effects of tree species grouping in tropical rainforest modelling: simulations with the individual-based model FORMIND. Ecol. Modell. 109, 301-321.

Kohler, P., and A. Huth, 2004. Simulating growth dynamics in a South-East Asian rainforest threatened by recruitment shortage and tree harvesting. Climatic Change. 67, 95–117.

Kohler, P., T. Ditzer, R. C. Ong, and A. Huth, 2001. Comparison of measured and modelled growth on permanent plots in Sabahs rain forests. For. Ecol. Manage. 144, 101–111.

Kohler, P., J. Chave, B. Riera, and A. Huth. 2003. Simulating the long-term response of tropical wet forests to fragmentation. Ecosystems 6, 114–128.

Larocque, G. R., L. Archambault, and C. Delisle. 2006. Modelling forest succession in two southeastern Canadian mixedwood ecosystem types using the ZELIG model. Ecol. Model. 199, 350-362.

Larocque, G. R., L. Archambault, and C. Delisle. 2011. Development of the gap model ZELIG-CFS to predict the dynamics of North American mixed forest types with complex structures. Ecol. Model. 222: 2570-2583.

Laurance, W.F. 1997. Hyper-disturbed parks: edge effects and the ecology of isolated rainforest reserves in tropical Australia. *In*: Laurance WF, Bierregaard RO, (eds) Tropical forest remnants: ecology, management, and conservation of fragmented communities. Chicago: University of Chicago Press. pp. 71–83.

Laurance, W. F. 2007. A new initiative to use carbon trading for tropical forest conservation. Biotropica. 39, 20-24.

Laurance, W. F., Yensen E. 1991. Predicting the impacts of edge effects in fragmented habitats. Biol Cons, 55, 77–92.

Laurence, J. A., W. A. Retzlaff, J. S. Kern, E. H. Lee, W. E. Hogsett and D. A. Weinstein. 2001. Predicting the regional impact of ozone and precipitation on the growth of loblolly pine and yellow-poplar using linked TREGRO and ZELIG models. For. Ecol. and Manage. 146, 247-263.

Lebrija-Trejos, E., F. Bongers, E. A. Perez-Garcia, and J. A. Meave. 2008. Successional change and resilience of a very dry tropical deciduous forest following shifting agriculture. Biotropica. 40, 422-431.

Levenson, J. B. 1981. Woodlots as biogeographic islands in southeastern Wisconsin. *In* Forest Island Dynamics in Man-dominated Landscapes, ed. R. L. Burgess and D. M. Sharpe. Springer-Verlag, New York, pp. 13-39.

Little, E.L.; Woodbury, R.O.; Wadsworth, F.H. 1974. Trees of Puerto Rico and the Virgin Islands. Agric. Handb. 449. Washington, DC: U.S. Department of Agriculture Forest Service. 1,024 p.

Lugo, A. E., J. A. Gonzalez-Liboy, G. Cintron, and K. Dugger. 1978. Structure, productivity and transpiration of a subtropical dry forest in Puerto Rico. Biotropica 10, 278-291.

Lugo, A. E., and P. G. Murphy. 1986. Nutrient dynamics of a Puerto Rican subtropical dry forest. J. of Trop. Ecol. 2, 55-72.

Lugo, A. E. and F. N. Scatena. 1996. Background and Catastrophic Tree Mortality in Tropical Moist, Wet, and Rain Forests. Biotropica. 28, 585-599

Lugo Camacho, J.L. 2005. The soil Climate Regimes of Puerto Rico-Reassessment and Implications. Master's Thesis. University of Puerto Rico, Mayaguez, PR.

Miles L., A. C. Newton, R. S. DeFries, C. Ravilious, I. May, S. Blyth, V. Kapos , and J. E. Gordon. 2006. A global overview of the conservation status of tropical dry forests. J. of Biogeo. 33, 491-505.

Miles L. and V. Kapos. 2008. Reducing greenhouse gas emissions from deforestation and forest degradation: global land-use implications. Science. 320, 1454-1455.

Ming, Y., Z. Zhangcheng, L. Jinchun. 2007. Habitat fragmentation impacts on biodiversity of evergreen broadleaved forests in Jinyun Mountains, China. Front. Biol. China 2, 62-68.

Molina Colón, S. and A. E. Lugo. 2006. Recovery of a Subtropical Dry Forest After Abandonment of Different Land Uses. Biotropica 38, 354-364.

Molina Colón, S. 1998. Long-term recovery of a Caribbean dry forest after abandonment of different land uses in Guánica, Puerto Rico. PhD Dissertation. University of Puerto Rico, Rio Piedras.

Mollicone, D., A. Freibauer, E. D. Schulze, S. Braatz, and G. Grassi. 2007. Elements for the expected mechanisms on 'reduced emissions from deforestation and degradation, REDD' under UNFCCC. Environ. Res. Lett. 2, pp. 7.

Murphy, P. G. and A. E. Lugo. 1986a. Structure and Biomass of a Subtropical Dry Forest in Puerto Rico. Biotropica. Vol. 18, 89-96

Murphy, P. G. and A. E. Lugo. 1986b. Ecology of tropical dry forest. Annual Review of Ecology and Systematics 17, 67-88.

Murphy, P. G., A. E. Lugo, A. J. Murphy, and D. C. Nepstad. 1995. The dry forests of Puerto Rico's south coast. In Tropical Forests: Management and Ecology. Eds. A. E. Lugo and C. Lowe. Springer-Verlag, New York. pp. 178-209.

Nakayama, T. 2008. Shrinkage of shrub forest and recovery of mire ecosystem by river restoration in northern Japan. For. Ecol. and Manage. 256, 1927-1938.

O'Brien, S.T., B.P. Hayden, H.H. Shugart. 1992. Global change, hurricanes and a tropical Forest. *Climatic Change* 22, 175-190.

Pabst, R.J., M.N. Goslin, S.L. Garman, and T.A. Spies. 2008. Calibrating and testing a gap model for simulating forest management in the Oregon Coast Range. For. Ecol. Manage. 256, 958–972.

Parés-Ramos, I. K., W. A. Gould, and T. Mitchell Aide. 2008. Agricultural abandonment, suburban growth, and forest expansion in Puerto Rico between 1991 and 2000. Ecology and Society 13(2), 1.

Pausas J.G. 1999. Mediterranean vegetation dynamics: modelling problems and functional types. Plant Ecology 140, 27–39.

Pereira, I. M., L. A. Andrade, E. S. B. V. Sampaio, and M. R. V. Barbosa. 2003. Use-history effects on structure and flora of Caatinga. Biotropica 35, 154–165.

Perez Martinez, F. O. 2007. Effects of exotic canopy on understory species composition in degraded subtropical dry forests of Puerto Rico. Master's Thesis. University of Puerto Rico, Mayaguez.

Priestly, C. H. B., and R. J. Taylor. 1972. On the assessment of surface heat flux and evaporation using large scale parameters. Mon. Weather Rev. 100, 81-92.

Ranney, J. W. 1977. Forest islands edges: their structure, development, and importance to regional forest ecosystem dynamics. EDFB/IBP-77/1. Oak Ridge National Laboratory, Oak Ridge, Tennessee.

Ranney, J. W., Bruner, M. C. and Levenson, J. B. 1981. The importance of edge in the structure and dynamics of forest islands. Pp. 67-95 in Burgess, R. L. and Sharpe, D. M. (eds). Forest island dynamics in Man-dominated landscapes. Springer-Verlag, New York.

Risch, A.C., Heiri, C., Bugmann, H. 2005. Simulating structural forest patterns with a forest gap model: a model evaluation. Ecol. Model. 181, 161-172.

Ruiz, J., M. C. Fandino, and R. L. Chazdon. 2005. Vegetation structure, composition, and species richness across a 56-year chronosequence of dry tropical forest on Providencia Island, Colombia. Biotropica 37, 520– 530.

Scarano, F. 2000. Puerto Rico Cinco Siglos de Historia. McGraw Hill/Interamericana Editores, S.A. de C. V.

Shugart, H. H. and D. C. West. 1977. Development of an Appalachian Deciduous Forest Succession Model and its Application to Assessment of the Impact of the Chestnut Blight. J. of Environ. Manage. 5, 161-179.

Shugart, H. H., M.S. Hopkins, I. P. Burgess, and A. T. Mortlock. 1980. The development of a succession model for subtropical rain forest and its application to assess the effects of timber harvest at Wiangaree State Forest, New South Wales. J. Environ. Manage. 11, 243-265.

Sollins, P., D. E. Reichle, and J. S. Olson. 1973. Organic matter budget and model for a southern Appalachian *Liriodendron* forest. EDFB/IBP-73/2. Oak Ridge National Laboratory, Oak Ridge, TN.

Tanner, E. V. J., V. Kapos, and J. R. Healey. 1991. Hurricane effects on forest ecosystems in the Caribbean. Biotropica. 23, 513-521.

Tietjen, B. and A. Huth. 2006. Modelling dynamics of managed tropical rainforests-An aggregated approach. Ecol. Model. 199, 421-432.

Urban, D.L., 1990. A Versatile Model to Simulate Forest Pattern: A User's Guide to ZELIG Version 1. 0. University of Virginia, Charlottesville, Virginia.

Urban, D.L., 2000. Using model analysis to design monitoring programs for landscape management and impact assessment. Ecol. Appl. 10, 1820–1832.

Urban, D.L., Bonan, G.B., Smith, T.M., Shugart, H.H., 1991. Spatial applications of gap models. Forest Ecol. Manage. 42, 95–110.

Urban, D. L., Harmon, M. R., and Halpern, C. B. 1993. Potential Response of Pacific Northwestern Forests to Climatic Change, Effects of Stand Age and Initial Composition. Clim. Change 23, 247-266.

Uriarte, M., C. D. Canham, J.Thompson, J. K. Zimmerman, L. Murphy, A. M. Sabat, N. Fetcher, and B. L. Haines. 2009. Understanding natural disturbances and human land use as determinants of tree community dynamics in a subtropical wet forest: results from a forest simulator. Ecological Monographs. 79, 423-443.

USDA. 2006. Forest inventory and analysis: national core field guide. Volume 1: Field data collection procedures for phase 2 plots. Caribbean Version 3.0.

USDA. 2008. United States Department of Agriculture, Natural Resources Conservation Service. Soil Survey of San Germán Area, Puerto Rico. Accessible online at: http://soils.usda.gov/survey/printed_surveys/.

Van Bloem, S.J., P.G. Murphy and A.E. Lugo 2003. Subtropical dry forest trees with no apparent damage sprout following a hurricane. Tropical Ecology. 44, 137-145.

Van Bloem, S. J. 2004. Multiple scale patterns in growth and structure of subtropical dry forests: soils, trees, and hurricanes. PhD. Dissertation. Michigan State University.

Van Bloem, S. J., P. G. Murphy, A. E. Lugo, R. Ostertag, R. Rivera Costa, I. Ruiz Bernard, S. Molina Colon, M. Canals Mora. 2005. The influence of hurricane winds on Caribbean dry forest structure and nutrient pools. Biotropica 37, 571-583.

Van Bloem. S. J., P. G. Murphy, A. E. Lugo. 2007. A link between hurricane-induced tree sprouting, high stem density and short canopy in tropical dry forest. Tree Physiology. 27, 475-480.

Van Daalen, J. C. and H. H. Shugart. 1989. OUTENIQUA – A computer model to simulate succession in the mixed evergreen forests of southern Cape, South Africa. Landscape Ecology. 2, 255-267.

Vesk, P.A. and Westoby, M. 2004. Sprouting ability across diverse disturbances and vegetation types worldwide. J. of Ecology 92, 310–320.

Wadsworth, F.H. 1950. Notes on the climax of Puerto Rico and their destruction and conservation prior to 1900. Caribb. Forester 11, 38-56.

Walker, L. R. 1995. Timing of post-hurricane tree mortality in Puerto Rico. J. of Tropical Ecology. 11, 315-320.

Wolfe, B. 2009. Post-fire regeneration in subtropical dry forest of Puerto Rico. Masters Thesis. University of Puerto Rico Mayaguez.

Yan, H. and H. H. Shugart. 2010. An air relative-humidity-based evapotranspiration model from eddy covariance data. J. of Geophy. Resear. 115:D16106.

Yaussy, D. A. 2000. Comparison of an empirical forest growth and yield simulator and a forest gap simulator using actual 30-year growth from two even-aged forests in Kentucky. For. Ecol. and Manage. 126, 385-398.

Zimmerman, J. K., M. R. Wilig, L. R. Walker, W. L. Silver. 1996. Introduction: disturbance and Caribbean Ecosystems. Biotropica. 48, 414-423.

Chapter 3 Simulating hurricane disturbances in climate change scenarios: biomass and net primary productivity changes for a subtropical dry forest.

3.1 Introduction

This paper develops and implements hypothetical hurricane simulations that are used in ZELIG-TROP, an individual-based gap model that simulates the Puerto Rican subtropical dry forest. Hurricane strength and frequency are dependent upon climate and could be altered due to climate change (IPCC 2007), and there is a consequent need to understand long term effects of various storms on vegetation dynamics. Individual-based forest gap models have been applied to simulate vegetation dynamics in response to global change (Solomon 1986, Smith and Urban 1988, Smith and Tirpak 1989, Overpeck et al. 1990, Shugart et al. 1992).

The impact of actual hurricane disturbances on tropical forests, where disturbance is defined as an abrupt event that kills individuals and strongly alters ecosystems, has been studied in detail. Researchers have examined forest recovery from hurricane damage in forest types classified as dry, moist, and wet forests specifically in Central America and the Caribbean (Lugo et al. 1983, Whigham et al 1991, Walker et al. 1991, Harrington et al 1995, Imbert et al 1996, Granzow de la Cerda et al. 1997, Reilly 1998, Vandermeer et al. 1998, Sanchez-Sanchez and Islebe 1999, Mascaro 2005). Other research has reported the damage and recovery of vegetation from hurricane disturbances specifically for the wet forests of Puerto Rico (Brokaw and Walker 1991, Basnet et al. 1992, Zimmerman et al. 1996, Dallmeier et al. 1998, Frangi and Lugo 1998, Foster et al. 1999).

A major challenge has been to compare storm effects on vegetation from multiple storm occurrences over a long period of time (decades and centuries) (Everham and Brokaw 1996). Studies are often limited to only one individual hurricane. The infrequency of storms, the limited sampling size and, particularly, the relatively low number of locations with forest data before and after a storm, limits these studies to the assessment of just one or two vegetation responses from a hurricane disturbance. The absence of detailed data that describes multiple vegetation responses from varying impacts and across longer time scales makes it difficult to evaluate the role hurricane disturbances play in forest dynamics. For example, it is difficult to determine if hurricane disturbances are natural events that help in maintaining the ecological integrity of these forests or if changes in the intensity or frequency of hurricanes may result in new transitions of forest succession. Simulation modeling with a detailed individual-based model can be used to evaluate these effects. Individual-based models have the capability to assess both individual- and ecosystem-level changes because they incorporate tree/climate interactions and allow for each tree to alter the local microenvironment (Whitmore 1982, Brokaw 1985, Silvertown and Smith 1988). Micro-environmental adjustments can be driven by the interactions between plants and soil water and nutrient conditions and available light, which in turn influence tree growth, survival, and regeneration (Pastor and Post 1986, Shugart 2002). As an individual based model, ZELIG-TROP is an appropriate choice to help determine the effects of varying hurricane disturbances on tropical forest biomass and productivity, the two variables that will be the focus of this study, in a globally changing environment.

3.1.1. Hurricanes in Puerto Rico

Hurricane frequency in Puerto Rico is high for the Caribbean region and the North Atlantic basin (Neumann et al. 1987), 33 storms in the last century. It is typical for tropical storms to approach from the east to southeast and take a westward path across the island. The island of Puerto Rico is the furthest east of the Greater Antilles. Lacking a large body of land between a storm path and the island to interrupt storm development, Puerto Rico is located in a vulnerable position for the Cape Verde hurricanes that develop off the west coast of Africa, or that originate nearby.

Puerto Rico has had numerous studies of hurricane-disturbance effects, mostly within the context of wet and moist forests (listed above), but only a few studies have addressed hurricane impacts in dry forest life zones within Puerto Rico (Van Bloem et al. 2003, 2005, 2006). Van Bloem et al. (2006) described the direct and short term effects of hurricanes on the subtropical dry forest of Puerto Rico, within Guanica State Forest, and concluded that the Puerto Rico dry forests have probably adapted to effects from hurricanes. One adaption is widespread basal-sprouting in these forests that is induced by bending, stem breaking and uprooting, and increased ethylene production that follows a hurricane with sustained winds surpassing a minimum speed of 119 km/h. Van Bloem et al. (2005) quantified the proportion of damage to large vs. small stems, and concluded that disproportionately higher damage occurred on larger stems.

These previous studies document local changes and forest response to historical hurricanes. Based off the past records, the ZELIG-TROP model was parameterized with field data of damage effects according to species. Previous studies report either short term responses (<2 years) or longer term responses (5yrs-10yrs). To better predict future forest dynamics in response to changing hurricane or climate scenarios, there is a logical application of simulation modeling to evaluate long term effects (+100 years).

3.1.2. Hurricane Modeling

There is still on-going debate and research about the history, current forecast, and future predictions of hurricane intensity and frequency with respect to human induced climate change, a topic of immediate concern. Some studies state that the human-induced increase in greenhouse gases and warming has caused an increase in tropical cyclone intensity (Goldberg et al. 2001, Emanuel 2005, 2006, Knight 2006, Mann and Emanuel 2006, IPCC 2007, Bender et al. 2010). Emanuel (2006) stated that the destructiveness of cyclones has doubled over the past 30 years and attributes it to human induced warming and increased sea-surface temperatures (SSTs) (Emanuel 2005). Additional studies imply that we are currently experiencing the highest hurricane activity known to date, with a fivefold increase in the Caribbean over a 6 year period from 1995-2000 (Goldberg et al. 2001).

Conversely, other studies conclude that intense hurricanes are not caused by human-induced warming (Vecchi & Soden 2007a, 2007b) or that cyclones are in fact changing, but due to natural causes. These causes include oscillations between La Niña years and strong West African monsoon seasons (Donnelly & Woodruff 2007), variability in the Atlantic Multidecadal Oscillation (AMO), in which a warmer AMO can increase hurricane formation (Knight 2006), increased Sahel rainfall events, increased

SSTs, and faster thermohaline circulations (Bengtsson et al. 2006, Knight 2005, Zeng et al. 2009). In contrast to storms increasing with climate change, Knutson et al. (2008) and Zhao et al. (2009) concluded that after analyzing computer simulation runs, there was a reduction in tropical cyclone frequency with climate change. Evaluating vegetation response to potential hurricane scenarios by varying intensity and frequency is critical to our understanding of effects from changes in climate.

Several studies have modeled hurricane disturbance of the wet subtropical forest of Puerto Rico (Luquillo Forest) and the response to varying storm disturbances (Doyle 1981, O'Brien et al. 1992, Boose et al. 2004, Uriarte et al. 2009). Boose et al. (2004) used a meteorological model to reconstruct the impact of 43 historical hurricanes since 1851, reporting the annual, decadal, and centennial trend in hurricane frequency. Hurricane effects were dependent on topography, land-use history, and effects of previous hurricanes.

Previous studies using individual based gap models have incorporated hurricane disturbances into the forest simulators (Doyle 1981, O'Brien et al. 1992, Uriarte et al. 2009) for the subtropical wet forest (Luquillo Experimental Forest). Model simulations showed stem densities and species richness increased when hurricanes were introduced compared to the absence of hurricanes (Doyle 1981). This is likely the result of more treefalls opening space for pioneer species and more trees of different species in lower size classes. O'Brien et al. (1992) used an earlier version of ZELIG to simulate a range of hurricane disturbances that would affect wet forest composition. Upon implementing a range from no hurricane effects to 100% tree mortality, simulation results from ZELIG predicted forests that ranged from mature with large trees to a forest in which trees never reach maturity. Recently, Uriarte et al. (2009) used the existing SORTIE gap model and applied natural disturbances (hurricanes) and human land use legacies to predict changes to forest dynamics in the subtropical wet forest of Puerto Rico. By analyzing stem density of eleven simulated species, Uriarte et al. (2009) noted, as did Doyle (1981) and O'Brien et al. (1992), that the periodicity and intensity of hurricanes played a role in abundance of species. While gap models have been developed for the wet montane forests of Puerto Rico, this is the first attempt to model hurricane effects for the rather different subtropical *dry* forests of Puerto Rico.

3.1.3. Changes in forest biomass and productivity with disturbances

The total carbon in dry tropical forest vegetation is relatively low (49.7 Pg, 8-9% of total carbon), and less than that of wet tropical forests, temperate forests, and boreal forests (Schlesinger 1997). While the total carbon in the vegetation is less, dry tropical forests have an average net primary production (NPP) of 6.20 Mg C ha^{-1} yr^{-1} that is second only to wet tropical forests (Schlesinger 1997). Other reports have estimated NPP for a tropical savanna at 6.61 Mg C ha^{-1} yr^{-1} and tropical deciduous forest to be 7.59 Mg C ha^{-1} yr^{-1} (Cao and Woodard 1998), while Clark et al. (2001) estimated the NPP for Guanica Forest in Puerto Rico to be 4.50 Mg C ha^{-1} yr^{-1}. With a high NPP, fluxes that would alter carbon allocation and plant respiration such as removal of plant material by harvesting, disturbance or herbivory are especially important to dry tropical forests compared to other forests.

Biomass density is a useful variable when comparing forest structural and functional traits to changing environmental conditions (Brown 1997, Brown & Lugo 1984, Brown et al. 1989). Previous studies evaluated the importance of quantifying the effects of multiple disturbance frequencies and intensities in different vegetative systems (Baker et al. 1995, Govender et al. 2006, Oluwole et al. 2008). It is critical to better understand large, infrequent disturbance effects on dry tropical forests (Turner and Dale. 1998). The manipulation of fire regimes and return intervals has aided in understanding the effects of fire disturbance on vegetation in African-savanna systems (Scholes and Walker 2004, Govender et al. 2006, Oluwole et al. 2008).

The research conducted here can be used for climate change mitigating tools like the United Nations supported REDD+ (Reducing Emissions from Deforestation and Degradation). REDD+ has been successful at measuring, reporting, and verifying carbon emissions and flows from tropical forests in *some* parts of the world (Gibbs et al. 2007, Angelsen 2008, Canadell and Raupach 2008), but not in all locations, typically due to a lack of data. A large amount of uncertainty still remains in our knowledge of tropical forests for a global program like REDD+ (Grainger 2010). REDD+ poorly understands the dynamics of *dry* tropical forests (which make up the largest area of tropical forests) as well as response to large-scale hurricane disturbances (permanence issues). Due to the large extent and differences in tropical forests all over the world, there is no one method to measure carbon stocks in all tropical forests for REDD+. Satellite and airborne mapping (LiDAR) have provided a route to estimate carbon stocks over large areas (Asner 2009), but for these methods to be successful, initial forest carbon levels need to be quantified. Simulation modeling and detailed carbon prediction used in this research (at the local and landscape scale) can supply initial carbon levels. The simulation models used here should be added as a methodology to project carbon stocks and emissions.

Hurricanes are important for maintaining dry forest structure in Puerto Rico. Hurricanes are episodic and range in damage severity and frequency. The consequences of these events are important and difficult to predict. This paper will particularly report on the interactions taking place within the ecosystem and the changes in biomass and forest productivity for a subtropical dry forest after simulating increased and decreased hurricane intensities and frequencies.

3.2 Methods

3.2.1 ZELIG-TROP Model

The individual-based gap model ZELIG-TROP was used to simulate the effects of hurricane disturbances on subtropical dry forests. The original model ZELIG has been used to simulate many forested locations and for different applications (Urban 1990, 2000, Urban et al. 1991, 1993, Cumming and Burton 1993, Larocque et al. 2006, Pabst et al. 2008). ZELIG-TROP was parameterized with species and site-specific parameters for the Guanica Dry Forest, in southwestern Puerto Rico, and validated by directly comparing model results to observed field data (computing correlation coefficients and percent differences), and reproducing a similar modeled forest structure to existing forests (Holm et al. in press). ZELIG-TROP uses functional relationships for annual computations of tree establishment, growth, survival, and death. Also, the crown interaction algorithm developed in ZELIG-CFS was integrated into ZELIG-TROP (Larocque et al. 2011b).

The processes of each individual tree were modeled as functions of environmental constraints (i.e. available light, soil moisture, soil nutrient resources, and temperature). Tree growth and regeneration was incremented as a function of tree size, site specific climate, available light, soil moisture, temperature, and competition. Tree mortality was a function of age (1.5% of trees are able to survive to their maximum age), stress (site/environmental stress or suppression), and disturbance (hurricane events).

3.2.2. ZELIG-TROP and Stand Visualization System

The Stand Visualization System (SVS), originally developed by Robert J. McGaughey and the USDA Forest Service (McGaughey 1997), was updated to produce visual images to depict the Puerto Rican subtropical dry forest. SVS generates realistic community representations made up of individual plants and stand components, using detailed geometric models. The visual forest community was shown at the plot level, which was user-specified. SVS and ZELIG-TROP have the capability to synchronize and run simultaneously, because ZELIG-TROP is spatially explicit, tracking the x-y coordinates of each individual tree over its lifetime. The synchronization was done through a graphic user interface that allowed the outputs of ZELIG-TROP to be visually seen in SVS[*]. Linking has been accomplished so that the tree density, each individual’s DBH, height, leaf area, crown width, crown length, and geographic position in the plot which was produced from ZELIG-TROP was reported by SVS in the image.

---

[*] The development of the graphic user interface that synchronizes ZELIG-TROP and SVS was led by G.R. Larocque at Natural Resources Canada.

To develop each individual tree realistically, detailed tree parameters specific to each of the 18 Puerto Rican species present in ZELIG-TROP were inputted into SVS. These parameters are: average crown ratio, crown radius, height, location of branching point relative to base of live crown, branch angle increment between branches and leaf structure, branch angle at top and bottom of crown, number of branches and leaves, number and distribution of branch whorls depending on plant form, high and low points of the tree crown in both the x and y position, stem color, branch color, foliage color for 75% of leaves, foliage color for 25% of leaves, and overall plant form. Plant form is critical for controlling the growth form of the tree in terms of branching characteristics and presence/position of leaves. For example a plant form can consist of a “single leader form” or “multiple leader form,” where leader refers to the main stem of the tree. Single leader tree forms are typically coniferous species and have one central stem. Single leader tree form classification was not used for the Puerto Rican species. Multiple leader forms are typically deciduous species with a central stem below the crown and branches either uniformly distributed throughout the crown, branches located in the bottom of the crown, or no central leader inside the crown.

3.2.3. Hurricane Data Collection and Modeling

Meteorological data for past tropical storms were retrieved from the Hurricane database, HURDAT, controlled by the U.S. National Hurricane Center and the National Oceanic and Atmospheric Administration (NOAA). The HURDAT database provides information on storms from 1851 to present for all tropical cyclones in the Atlantic

Ocean, Gulf of Mexico, and Caribbean Sea. The database reports the direction (degrees), latitude, longitude, speed (mph and kph), wind (mph and kph), pressure (mb), and classification name at six hour interval throughout the duration of the storm. HURDAT was created in the 1960s and since its creation there have been new data additions and a re-analysis project conducted by Landsea et al. (2002). To verify the accuracy of the HURDAT database for Puerto Rican hurricanes, results were confirmed with Puerto Rican field studies of hurricane reports (Millas 1968, Quninos 1992, Boose et al. 2004).

In the past 158 years (since first available recordings in HURDAT) there have been 12 storms that have had a direct or partial passing over Guanica Forest (7.6 storms per century). To avoid over-estimating hurricane damage, a slightly more conservative definition of a direct and partial hit were used compared to the National Hurricane Center's (NHC) definition. The definition of radius of maximum wind was used to determine if a storm passed over the study site; defined as the radial distance from the storm center to the region of maximum wind speed (Hsu and Yan 1998, NHC). In this report, a direct hit occurred if any portion of the radius of maximum wind of the storm passed over Guanica Forest. A partial hit occurred if any portion from the outer edge of the radius of maximum wind to the storm's exterior wind bands passed over Guanica. If intact storm wind bands did not pass over the southwestern portion of the island (indirect hit), the storm was not included in the list. Figure 3.1 represents our classification of direct and partial hits of 12 storms that have passed through Guanica over the past 158 years. The storms include: four category-1 hurricanes, five category-2 hurricanes, and three category 3 to 5 hurricanes, according to the Saffir-Simpson scale, during time of passing over Guanica. In total, 33 hurricanes had an impact on Puerto Rico in the last century. In this study the Saffir-Simpson was replaced with a categorical scale of hurricane levels with a numerical scale based on wind speed. A sample hurricane disturbance was selected from a distribution of continuous wind speeds ranging from 119 km/hr to 300 km/hr.

Hurricane return times (intervals between hurricane events in years) for the historical pattern of storms in each wind speed category was first implemented in model simulations (Table 3.1) and used as the control. In addition to the control simulations, ten forced hurricane scenarios, or treatments, (Table 3.1) were simulated that were congruent with observed and predicted increases in storms (Sanford et al. 1991, Goldenberg et al. 2001, Emanuel 2005, Webster 2005, IPCC 2007, Bender et al. 2010). We test aboveground biomass and NPP as a response variable. Each treatment was run 20 times to generate average responses.

An array of plausible hurricane scenarios were simulated in order to take a comprehensive approach, and partially due to the fact that studies remain inconclusive on the long-term changes in storm patterns (Henderson-Sellers et al. 1998, Vecchi et al. 2008, Landsea et al. 2010). While past studies have shown that storm intensity might be increasing more than storm frequency (Emanuel 2005, 2006, Bender et al. 2010), it was chosen to additionally model increases in storm frequency (as well as a decrease in storms) to evaluate the changes in forest biomass and productivity with multiple hurricane treatments.

There were four total scenarios where the effects of changes in storm intensity and frequency were compared with the results of the control disturbance regime. Two scenarios isolated either intensity or frequency; one where intensity was increased and overall storm frequency was held constant, and the second where the distribution of intensities remained true to historical levels and frequency was increased. The other two scenarios synchronized 1) an increase in intensity and frequency and 2) a decrease in intensity and frequency.

To simulate increased intensity the total number of storms per century remained consistent with the historical trends, but the occurrence of severe storms (178 to >250 km/hr) increased and the occurrence of weaker storms (119-177 km/hr) decreased. Storms greater than 178 km/hr were increased by 25%, 50%, and 100% - values consistent with previous hurricane simulations using an individual based gap model (O'Brien et al. 1992).

The frequency of hurricane events (or deceased return time) were increased evenly for each wind speed category (5 categories ranging from 119 to >250 km/hr). The frequency of storms in each wind speed category was increased by 25%, 50%, and 100%. For the third scenario both the frequency of all storms and intensity of severe storms were increased. So that all simulation outputs had a consistent hurricane history, the increased hurricane frequency used in the second scenario was maintained (increasing frequency by 25%, 50%, and 100%), but also storms greater than 178 km/hr increased by 25%, 50%, and 100%. This method created both an increase in intensity, in addition to increased frequency of storms. Last, one scenario of decreasing the historical hurricane frequency and intensity of severe storms by 50% was implemeted. To investigate the disturbance severity effect on aboveground biomass (AGB) a one-way analysis of variance on the data from each of the four treatments with the control data was performed, and compared categorical means with Tukey post-hoc tests.

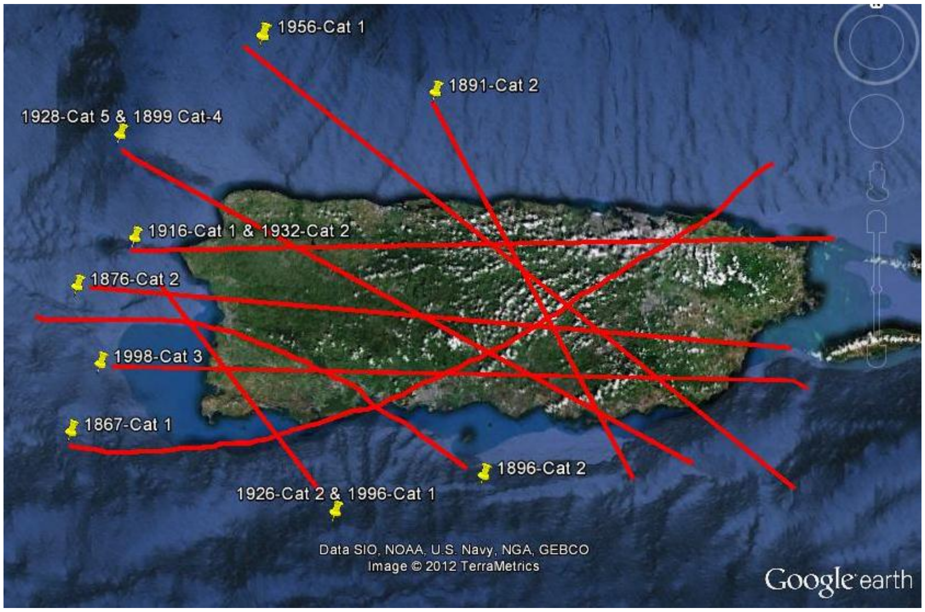


Figure 3.1. Map of Puerto Rico with 12 hurricane paths (including date and category level provided by HURDAT), all which had a direct or partial pass over Guanica Forest, from 1867 to present.

Table 3.1. Return interval (years) for storm events in five wind classes between 119 and >250 km/hr, and total number of storms to pass over the southwestern portion of Puerto Rico. Return intervals are for historical scenarios and ten treatments deviating from the control. These include treatments of increasing intensity of only the severe storms, increasing frequency of all storms, and increasing both the frequency of all storms and the intensity of severe storms all by 25%, 50%, and 100%, and also decreasing the frequency and intensity of severe storms only by 50%.

Treatments	119-153 km/hr	154-177 km/hr	178-209 km/hr	210-249 km/hr	> 250 km/hr	All Storms
Historical/Control	40	32	158	158	158	13
Intensity +25%	43	35	126	126	126	13
Intensity +50%	47	38	105	105	105	13
Intensity +100%	59	48	79	79	79	13
Frequency +25%	32	25	126	126	126	11
Frequency +50%	26	21	105	105	105	9
Frequency +100%	20	16	79	79	79	7
Inten. & Freq. +25%	35	26	106	106	106	11
Inten. & Freq. +50%	29	24	80	80	80	9
Inten. & Freq. +100%	25	19	53	53	53	7
Inten. & Freq. -50%	79	63	316	316	316	26

3.2.4. Hurricane Disturbance Simulations and Modifications

The model simulated tree communities on 0.04-ha plots, and all simulations were run for 800 years and replicated for 20 plots. Simulations were started from bare ground, with ZELIG-TROP running for a spin-up period (also known as transient period) of 200 years to allow the model to reach equilibrium. Therefore all results were reported for the last 600 years of simulations. Eighteen of the most important tree species found in the subtropical dry forests of Puerto Rico (Murphy and Lugo 1986b) was simulated. Python programming was used to randomly generate hurricane events over the 800 year time period. The Python program randomly determined if a hurricane occurred on a given year based on the return interval (years) in Table 1. For example when running a historical hurricane regime a hurricane between wind speeds of 119-153 km/hr would hit the forest once randomly during a 40 year period. Our version of the model allows for multiple hurricanes to hit during any given year, as this has been occasionally observed. When a hurricane event occurred the “hurricane effect” function was initiated in ZELIG-TROP during that yearly time step. Abundance of individuals (stems ha^{-1}), stand biomass (Mg ha^{-1}), stand basal area (m^{2} ha^{-1}), and NPP (Mg C ha^{-1} yr^{-1}) were reported on an annual time step for each storm scenario.

In real hurricane events effects on individual trees in a forest are typically heterogeneous across the landscape. The amount of damage to within and among species and biomass lost are not constant. Therefore model parameters for hurricane damage were derived from past local measurements taken in Guanica Forest after Hurricane Georges hit the southwestern portion of Puerto Rico in 1998 (Van Bloem et al. 2005). Van Bloem et al. (2005, 2007) quantified species specific damage in multiple damage classes (no damage, defoliation, stem snapped, uprooted, and dead), and total sprouting stems post hurricane. In previous disturbance modeling studies there has been difficulty in obtaining local measurements for species specific effects (Doyle 1981, O’Brien et al. 1992). An advantage of effect parameterization being species specific is the ability to produce a forest composite and structure that is potentially more realistic. Damage to each individual also varied depending on the DBH of the individual at the time of disturbance. A tree with a smaller DBH did not receive as much wind damage as a larger tree. Field data records of forest response to historical hurricanes were used as a basis to test the validity of our simulation results and make accurate assessments of our model simulations.

There were six separate damage types that could possibly occur to each individual, for the 18 species in the model. These damage classifications were 1) no apparent damage, 2) loss of foliage, 3) branch damage, 4) main stem snapped, 5) tree uprooted, or 6) dead. Loss of foliage was either 50% or 100% foliage lost depending on DBH size. Branch damage and snapped stems consist of an individual losing 50% of crown width and crown length, respectively. Each individual has the potential to receive one or more of these damage classifications during a hurricane simulation. All individuals that were present at the beginning of the time period had an equally random chance of receiving simulated damage, but we know that stems >7.5cm DBH had 50% higher rate of stem snapped and uprooted. Damage received was randomly selected within the model, and damage values for each individual ranged from 0.0-1.0 based on the severity of the hurricane disturbance (wind level in the model), species type based on observed local measurements, and individual DBH. Once an individual was randomly damaged by the simulated hurricane, its new tree geometry was updated into the next time step, with new growth occurring based on its reduced damage state. Therefore, new canopy structure (length and width), leaf area and foliage amount after a hurricane was accounted for in the years following a hurricane. Death of an individual was a less likely occurrence. Complex interactions (i.e. age of tree, existing disease or fungus) would lead to difficult predictions for tree death. If an individual was classified as uprooted, a proportion of these individuals were also categorized to die, reducing possible error in assumption biases. Of the proportion of uprooted trees that did not die, the main stem was removed from the model, but basal-sprouting could occur. A new basal-sprouting routine was added to ZELIG-TROP (Holm et al. in press) allowing for sprouts to grow from stumps and downed trees. Individuals that were randomly picked to have a stem snapped also had the ability to sprout new stems from the old trunk, based on their sprouting ability from field data.

3.2.5. Net Primary Productivity Model Additions

Net primary productivity (NPP) is defined as the net carbon gain by vegetation. NPP equaled gross primary production minus autotrophic respiration, where gross primary production is total assimilation of CO_2 by a plant, including the amount later lost through respiration (Newbould 1967, Clark et al. 2001). Newbould (1967) defined NPP as sum of new biomass in photosynthetic plants between two time periods, incorporating loss to death, shedding, respiration, and loss to human harvest and consumption by animals already accounted for. Therefore, litterfall was not subtracted from NPP, and NPP was an estimation of the organic matter production over a time interval with plant respiration taking place. In accordance with Newbould (1967) and Clark et al. (2001), I defined NPP as the following equation (3.1):

$$NPP = \sum D_i + L_i + S_i \qquad \text{Equation 3.1}$$

Where D is new wood/biomass growth through diameter increment, L is new leaves/leaf growth, and S is biomass from new basal sprouts over the one year time period (Mg C ha^{-1} yr^{-1}), for each individual (i). NPP was only calculated for aboveground tissue, and did not include the belowground portion. In order to calculate the three components of NPP, new additions within ZELIG-TROP were implemented to track these changes in carbon. Aboveground biomass was calculated using a dry forest allometric equation specific to Puerto Rico (Brandeis et al. 2006). It is assumed that carbon was 50% biomass (Schlesinger 1997). To investigate the disturbance severity effect on NPP, two-way analysis of variances on the data with increases in hurricane intensity and frequency as the main effects were performed.

3.3 Results

3.3.1 ZELIG-TROP with Hurricane and SVS Results

The Stand Visualization System (SVS) was able to produce a plot level (400 m^2) graphical representation of Guanica Forest (Figure 3.2). Simulations of the dry forest before and after hurricane events can be seen visually, showing the number of trees present and the gaps caused by damage. Only small saplings were present after simulation year 1 (Figure 3.2a). The total number of individuals was 77 trees, crown cover was 15%, and the average sapling height was 2.5m (Figure 3.2a).

At year 226 with hurricanes implemented in the model, there were 342 individual stems in the plot (8550 per ha), and canopy coverage was calculated to be 95% (Figure 3.2b). A category 5 hurricane occurred in year 227. The results showed in year 228 the number of individuals decreased to 306 in the 400m^2 plot (7650 per ha), an 11% decrease in abundance. The canopy coverage decreased to 91% (Figure 3.2c). The SVS overhead view in Figure 3.2c illustrates locations where larger, dominant trees have died and left gaps in the forest.

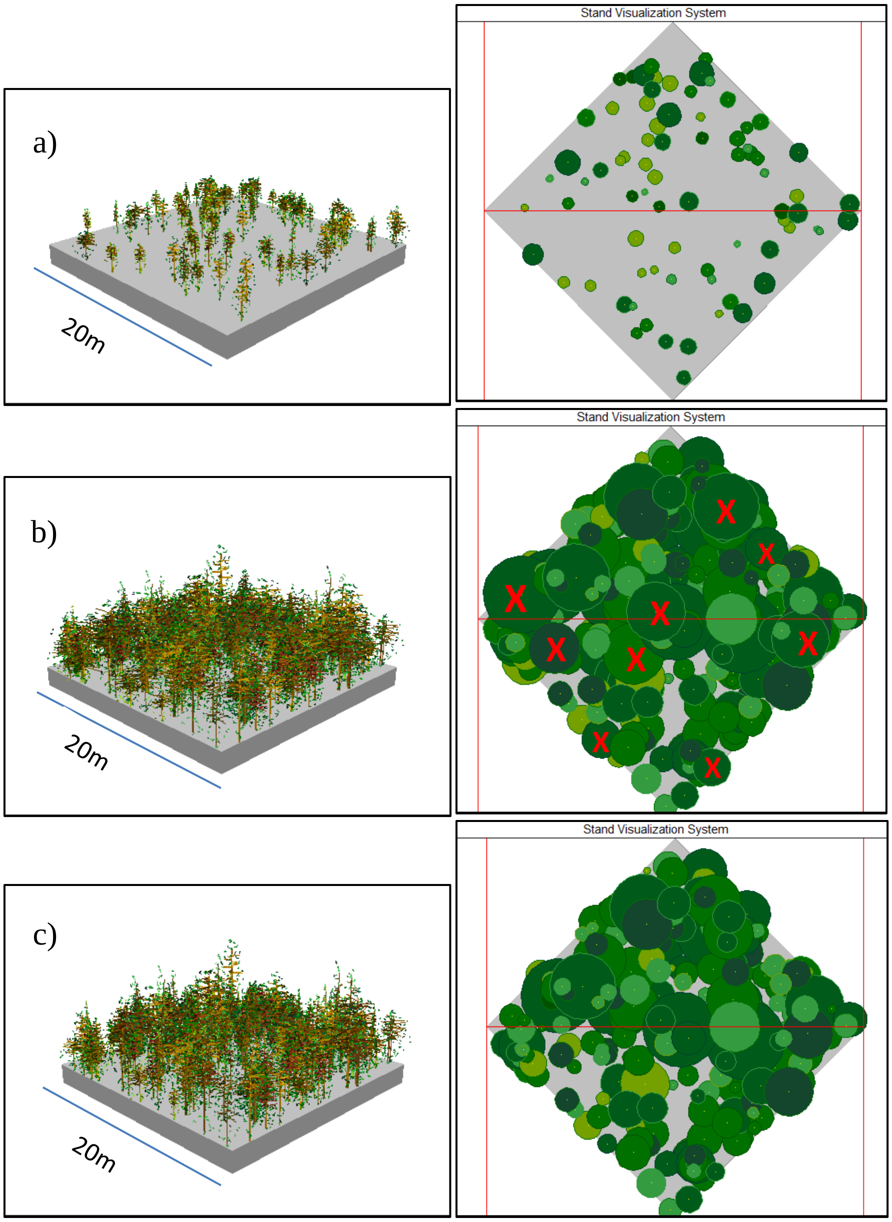


Figure 3.2. Forest structure images (perspective and overhead view) on a 400 m^2 plot, from three separate years provided by Stand Visualization System (SVS) and in conjunction with ZELIG-TROP. All from simulations with increase in storm frequency by 50%. a) Year 1 after starting simulation from bare ground; average tree height: 2.5m, b) year 226 after a period of low hurricane disturbance; average tree height: 4.8m , with red X marks over a subset of individuals that died in the next year, and c) year 228 after a hurricane level 5 occurred the previous year; average tree height: 4.1m.

3.3.2 Disturbance Simulations

ZELIG-TROP reported forest stand results for each hurricane treatment; results were reported in stand basal area (m^2 ha^{-1}), abundance of individuals (stems ha^{-1}), aboveground biomass (Mg ha^{-1}), and NPP (Mg C ha^{-1} yr^{-1}) (Table 3.2). These forest variables were an average of 600 years of simulation after the model was spun up for 200 years to reach a mature forest state started from bare ground. The majority of the forest variables reported from the historical hurricane scenario (control) matched the observed forest values more accurately than the original ZELIG-TROP, which was void of a disturbance module (results from Holm et al. in press) (Table 3.2). Thus, simulations incorporating hurricane disturbances appropriately represented the real-world dynamics which also experience hurricanes. The “no disturbance” scenario in ZELIG-TROP still produces death of large trees and natural tree gap disturbances, but any other disturbance (anthropogenic, disease, storms, grazing, etc.) is not simulated.

After simulating the historical hurricane regime both basal area and stem density increased to values that more closely resembled the observed forest. After hurricane disturbances were introduced in ZELIG-TROP average basal area reached 20.02 m^2 ha^{-1} (observed basal area is 20.15 m^2 ha^{-1}). Following an increase in the intensity of severe storms, all values stayed very similar to historical/control storm levels, or increased only slightly (1-7% relative effect of treatment). The treatment of intensity increasing to 100% caused a drop in basal area and aboveground biomass. Stem density always increased with increasing storm intensity treatments. After increasing frequency of hurricanes and also both intensity and frequency, all forest variable levels decreased, compared to the historical hurricane disturbance. The relative effect of each treatment ranged from decreasing forest variables by 4-40%, with a higher effect seen with increasing frequency of storms. Stem density had the smallest decrease in value (Table 3.2).

Treatments	Basal Area (m^2 ha^{-1})	Stem Density (stems ha^{-1})	AGB (Mg ha^{-1})	NPP (Mg C ha^{-1} yr^{-1})	Relative Effect of Treatment % (Basal Area)	Relative Effect of Treatment % (Stem Density)	Relative Effect of Treatment % (Biomass)	Relative Effect of Treatment % (NPP)
Observed Values (1981-2009)	20.15 (2.3)	9322 (1552.8)	64.8 (11.9)	4.5**	NA	NA	NA	NA
No Disturbance *	19.17 (1.7)	8506 (798)	69.0 (2.8)	NA	NA	NA	NA	NA
Historical Hurricanes	20.02 (2.1)	9936 (1175)	75.3 (7.8)	3.04 (0.19)	NA	NA	NA	NA
Hurricane Intensity +25%	20.37 (2.4)	10226 (1563)	76.5 (9.3)	3.08 (0.23)	1.73	2.88	1.58	1.16
Hurricane Intensity +50%	20.54 (2.7)	10744 (1714)	77.1 (10.3)	3.11 (0.26)	2.56	7.81	2.36	2.12
Hurricane Intensity +100%	19.72 (2.8)	10137 (1456)	74.5 (10.2)	3.06 (0.24)	-1.51	2.00	-1.07	0.56
Hurricane Frequency +25%	18.92 (1.8)	9516 (1076)	71.0 (6.7)	5.10 (0.36)	-5.65	-4.32	-5.88	50.58
Hurricane Frequency +50%	16.54 (1.4)	8214 (606)	62.6 (5.3)	4.73 (0.31)	-19.04	-18.98	-18.42	43.35
Hurricane Frequency +100%	14.64 (1.1)	7248 (365)	55.7 (4.2)	4.39 (0.27)	-31.04	-31.29	-29.92	36.36
Intensity & Frequency +25%	18.27 (1.9)	9247 (1096)	68.9 (6.9)	5.00 (0.37)	-9.14	-7.18	-8.88	48.73
Intensity & Frequency +50%	16.00 (1.6)	8199 (658)	60.5 (5.9)	4.67 (0.34)	-22.32	-19.16	-21.80	42.24
Intensity & Frequency +100%	13.22 (1.3)	7021 (465)	50.2 (4.7)	4.21 (0.30)	-40.91	-34.38	-40.00	32.17
Intensity & Frequency -50%	20.84 (1.4)	10231 (779)	78.0 (5.0)	5.39 (0.25)	4.01	2.93	3.52	55.72

Table 3.2. Average basal area, stem density, aboveground biomass, and NPP for the observed Puerto Rico forest, simulations with no disturbance, historical hurricane events, and ten storm treatments (standard deviation in parentheses) from 600 years, after an initial spin-up of 200 years starting from bare ground. Relative effect of each treatment from the control (%), with a negative value meaning the treatment caused a decrease in value. N=20 model runs for each treatment.

3.3.3 Effects of Hurricane Treatments in Climate Change Scenarios

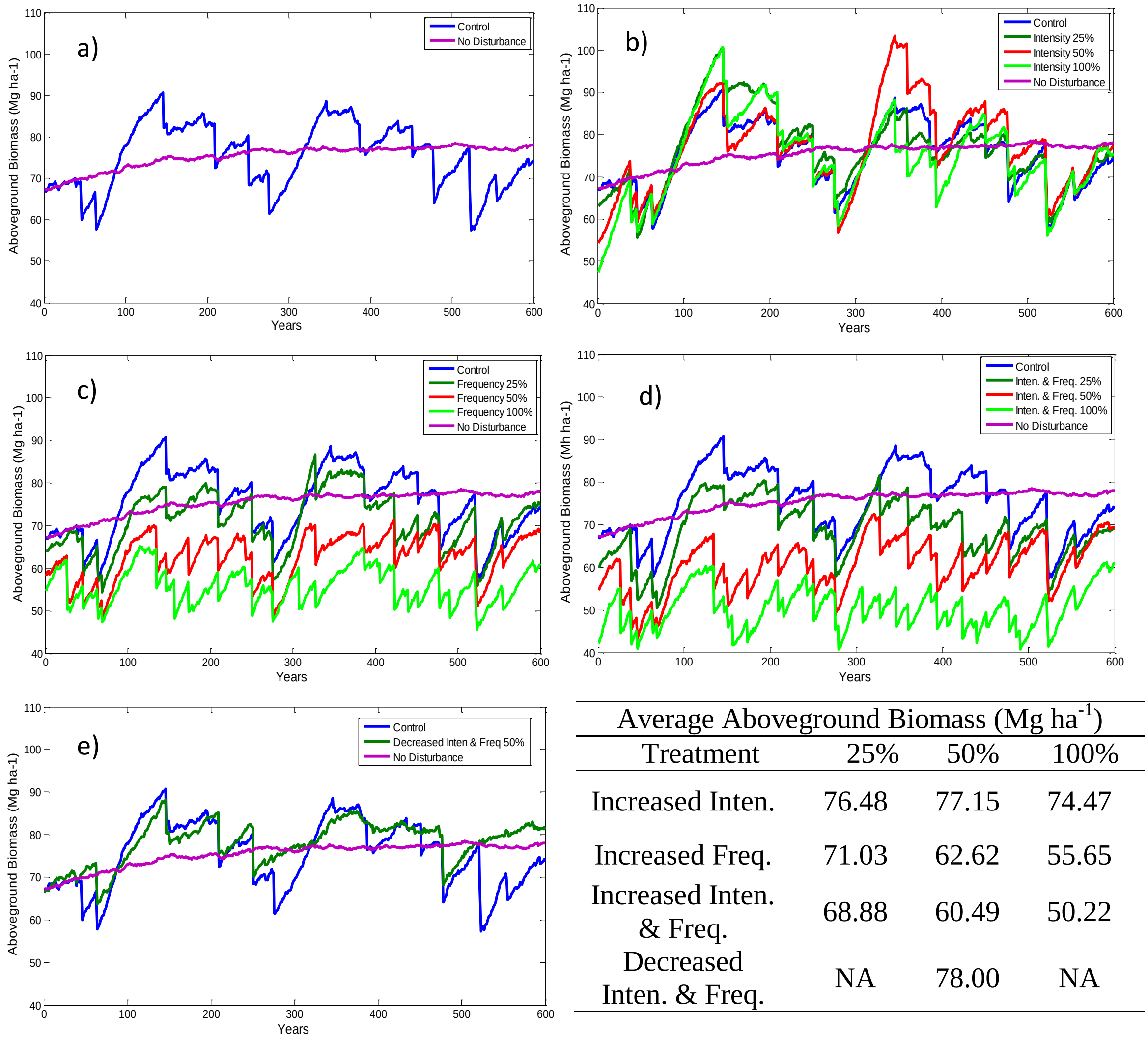
The changes in aboveground biomass (AGB) levels over time (Mg ha^{-1}) after all hurricane disturbances and treatments can be seen in Figure 3.3. The control AGB fluctuates from 57 to 90 Mg ha^{-1} (average AGB 75.3 Mg ha^{-1}), around a simulation with no hurricane disturbance (Figure 3.3a). A hurricane event results in a sudden decrease in AGB followed by a sharp increase during the recovery process, however, during the absence of hurricanes the AGB remains constant. Increasing the intensity of severe hurricanes caused the AGB biomass to fluctuate from 47 to 101 Mg ha^{-1}, allowing for large transient increases in AGB. This is most likely due to the forested landscape growing and developing in synchrony after a storm, breaking away from a quasi-equilibrium state (Shugart 1998). After a severe storm both the early and late successional species were damaged, and therefore the landscape is not a mosaic of different patches (quasi-equilibrium state) as seen during simulations void of hurricanes, but instead produces a less predictable, non-equilibrium landscape where AGB can reach higher levels compared to results with no hurricanes hitting the dry forest.

Increasing the intensity of severe hurricanes from 25% to 100% subtly changed the average AGB levels from the control. A one-way analysis of variance showed that increasing storm intensity from the control did not significantly change AGB: ($F(_{79, 2.7}) = 0.487$, $p=0.692$, $r^2=0.019$). Increasing the intensity of severe storms by 25% and 50% increased the AGB by 1.6% and 2.5% over the control (75.3 Mg ha^{-1}) (Figure 3.3b). Increasing the intensity of severe storms by 100% decreased the AGB by 1.1% (74.5 Mg ha^{-1}).

Increasing the frequency of storm events from the control altered the biomass levels more strongly and significantly than increased intensity; ($F_{(79,2.7)} =72.15$, $p<0.001$,

r^2=0.74). The changes in increasing storm frequency explained 74% of the variation in AGB, and following a Tukey's ad hoc test all treatments had means that were significantly different from each other. Average AGB was decreased by 5.8%, 18.3%, and 29.9% for increasing frequency by 25%, 50%, and 100%, respectively (average 71.0, 62.6, and 55.6 Mg ha^{-1}) (Figure 3.3c). While average biomass levels were lower with increased frequencies than increased intensities, the fluctuations in biomass were not as strong when compared to increased intensities. The maximum and minimum AGB were more pronounced with increased intensity of storms. The combination of increasing both hurricane frequency and intensity of severe storms generated the greatest decrease in AGB: 8.9%, 21.8%, and 39.9% decrease for increasing frequency and intensity by 25%, 50%, and 100% respectively (average 68.9, 60.5, and 50.2 Mg ha^{-1}) (Figure 3.3d). A storm scenario of *decreasing* the frequency and intensity of severe storms by 50% from the control level increased AGB by 3.6% (78.0 Mg ha^{-1}) (Figure 3.3e), but this was not significant ($F_{(39,4.1)}$ =2.066, p=0.159, r^2=0.05%). The reduction in storm frequency and intensity produced the smallest fluctuation in AGB (63.6 to 88.2 Mg ha^{-1}); a smaller difference in extreme levels compared to treatments with increased hurricane intensity and frequency. Results from the one-way ANOVA can be found in Appendix 3.1.

Extreme differences between overall aboveground biomass gain and lost (over 600 years) were seen more often with climate change scenarios of increased storm intensity (Appendix 3.2). The difference between AGB gained and lost, net change in biomass, is 12.0, 23.6, and 28.6 Mg ha^{-1}, respectively for increases of storm intensity by 25%, 50%, and 100%. The net change in AGB is less extreme in climate change scenarios of increased storm frequency, allowing a more mild change in biomass between hurricane events and over the 600 simulated years. The difference between AGB gained and lost is 11.5, 11.1, and 6.2 Mg ha^{-1}, for increases of storm frequency by 25%, 50%, and 100%. The amount of biomass after storm recovery is always greater than the biomass lost; therefore forest recovery is not limited by severe hurricane damage. For the control treatment (historical hurricane regime) the difference in AGB gained and lost is minimal, 7.5 Mg ha^{-1}, similar to treatments with increased storm frequency.



Average Aboveground Biomass (Mg ha^{-1})			
Treatment	25%	50%	100%
Increased Inten.	76.48	77.15	74.47
Increased Freq.	71.03	62.62	55.65
Increased Inten. & Freq.	68.88	60.49	50.22
Decreased Inten. & Freq.	NA	78.00	NA

Figure 3.3. Average aboveground biomass (Mg ha^{-1}) over 600 years, for a total of 11 hurricane treatments and no disturbance after spinning up the model for 200 years starting from bare ground. a) Control, b) control and increasing storm intensity, c) control and

increasing storm frequency, d) control and increasing both storm intensity and frequency, e) control and decreasing both storm intensity and frequency. Control values based on historical patterns. Historical and observed AGB was 75.3 and 64.8 Mg ha^{-1}.

3.3.4 Effects of Disturbance on Net Primary Production (NPP)

The average NPP under historical hurricane disturbance (the control) was 3.04 Mg C ha^{-1} yr^{-1}. Increasing the intensity of severe storms by 25%, 50%, and 100% only had a very slight effect on average NPP. Similar to biomass results, a two-way analysis of variance found the main effect of increase in intensity non-significant ($F(_{1, 316}) = 0.719$, $p=0.397$, Figure 3.4). The main effect of increase in frequency of storm events was significant, and substantially increased NPP ($F(_{1, 316}) = 54.18$, $p<0.001$, Figure 3.4), but there was not an interaction effect between increased intensity and frequency ($F(_{1,316}) = 0.431$, $p=0.512$, Appendix 3.3).

Increasing intensity of storm by 25%, 50%, and 100% over the control yielded an average of 1.2%, 2.1%, and 0.6% increase in NPP (3.08, 3.11, and 3.06 Mg C ha^{-1} yr^{-1} respectively). During long-term simulations (over the course of 600 years) the NPP from treatments with increased storm intensity dropped to levels below the control, demonstrated by the negative percent difference (Figure 3.4). The increase in storm frequency accounted for 17% of the variation in NPP seen in the Puerto Rico forest. NPP increased by 50.6%, 43.4%, and 36.4% with increasing frequency of 25%, 50%, and 100% (5.1, 4.7, 4.4 Mg C ha^{-1} yr^{-1} respectively). One-way ANOVAs were used for the remaining two hurricane treatments. Increasing both hurricane frequency and intensity significantly increased NPP values over the control ($F(_{79, 2.7}) = 589.79$, $p<0.001$, $r^2=0.96$).

NPP increased by 48.7%, 42.2%, and 32.2% with increasing frequencies and intensities of 25%, 50%, and 100% (5.0, 4.7, and 4.2 Mg C ha^{-1} yr^{-1} respectively). Decreasing the frequency and intensity of severe storms by 50% from the control levels produced the largest, significant, average NPP value, 5.39 Mg C ha^{-1} yr^{-1}, a 55.7% increase in NPP from the control ($F(_{39,\,4.1}) = 1163.08$, $p<0.001$, $r^2=0.97$, Figure 3.4). Results from the one-way ANOVA can been found in Appendix 3.4.

Figure 3.5 illustrates the comparison of average NPP for all combinations of storm treatments in a 3D-grid format. The y-axis is average NPP (Mg C ha^{-1} yr^{-1}), the x-axis is changes to storm intensity, and the z-axis is changes to storm frequency. The only substantial difference in NPP was seen during treatments that increased in storm frequency (z-axis). NPP was not affected by increases in storm intensity (x-axis). Higher levels of NPP and higher frequency of storms were negatively correlated, such that the highest level of NPP was seen with the smallest simulated increase in storm frequency, 25%. The lowest NPP was observed when only intensity of storms was increased, but frequency was not altered (back row along x-axis, Figure 3.5). NPP (Mg C ha^{-1} yr^{-1}) increases as a function of increasing aboveground biomass (Mg ha^{-1}) (Figure 3.6); further highlighting that hurricane treatment plays a major role in NPP levels.

A climate change scenario with more frequent storms was able to produce a higher NPP value due to 1) more frequent thinning and recovery episodes, and 2) recovery from less intense storms, compared to the treatments that increased the intensity of storms. This is likely due to smaller differences in extreme levels of high and low aboveground biomass, which is observed when there is an increase in severe storms but not when there is an increase in frequency of storms.

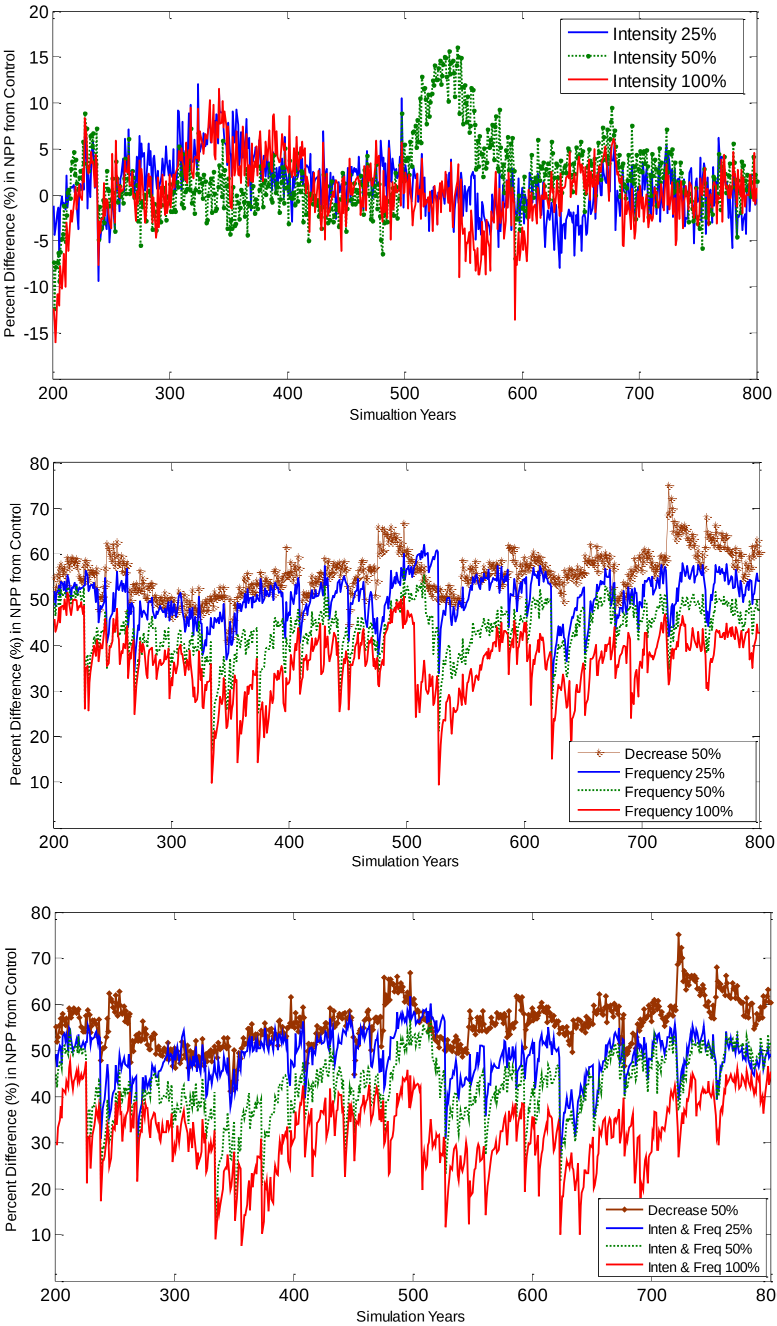


Figure 3.4. Net primary productivity measurements (Mg C ha^{-1} yr^{-1}) as a percent difference from the control hurricane treatment, for ten hurricane treatments over 600 years (after an initial spin-up of 200 years starting from bare ground). Treatments consist of decrease in

frequency and intensity, increased frequency, increased intensity, and both increased frequency and intensity of hurricanes.

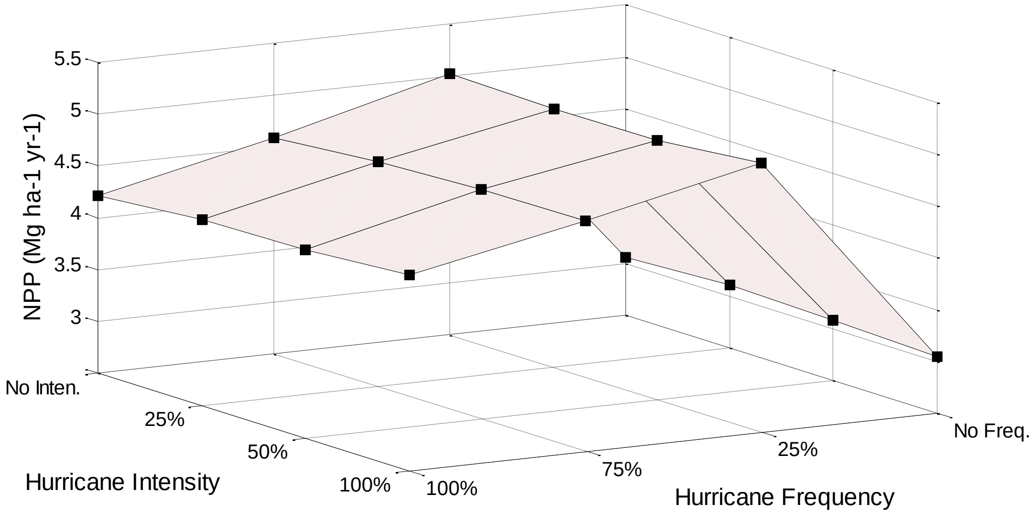


Figure 3.5. Average NPP (Mg C ha^{-1} yr^{-1}) for a mature forest over 600 years (after an initial spin-up of 200 years after starting from bare ground) for the 16 simulated hurricane treatments including the control treatment and all combination of increasing hurricane intensity and frequency by 25%, 50%, and 100% (shown on the x-axis and z-axis).

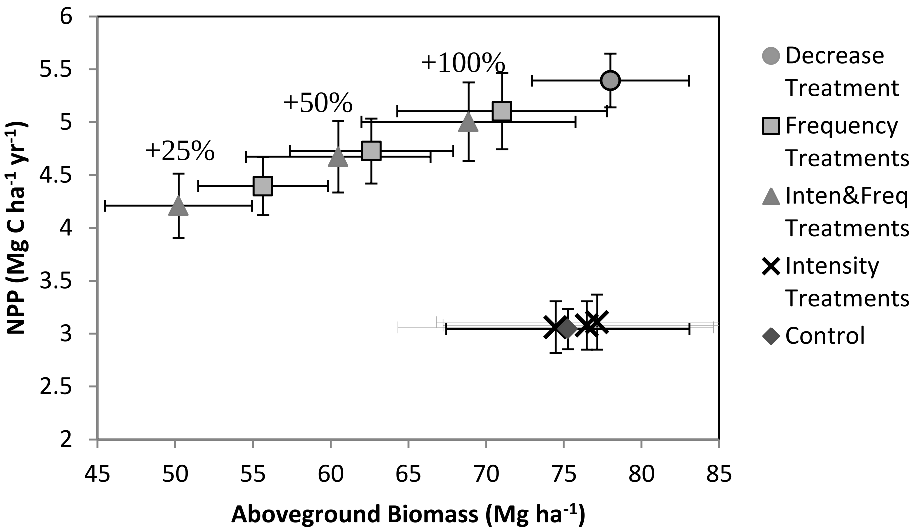


Figure 3.6. Relationship between average aboveground biomass (Mg ha^{-1}) and average NPP (Mg C ha^{-1} yr^{-1}) over 600 years, for the control and ten hurricane treatments under climate change conditions.

3.4 Discussion

3.4.1 Hurricane Treatments

In ZELIG-TROP hurricane simulations, increased intensity of storms does not result in a shift in forest conditions from those simulated by the control treatment and based on historical records. All simulations with increased storm intensities (25%, 50%, and 100%) produced forest structure and function (basal area, density, aboveground biomass and NPP), which were consistent with the control values (Table 3.2 and Figure 3.3b). The single difference between higher storm intensities and control values were larger fluctuations in extreme levels of biomass loss and gain over the 600 year model cycle (Appendix 3.2).

Simulations with increased storm frequency showed decreasing basal area, stem density, aboveground biomass, but NPP increased from the control scenario (Table 3.2 and Figure 3.3c). A decrease in both the frequency and intensity of severe storms by 50% produced the largest increase in basal area, aboveground biomass, and NPP. The increase in forest structure (biomass, basal area) and forest productivity (NPP) with decreased storms was larger than all other treatments, including the control (Figure 3.3e).

Past studies have shown that the hurricane power dissipation or storm destructiveness has been increasing over the past two to three decades, coinciding with increasing sea surface temperatures and increasing climatic warming (Mann and Emanuel 2006, Emanuel 2007, IPCC 2007). The annual average storm peak wind-speed has increased by 50%, so there is an increase in net power (Emanuel 2005). Simulations showed increased wind speeds did *not* have a large effect on the dry forest system of Puerto Rico. The stronger winds of intense storms did not alter the simulated average aboveground biomass or NPP over a long time period (centuries). There was also not an observable change in successional direction.

This study was able to manipulate the intensity of severe storms hitting the Puerto Rican forest and, the frequency or return interval of a range of storm types, using simulations of hurricane disturbance patterns, consistent with expectations for future climate change scenarios. Another achievement was being able to compute the responses from changes in both intensity and frequency of storms. The model results presented above do not include the effects of changes to temperature and precipitation that might be associated with alternate hurricane regimes.

Over the 600 year simulations a mild net change in total biomass was seen (Appendix 3.2), but in shorter observational intervals, there was evidence for extreme fluctuation in biomass (Figure 3.3), particularly in treatments with higher increases in storm intensity (50% and 100% increase). This supports field studies from other forest types that have reported a reduction in biomass from short time periods, but five years following the severe storm, aboveground biomass accumulated at faster rates than pre-hurricane rates (Frangi and Lugo 1998). One of the advantages of augmenting simulation models with field studies was the capacity to inspect dynamics over longer periods than those used in field studies. Over the long-term, average forest structure did not significantly shift from the control condition.

Linkages between climate change (warming) and increased hurricane destructiveness are still in question. Some climate simulation studies have shown a reduction in intensity compared to the historical observed level, and other studies have indicated intense hurricanes are not increased under climate change effects (Knutson et al. 2008, Vecchi and Soden 2007a, 2007b, Zhao et al. 2009). Furthermore, large scale ocean-atmosphere modeling reports show that vertical wind shear will increase with increasing atmospheric temperature. Such increased vertical wind shear is known to weaken hurricanes (Pielke 1990). Because of the alternative predictions from climate models, I also modeled a decrease in storm intensity (possibly due to the effect of vertical wind shear increasing) and decreased storm frequency. With this treatment, there was the largest increase in forest biomass and productivity, and mild fluctuations between annual biomass (Figure 3.3e).

Boose et al. (2004) used a meteorological model to reconstruct the impact of 43 actual hurricanes which have crossed the island of Puerto Rico since 1851. This modeling was on a century time scale (similar to this study) and included a summary of all past hurricanes and damage caused by those hurricanes. After reconstructing 43 storms, Boose et al. (2004) showed that there were repeated minor effects on the scale of years, with loss of foliage and branches occurring regularly from 4-6 years. Major effects or mortality, from larger storms, was on a scale of decades. Effects on forest were dependent on topography, land-use history, and presence of recent hurricanes. Our study agreed with the results in Boose et al. (2004) that increased forest effects were dependent on effects of recent hurricanes and that shorter return intervals of storms have a larger effect on decreasing forest biomass. Our findings concurred with Boose et al. (2004) in that storm effects on forests were not always a byproduct of how intense the storm was, but more dependent on legacy factors.

The disturbance modeling employed here was similar to another simulation modeling experiment conducted in the wet tropical forest of Puerto Rico by O'Brien et al. (1992). Two major differences between the studies were that our experiment involved more accurate species-specific damage data in six damage classes as opposed to randomly assigning the same mortality to all species, and the initialization point from which to increase storm intensity and frequency was from the historical level of hurricanes and not zero occurrences of hurricanes. A major difference between the simulations from the dry forest and the O'Brien et al. simulations of wet forest was that after very intense hurricane treatments (increasing hurricanes by 100%), the dry forest did not experience the losses to basal area, biomass, and leaf area index observed in the model simulations of the wet forest (where basal area, biomass, and leaf area came close to zero). The dry forest on Puerto Rico appeared to be more resistant to large, infrequent disturbances like hurricanes (Van Bloem et al. 2003). This resiliency in the model and in the actual ecosystems appeared to be due to the inclusion of sprouting in simulations. Verifying these results for additional dry tropical forests could be of interest, as post-hurricane sprouting has been noted in other dry tropical forests.

3.4.2. Effects of Disturbance on Net Primary Productivity

I evaluated the long-term change in forest carbon assimilation after varying disturbance treatments, which could interact with forest-based carbon mitigation strategies that aim to reduce carbon emissions (REDD+: Reducing Emissions from Deforestation and Degradation, Miles and Kapos 2008, Venter et al. 2009). Modeling terrestrial-production processes promotes understanding of the factors that contribute to the long-term carbon accumulation in ecosystems. Reduced carbon uptake occurs during the initial damage phase in these forests (seen by decrease in NPP). With increases in hurricane disturbances, there were larger initial increases in NPP due to recovery and therefore greater carbon sequestration (Figure 3.4).

This study further validated that there was a dynamic relationship between aboveground biomass and NPP, with the relationship changing depending on the hurricane treatment. Treatments that resulted in low average biomass level, due to damage, produced high average NPP due to recovery (an inverse relationship, Figure 3.6). Conversely, when aboveground biomass levels were high due to less damage, the NPP was low. The pattern of higher NPP in stands with decreased biomass is analogous to the self-thinning theory (Yoda et al. 1963), as well as productivity being a function of stand structure (Sprugel 1984, Luyssaert et al. 2008). Under self-thinning during simulated hurricane regimes with increased storm frequencies, there was a pronounced drop in stand density and the aboveground biomass of the forest. With this decrease there was a corresponding increase in carbon uptake during the recovery process, and consequently higher NPP. This recovery period allowed for new development and higher net primary production in the forest and thus higher carbon sequestration, matching results found by field studies in wet forests of Puerto Rico (Scatena et al. 1996). It has been observed that debris after a hurricane will decompose quickly followed by a rapid regrowth of vegetation transferring the nutrients from the floor back into the aboveground growth, and primary productivity rates can be triple that prior to the hurricane (Scatena et al. 1996), but not observed to date in dry forests.

During scenarios that have increased hurricane intensity, there was also a recovery process after each hurricane, but there was no substantial increase in NPP (Figure 3.4, 3.5). During treatments when only severe storms increased, the damage effects were more extreme and infrequent. Additionally, between the severe storms, smaller storms still occurred. Any recovery from the extreme damage was further reduced with each subsequent storm, explaining the lack of increase in NPP. When disturbances were small or frequent, such as during treatments in which storms of all wind speeds increased in frequency, the disturbance became incorporated into the environment. During scenarios when storms were frequent and weaker in severity, a different pattern occurs: less extreme damage and recovery periods, with a mosaic landscape reminiscent of a quasi-equilibrium state (Shugart 1998).

After evaluating our modeling results, it was concluded that recovery trends in NPP are similar to a field study that examined forest recovery after Hurricane Hugo in Puerto Rico (Scatena and Lugo 1995). Scatena and Lugo (1995) found that nutrient accumulation on the forest floor and biomass recovery occurs over similar time periods and parallel patterns of return interval of storms. Under this assumption, that the lengths of time for both forest recovery and storm return interval were similar, then during scenarios with more frequent storms there is less damage, and faster turnover rates, promoting faster recovery (favoring higher NPP). Therefore, in treatments when the severity of the storm was high, there was higher damage, and would require longer recovery periods. Simulations showed that when these longer recovery period requirements are interrupted by another storm event, full recovery was not reached, and there was a decrease in overall biomass and carbon acquisitions.

3.4.3. Simulation modeling in comparison to field studies

The forest response to historical hurricane regimes reported here were similar to what was reported in field studies from Puerto Rico. The long term forest effects from many modeled hurricane events of varying strengths were reported as opposed to results from one or two storms, but the trends were related.

Van Bloem et al. (2003, 2007) observed widespread sprouting, induced by bending, wind throw, and increased ethylene production after a hurricane when sustained winds surpassed a minimum threshold of 178 km/h (category 3). Field results also found that hurricanes reduced the number of large diameter stems by uprooting or snapping, but increased sprouting which in turn minimized overall mortality rates (Van Bloem et al.

2005). Due to a new basal-sprouting routine included in the model simulations, stem density remained high after multiple hurricane events (Table 2) and made for more realistic model results confirming field studies. The density of stems never dropped to a critically low level, and abundance was able to return after a storm, even to levels higher than observed. After running simulations with increased storm frequency, the average basal area (m^2) decreased below both the control treatment and the treatment with absence of disturbance (Table 3.2), confirming a reduction in large diameter stems over time similar to field observations. The number of stems in smaller DBH size classes increased with increasing hurricane frequency. Our results were also consistent with Van Bloem et al. (2007), who found that 7 years after a hurricane, sprouting was still observed. Spouts were surviving and growing, and 13% of surviving sprouts had reached the sub-canopy. An increase in growth, recovery, and stem abundance up to 7 years and longer in our simulations was observed, supporting that dry forests are adapted to hurricane disturbances.

Lugo (2000) predicted the effects and outcomes of hurricane disturbances on Puerto Rico in a climate change scenario, similar to climate change scenarios used here. Among his many conclusions he predicted that with increased intensity and frequency of storms “a large fraction of the landscape would be set back in successional stage, or more secondary forests,” and each of the following will occur: forest aboveground biomass and height will decrease, faster rates of biomass turnover (Frangi and Lugo 1991), sudden and massive tree mortality, alternative methods of forest regeneration (such as regeneration from large vs. small gaps or on mineral exposed soils), and more pronounced diversity of age classes in forest stands (Scatena and Larson 1991). This study confirmed some of these predictions, while some were not specifically addressed here. Immediately after a hurricane event, a setback in forest conditions was seen. The aboveground biomass and basal area decreased, and there was a short period of decease in stem density and increase in open gaps as seen from the SVS outputs (Figure 3.2, Figure 3.3). Over time the forest regenerated to pre-storm conditions. The setback in successional stage or creation of secondary forests as predicted by Lugo (2000) with increasing storms was not observed in our simulations.

3.4.4. Strategies for disturbance management and monitoring

Challenges tend to arise when trying to coordinate management plans over large spatial scales and long term temporal scales in forest settings (McCarter et al. 1998, Larocque et al. 2011a). In hopes to ease these challenges, this report provided a tool to display the Puerto Rican forest in a visual and interpretive manner, which could serve as a beneficial resource for management purposes. The Stand Visualization System (SVS) was able to produce plot level images of the forest on annual time steps. The SVS tool could also quickly compute stand canopy cover (%), change in stem abundance from year to year, DBH distribution, and provided an array of visual viewpoints (overhead view, perspective view, stems only, realistic trees, geometric shaped trees). Graphically displaying the individual stand components (i.e. each tree) before and after each hurricane event can be beneficial for many audiences. The graphical snap-shot of the forest includes an accurate size and shape of each tree depending on its age and development. Therefore, the coupled SVS and ZELIG-TROP visualized the spatial pattern of the disturbance to the landscape, and monitored when larger or smaller trees were removed after a disturbance. Identifying habitats that are vulnerable to a disturbance over a large spatial scale can benefit management of fragmented forests, as suggested by Turner et al. (1989). SVS was a useful tool for managing forests under hurricane treatments in climate change scenarios.

The modeling approach demonstrated here can be used as a tool for entities and political issues such as REDD+ (Laurance 2007). Quantifying NPP and vegetation carbon content for desired future time frames (5 years, 10 years, or 100 years) with varying disturbance levels or no disturbance was achieved with ZELIG-TROP. This study contributed to the global knowledge of modeling tropical forest land cover change and estimating carbon emissions, a topic in need of more clarity (Grainger 2010). Tropical forests can sequester large amounts of carbon each year, especially during forest regeneration (DeFries et al. 2002, Achard et al. 2004), but the amount of carbon sequestration during the recovery from disturbance needs further examination. ZELIG-TROP found that the recovery process allows for more carbon to enter the forest system compared to what leaves during the disturbance phase. This study only modeled theoretically stable forests that did not undergo deforestation, an occurrence which is still a major concern (Fearnside 2000, Houghton 2003). This study has the potential to add to the knowledge of quantifying the amount of carbon that can enter a forest after a disturbance and how forests can be used as a mitigation tool for climate change (Canadell and Raupach 2008).

A principal goal of applying 10 varying hurricane treatments was to determine which hurricane scenario would cause an increase or decrease in aboveground biomass and NPP. Some treatments would lead to either higher biomass or higher NPP, but through this method it was found that decreasing or weakening storms would enhance both variables. If climate change tends to increase hurricane frequency (Goldberg 2001) as opposed to increasing intensity (Emanuel 2005, 2006, Webster 2005) the consequences might not be negative, due to increases in NPP. This research provided examples that increases in disturbances will not solely be detrimental, and certain disturbance regimes can in fact benefit the ecosystem and lead to a viable and functioning landscape.

3.5 Conclusions

With the new hurricane disturbance routine implemented into the gap model ZELIG-TROP, the ability to assess long term dynamics of forests (centuries) in response to disturbances was achieved. ZELIG-TROP successfully manipulated hurricane return intervals and hurricane strength. With increasing hurricane intensity (even up to 100% increase) a large shift in aboveground biomass or NPP from the control treatment was not predicted. Therefore, while there is evidence and predictions that hurricane destructiveness has been increasing in the Atlantic Basin over the past 30 years and into the future (Emanuel 2006, IPCC 2007) ZELIG-TROP predicted the forest structure and productivity will not be largely affected. Although large net change between aboveground biomass loss and gain with increased intensity (well above the control) was observed and should be a point of concern with regard to short-term processes. The overall average aboveground biomass and NPP over 600 years remained at a constant level.

Treatments that increased the occurrence of storms have a larger effect (both negative and positive) on the forest. A 5%-40% decrease in aboveground forest biomass and 32%-50% increase in NPP, depending on treatment was found. The hurricane treatment which produced a suitable forest, in terms of producing the highest values of biomass and NPP, was a decrease in the intensity and frequency of storms by 50%. A reduction of storm occurrences and severity had the largest impact on increasing forest biomass and NPP. Using two forest variables (aboveground biomass and NPP), the model was able to access dynamic interactions with each hurricane treatment. It was found that hurricane treatments predicted by climate change scenarios always increased the NPP, with increased hurricane frequency producing larger NPP due to its recovery pattern. Two main trends were observed concerning the relationship between aboveground biomass and NPP depending on the treatment. There was an inverse relationship between AGB and NPP. But, with increasing biomass there was also opportunity for increasing NPP (positive relationship). This project presented two applications from this research which can be used for forest management purposes; SVS graphical outputs and applicability for REDD+. Disturbance simulation modeling, joined with SVS, graphically produced land cover change images for dry tropical forests. Furthermore, capability of predicting carbon stocks, emissions, and sequestration from natural disturbances in dry tropical forests was successful, and can be used by initiatives like REDD+.

3.6. Literature Cited

Angelsen, A. 2008. Moving ahead with REDD: issues, options and implications. CIFOR, Bogor, Indonesia.

Asner, G.P. 2009. Integrated Satellite and Airborne Mapping Approaches. Environ. Res. Letters. 4: 034009.

Baker WL, Walford GM. 1995. Multiple stable states and models of riparian vegetation succession on the Animas River, Colo- rado. Ann Assoc Am Geogr 85:320-38.

Basnet, K., G. E. Likens, F. N. Scatera, and A. E. Lugo. 1992. Hurricane Hugo: damage to a tropical rain forest in Puerto Rico. Journal of Tropical Ecology 8:47-55.

Bender, M.A., T.R. Knutson, R.E. Tuleya, J.J. Sirutis, G.A. Vecchi, S.T. Garner, I.A. Held. 2010. Modeled impact of anthropogenic warming on the frequency of intense Atlantic hurricanes. Science. 327: 454.

Bengtsson, L., et al., 2006. Storm Tracks and Climate Change. Journal of Climate, 19, 3518-3543.

Boose, E. R., M. I. Serrano, D. R. Foster. 2004. Landscape and regional impacts of hurricanes in Puerto Rico. Ecological Monographs. 74: 335-352.

Brandeis, T. J., M. Delaney, B. R. Parresol, and L. Royer. 2006. Development of equations for predicting Puerto Rican subtropical dry forest biomass and volume. For. Ecol. and Mang. 233, 133-142.

Brokaw, N. V. L. 1985. Treefalls, regrowth, and community structure in tropical forests. In The Ecology of Natural Disturbances and Patch Dynamics. Eds. S. T. A. Pickett and P. S. White. New York: Academic, pp. 101-108.

Brokaw, N. V. L. and L. R. Walker. 1991. Summary of the Effects of Caribbean Hurricanes on Vegetation. Biotropica 23:442-447.

Brown, S. and A. E. Lugo. 1984. Biomass of Tropical Forests: A New Estimate Based on Forest Volumes. Science 223:1290-1293.

Brown, S., Gillespie, A.J., Lugo, A.E., 1989. Biomass estimation methods for tropical forests with application to forest inventory data. Forest Sci. 35, 881–902.

Brown, S. 1997. Estimating biomass and biomass change in tropical forests. A primer. FAO Forestry Paper 134. Food and Agriculture Organization of the United Nations, Rome.

Canadell, J. G. and M. R. Raupach. 2008. Managing forests for climate change mitigation. Science. 320, 1456-1457.

Cao. M. and F.I. Woodard. 1998. Net primary and ecosystem production and carbon stocks of terrestrial ecosystems and their responses to climate change. Global Change Biology. 4: 185-198.

Chapin, F. S., P. A. Matson, H. A. Mooney. 2002. Principles of Terrestrial Ecosystem Ecology. Springer. New York.

Clark, D.A, S. Brown, D.W. Kicklighter, J.Q. Chambers, J.R. Thomlinson, J. Ni, E.A. Holland. 2001. Net primary production in tropical forests: an evaluation and synthesis of existing field data. Ecol. Applications. 11: 371-384.

Cumming, S. G. and Burton, P. J. 1993. A Programmable Shell and Graphics System for Forest Stand Simulation, Environ. Software. 8, 219-230.

Dallmeier, F., J. A. Comiskey, F. N. Scatena. 1998. Five years of forest dynamics following hurricane Hugo in Puerto Rico's Luquillo Experimental Forest. Pages 231-248 in F. a. J. A. C. Dallmeier, editor. Forest biodiversity in North, Central and South America, and the Caribbean. The Parthenon Publishing Group, Paris.

DeFries, R. S., R. A. Houghton, M. C. Hansen, C. B. Field, D. Skole, J. Townshend. 2002. Carbon emissions from tropical deforestation and regrowth based on satellite observations for the 1980s and 1990s. PNAS. 99, 14256-14261.

Donnelly, J.P., and J.D. Woodruff. 2007. Intense hurricane activity over the past 5,000 years controlled by El Niño and the West African monsoon. Nature, 447, 465-468.

Doyle, T. W.: 1981. ‘The Role of Disturbance in the Gap Dynamics of a Montane Rain Forest: An Application of a Tropical Forest Succession Model’, in West, D. C., Shugart, H. H., and Botkin, D. B. (eds.), Forest Succession: Concepts and Application, Springer, New York a.o., pp. 56–73.

Emanuel, K. 2005. Increasing destructiveness of tropical cyclones over the past 30 years. Nature 436:686-688.

Emanuel, K. 2006. Hurricanes: Tempests in a greenhouse. Physics Today 59:74-75.

Emanuel, K. 2007. Environmental factors affecting tropical cyclone power dissipation. J. Climate. 20: 5497-5509.

Everham, E.M. III and N.V.L. Brokaw. 1996. Forest damage and recovery from catastrophic winds. The Bot. Rev. 62: 113-185.

Fearnside, P. M. 2000. Global warming and tropical land-use change: Greenhouse gas emissions from biomass burning, decomposition and soils in forest conversion, shifting cultivation and secondary vegetation. Clim. Change 46: 115–145.

Foster, D.R., M. Fluet, E.R. Boose. 1999. Human or natural disturbance: landscapes scale dynamics of the tropical forests of Puerto Rico. Ecol. Application. 9: 555-572.

Frangi J.L. and Lugo AE. 1991. Hurricane damage to a flood plain forest in the Luquillo Mountains of Puerto Rico. Biotropica. 23:324-335.

Frangi, J. L. and A. E. Lugo. 1998. A flood plain palm forest in the Luquillo mountains of Puerto Rico five years after Hurricane Hugo. Biotropica 30:339-348.

Gibbs, H.K. S. Brown, J.O. Niles, J.A. Foley. 2007. Monitoring and estimating tropical forest carbon stocks: making REDD a reality. Environ. Res. Lett. 2: 045023.

Goldenberg, S. B., et al., 2001. The recent increase in Atlantic hurricane activity: causes and implications. Science, 293, 474-479.

Govender, N. W. S. W. Trollope, B. W. Van Wilgen. 2006. The effect of fires season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. J. of App. Eco. 43:748-758.

Grainger, A. 2010. Uncertainty in the construction of global knowledge of tropical forests. Progress in Physical Geography. 34, 811-844.

Granzow de la Cerda, I., Z. Nelson, J. Vandermeer, D. Boucher. 1997. Tree species diversity in the tropical moist forest (Caribbean of Nicaragua) seven years after hurricane Joan. . Revista de Biological Tropical 45:1409-1419.

Harrington, R. A., J. H. Fownes, P.G. Scowcroft, C.S. Vann. 1995. Impact of hurricane Iniki on native Hawaiian Acacia koa forests: damage and two-year recovery. J. of Trop. Ecol. 13:539-558.

Henderson-Sellers, A., H. Zhang, G. Berz. K. Emanual, W. Gray, C. Landsea, G. Holland, J. Lighthill, S-L. Shieh, P. Webster, K. McGuffie. 1998. Tropical cyclones and global climate change: A post-IPCC assessment. Bull. Amer. Meteor. Soc., 79, 19–38.

Holm, J.A., H.H. Shugart, S.J. Van Bloem, G. R. Larocque. In press. Gap model development, validation, and application to succession of secondary subtropical dry forests of Puerto Rico. Ecol. Model.

Houghton, R. A. 2003. Revised estimates of the annual net flux of carbon to the atmosphere from changes in land use and land management. Tellus 55B: 378–390.

Hsu, S.A and Z. Yan. 1998. A note on the radius of maximum wind for hurricanes. J. of Coastal Research. 14: 667-668.

Imbert, D., P. Labbe, A. Rousteau. 1996. Hurricane damage and forest structure in Guadeloupe, French West Indies. Journal of Tropical Ecology 12:663-680.

IPCC. 2007. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I, II, and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Core Writing Team, Pachauri, R.K. and Reisinger, A. (Eds.) IPCC, Geneva Switzerland.

Knight, J.R., R.J. Allan, C.K Folland, M.Vellinga, M. Mann. 2005. A signal of natural thermohaline cycles in observed climate. Geo. Research Letters 32: L20708.

Knight, J.R., C. K. Folland, A. A. Scaife. 2006. Climate impacts of the Atlantic Multidecadal Oscillation. Geo. Research Letters 33: L17706.

Knutson, T., J.J. Sirutis, S.T. Garner, G.A. Vecchi, I.M. Held 2008. Simulated reduction in Atlantic hurricane frequency under twenty-first-century warming conditions. Nature Geosciences, 1, 359 - 364.

Landsea, C., C. Anderson, N. Charles, G. Clark, J. Fernandez-Partagas, P. Hungerford, C. Neumann, and M. Zimmer. 2002. Atlantic hurricane re-analysis project. NOAA/Hurricane Research Division web page. Online: http://www.aoml.noaa.gov/hrd/hurdat.

Landsea, C.W., G.A. Vecchi, L. Bengtsson, T.R. Knutson. 2010. Impact of duration thresholds on Atlantic tropical cyclone counts. J. of Climate. 23: 2508 – 2519.

Larocque, G. R., L. Archambault, and C. Delisle. 2006. Modelling forest succession in two southeastern Canadian mixedwood ecosystem types using the ZELIG model. Ecol. Model. 199, 350-362.

Larocque, G. R., J.S. Bhatti, J.C. Ascough II, J. Liu, N. Luckai, D. Mailly, L. Archambault, A.M. Gordon. 2011a. An analytical framework to assist decision makers in the use of forest ecosystem model prediction. Environ. Model. & Soft. 26: 280-288.

Larocque, G.R., L. Archambault, C. Delisle. 2011b. Development of the gap model ZELIG-CFS to predict the dynamics of North American mixed forest types with complex structures. Ecol. Model. 222:2570-2583.

Lugo, A. E., M. Applefield, D. J. Pool, R. B. McDonald. 1983. The impact of hurricane David on the forests of Dominica. Can. J. of For. Res. 13:201-211.

Lugo, A. E. 2000. Effects and outcomes of Caribbean hurricanes in a climate change scenario. The Science of the Tot. Environ. 262: 243-251.

Mann, M.E. and K.A. Emanuel. 2006. Atlantic hurricane trends linked to climate change. EOS. 87: 233-244.

Mascaro J., I. P. O. B. D. H. B. I. G. d. l. C. J. R. J. V. 2005. Aboveground Biomass Accumulation in a Tropical Wet Forest in Nicaragua Following a Catastrophic Hurricane Disturbance. Biotropica 37:600-608.

McGaughey, Robert J. 1997. Visualizing forest stand dynamics using the stand visualization

system. In: Proceedings of the 1997 ACSM/ASPRS Annual Convention and Exposition; April 7-10, 1997; Seattle, WA. Bethesda, MD: American Society of Photogrammetry and Remote Sensing. 4:248-257.

Miles, L. and V. Kapos. 2008. Reducing greenhouse gas emissions from deforestation and forest degradation: global land-use implication. Science. 320: 1454-1455.

Millas, J. C. 1968. Hurricanes of the Caribbean and adjacent regions. Academy of the Arts and Sciences of the Americas, Miami, Florida, USA.

Neumann, C. J., B. R. Jarvinen, A. C. Pike. 1987. Tropical cyclones of the North Atlantic Ocean 1871-1986. Third revised edition. NOAA-National Climatic Data Center, Asheville, North Carolina, USA.

Newbould, P.J. 1967. Methods for estimating the primary production of forests. Blackwell Scientific, Oxford.

O'Brien, S.T, B.P. Hayden, H.H. Shugart. 1992. Global climatic change, hurricanes, and a tropical forest. Climatic Change. 22: 175-190.

Oluwole, F. A., J. M. Sambo, D. Sikhalazo. 2008. Long-term effects of different burning frequencies on the dry davannah grasslands in South Africa. African. J. of Agri. Research. 2: 147-153.

Overpeck, J. T. D. Rind, R. Goldberg. 1990. Climate-induced changes in forest disturbance in vegetation. Nature. 343: 51-53.

Pabst, R.J., M.N. Goslin, S.L. Garman, and T.A. Spies. 2008. Calibrating and testing a gap model for simulating forest management in the Oregon Coast Range. For. Ecol. Manage. 256, 958–972.

Pastor, J. and W. M. Post. 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. Biogeochemistry. 2: 3-27.

Pielke, R.A., 1990: The Hurricane. Routledge Press, London.

Quiñones, F. 1992. History of hurricanes in Puerto Rico, 1502-1989. Acta Cientifica 6:3-14.

Reilly, A. E. 1998. Hurricane Hugo: Winds of change...or not? Forest dynamics on St. John, U.S. Virgin Islands, 1986-1991. Pages 349-365 in F. a. J. A. C. Dallmeier, editor. Forest biodiversity in North, Central and South America, and the Caribbean. The Parthenon Publishing Group, Paris.

Sanchez-Sanchez, O. and G. A. Islebe. 1999. Hurricane Gilbert and sructural changes in a tropical forest in south-eastern Mexico. Global Ecology and Biogeography 8:29-38.

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

Scatena FN, Larsen MC. 1991. Physical aspects of Hurricane Hugo in Puerto Rico. Biotropica. 23:317-323.

Scatena FN, Moya S, Estrada C, Chinea JD. 1996. The first five years in the reorganization of aboveground biomass and nutrient use following Hurricane Hugo in the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico. Biotropica. 28:424-440.

Scatena F.N and A. E. Lugo. 1995. Relative scales of time and effectiveness of watershed processes in a tropical montane rain forest of Puerto Rico. In: Natural and anthropogenic influences in fluvial geomorphology. Geophysical Monograph 89. American Geophysical Union. Washington, DC. 103-111.

Schlesinger. W. H. 1997. Biogeochemistry: an analysis of global change. 2nd Edition. Academic Press. San Diego, CA.

Scholes, R. J. and B. H. Walker. 2004. An African Savanna: synthesis of the Nylsvley study. Cambridge University Press.

Shugart, H. H., T. M. Smith, W. M. Post. 1992. The potential for application of individual-based simulation models for assessing the effects of global change. Ann. Rev. of Eco. and Systematics. 23: 15-38.

Shugart, H.H. 1998. Terrestrial ecosystems in changing environments. Cambridge: Cambridge University Press, USA.

Shugart, H. H. 2002. Forest Gap Models. Vol. 2, The Earth system: biological and ecological dimensions of global environmental change. Eds. H. A. Mooney and J. C. Canadell in Encyclopedia of Global Environmental Change. John Wiley & Sons. pp. 316-323.

Silvertown, J. and B. Smith. 1988. Gaps in the canopy: the missing dimension in vegetation dynamics. Vegetatio. 77:57-60.

Smith, J. B., and D. A. Tirpak, 1989. Eds. The potential effects of global climate change on the U.S.: Appendix D – Forest. Off. Policy, Planning Eval. Washington, DC: US Environ. Protection Agency.

Smith, T. M. and D. L. Urban. 1988. Scale and the resolution of forest structural pattern. Vegetatio. 74:143-150.

Solomon, A. M. 1986. Transient response of forests to CO2-induced climate change: Simulations experiments in eastern North America. Oecologia. 68: 567-579.

Turner, M. G. and V. H. Dale. 1998. Comparing large, infrequent disturbances: what have we learned? Ecosystems. 1: 493-496.

Urban, D.L., 1990. A Versatile Model to Simulate Forest Pattern: A User’s Guide to ZELIG Version 1. 0. University of Virginia, Charlottesville, Virginia.

Urban, D.L., 2000. Using model analysis to design monitoring programs for landscape management and impact assessment. Ecol. Appl. 10, 1820–1832.

Urban, D.L., Bonan, G.B., Smith, T.M., Shugart, H.H., 1991. Spatial applications of gap models. Forest Ecol. Manage. 42, 95–110.

Urban, D. L., Harmon, M. R., and Halpern, C. B. 1993. Potential Response of Pacific Northwestern Forests to Climatic Change, Effects of Stand Age and Initial Composition. Clim. Change 23, 247-266.

Uriarte, M., C. D. Canham, J.Thompson, J. K. Zimmerman, L. Murphy, A. M. Sabat, N. Fetcher, and B. L. Haines. 2009. Understanding natural disturbances and human land use as determinants of tree community dynamics in a subtropical wet forest: results from a forest simulator. Ecological Monographs. 79: 423-443.

Van Bloem, S. J., P. G. Murphy, A. E. Lugo. 2003. Subtropical dry forest trees with no apparent damage sprout following a hurricane. Tropical Ecology 44:137-145.

Van Bloem, S. J., P. G. Murphy, A. E. Lugo, R. Ostertag, R. Rivera Costa, I. Ruiz Bernard, S. Molina Colon, M. Canals Mora. 2005. The influence of hurricane winds on Caribbean dry forest structure and nutrient pools. Biotropica 37:571-583.

Van Bloem, S. J., A. E. Lugo, P. G. Murphy. 2006. Structural response of Caribbean dry forests to hurricane winds: a case study from Guanica Forest, Puerto Rico. Journal of Biogeography 33:517-523.

Vandermeer J., A. B. I. G. C. 1998. Growth Rates of Tree Height Six Years after Hurricane Damage at Four Localities in Eastern Nicaragua. Biotropica 30:502-509.

Vecchi, G.A. and B.J. Soden. 2007a. Effect of remote sea surface temperature change on tropical cyclone potential intensity. Nature, 450, 1066-1071.

Vecchi, G.A. and B. J. Soden, 2007b. Increased tropical Atlantic wind shear in model projections of global warming. Geo. Research Letters.

Vecchi, G.A., K.L. Swanson, B.J. Soden. 2008. Whiter hurricane activity? Science. 322: 687-689.

Venter, O., W. F. Laurance, T. Iwamura, K. Wilson, R. A. Fuller, H. P. Possingham. 2009. Harnessing carbon payments to protect biodiversity. Science. 326: 1368.

Walker, L. R., D. J. Lodge, N. V. L. Brokaw, and R. B. Waide. 1991. An Introduction to Hurricanes in the Caribbean. Biotropica 23:313-316.

Webster, P.J., G.J. Holland, J.A. Curry, H.-R. Chang. 2005. Changes in tropical cyclone number, duration, and intensity in a warming environmental. Science. 309: 1844.

Whigham, D. F., I. Olmsted, E. Cabrera Cano, and M. E. Harmon. 1991. The impact of hurricane Gilbert on trees, litterfall, and woody debris in a dry tropical forest in the northeastern Yucatan Peninsula. Biotropica 23:434-441.

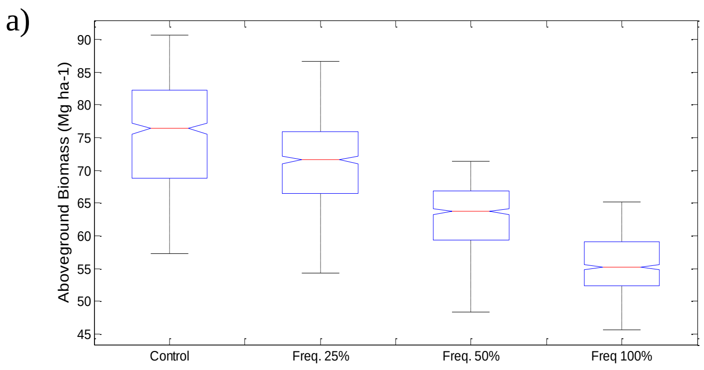
Whitmore, T. C. 1982. On pattern and process in forests. In The Plant Community as a Working Mechanism. Special Publ. No 1, Br. Ecol. Soc. Ed. E. I. Newman. Oxford: Blackwell Sci. pp. 45-59.

Yoda, K., T. Kira, H. Ogawa, and K. Hozumi. 1963. In- traspecific competition among higher plants. XI. Self-thinning in overcrowded pure stands under cultivated and nat- ural conditions. Journal of Biology of Osaka City University 14:107-129.

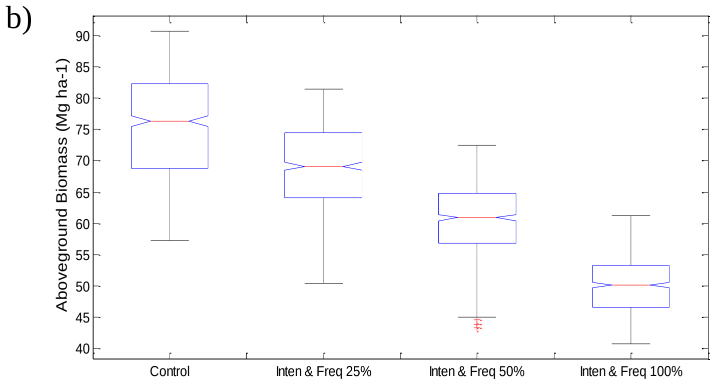
Zeng H., J. Q. Chambers, R. I. Negron-Juarez, G. C. Hurtt, D. B. Baker, M. D. Powell. 2009. Impacts of tropical cyclones on U.S. forest tree mortality and carbon flux from 1851 to 2000. PNAS. 106: 7888-7892.

Zimmerman, J.K., M.R. Willig, L.R. Walker, W.L. Silver. 1996. Introduction: Disturbance and Caribbean ecosystems. Biotropica. 28: 414-423.

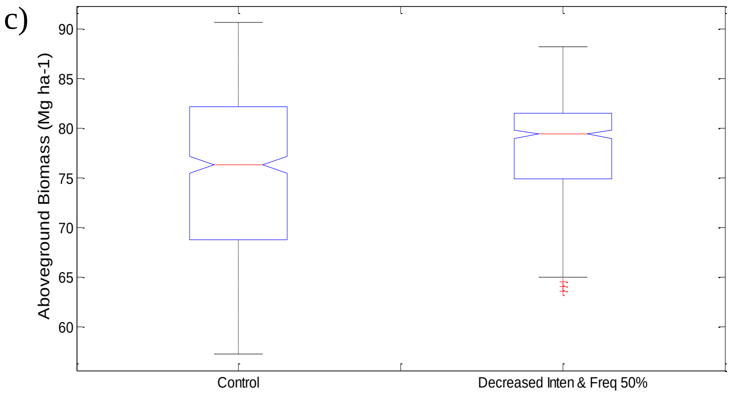
3.7 Appendix



AGB: $F_{(79,2.7)}$ =72.15, p<0.001, r^2=0.74



AGB: $F_{(79,2.7)}$ =117.43, p<0.001, r^2=0.82

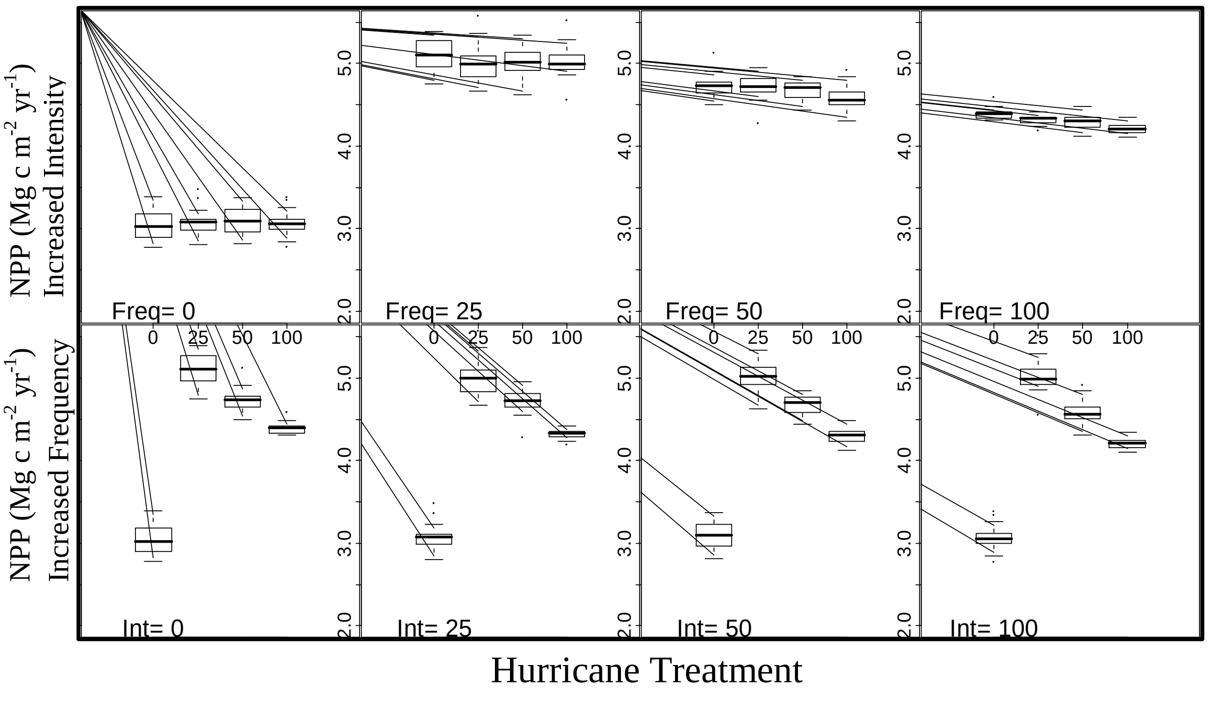


AGB: $F_{(39,4.1)}$ =2.066, p=0.159, r^2=0.05

Appendix 3.1. Boxplots with sample minimum, lower quartile, median, upper quartile, and sample maximum for three one-way ANOVA tests between differences in aboveground biomass for the control scenario and: a) increasing frequency, b) increasing intensity and frequency, and c) decreasing intensity and frequency.

Appendix 3.2. Net change in aboveground biomass (Mg ha^{-1}) over 600 years. Change in biomass calculated as difference between total biomass gain/recovery in-between all hurricane events minus the total biomass lost after all disturbances.

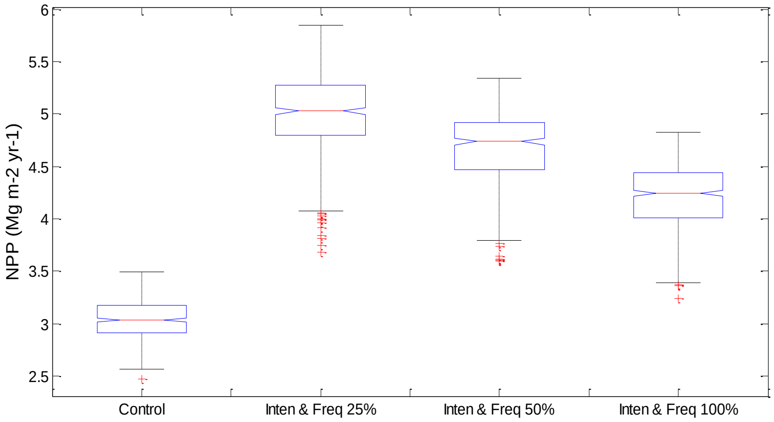
	Treatments		
Biomass (Mg ha^{-1})	25%	50%	100%
Biomass Lost (Intensity)	139.2	167.9	178.1
Biomass Lost (+Freq.)	157.4	177.1	192.9
Biomass Lost (+Inten. & Freq.)	163.4	196.7	218.0
Biomass Loss (-Inten. & Freq.)	NA	65.1	NA
Biomass Gain (+Intensity)	151.2	191.5	206.7
Biomass Gain (+Freq.)	168.9	188.2	199.1
Biomass Gain (+Inten. & Freq.)	172.9	211.8	237.8
Biomass Gain (-Inten. & Freq.)	NA	79.9	NA
Net Δ in AGB (+Intensity)	12.0	23.6	28.6
Net Δ in AGB (+Freq.)	11.5	11.1	6.2
Net Δ in AGB (+Inten. & Freq.)	9.5	15.1	19.8
Net Δ in AGB (-Inten. & Freq.)	NA	14.8	NA



Appendix 3.3. Boxplots with sample minimum, lower quartile, median, upper quartile, and sample maximum for a two-way ANOVA test of differences in NPP, with increased

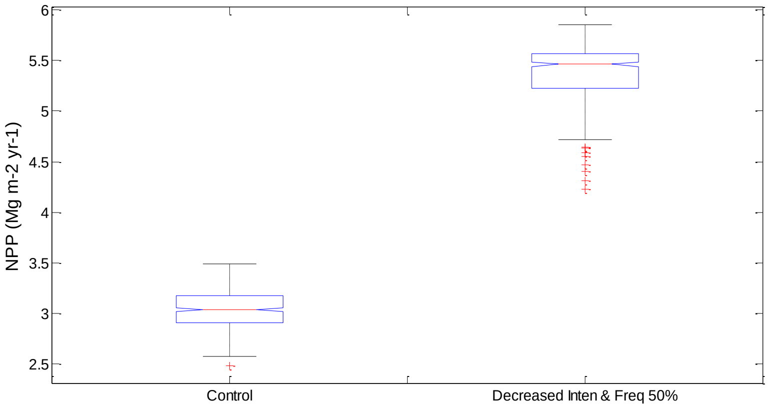
hurricane intensity and increased hurricane frequency as the main effects. Main effect of increased intensity (top row) and the interaction factor was not significant, but main effect of increased frequency (bottom row) was significant.

a)



NPP: F($_{79,\ 2.7}$) = 589.79, p<0.001, r^2=0.96

b)



NPP: F($_{39,\ 4.1}$) = 1163.08, p<0.001, r^2=0.97

Appendix 3.4 Boxplots with sample minimum, lower quartile, median, upper quartile, and sample maximum for two one-way ANOVA tests between differences in NPP for the control scenario and: a) increasing intensity and frequency, and b) decreasing intensity and frequency.

Chapter 4 Annual carbon production and functionality of a subtropical dry forest after hurricane disturbances

4.1 Introduction

Terrestrial forests act as a carbon source to the atmosphere by means of deforestation, land-use change, and disturbance (Fearnside and Laurance 2004, Houghton 2005, Bryan et al. 2010). However, this role has been regarded as one of the most uncertain components in climate change models, and needs to be further examined (Houghton et al. 2001, IPCC 2007). This uncertainty can represent a major source of carbon to the atmosphere, in addition to the carbon dioxide released from fossil fuel combustion and human activity, which is well described (Marland et al. 2000, IPCC 2007, Global Carbon Project 2011, Peters et al. 2011).

Tropical deforestation is estimated to produce large amounts of carbon emissions (or sink reductions); accounting for 15-25% of annual global greenhouse emission in the 1990s, and variability in deforestation rates leads to errors in carbon balance estimates (Fearnside and Laurance 2003, 2004, Houghton 2003, 2005, Gibbs et al. 2007, Global Carbon Project 2011). The range of carbon emissions from tropical deforestation was 0.6 to 2.5 Pg yr^{-1} from the 1980s (IPCC report in Prentice et al. 2001) and averaged 0.9 Pg yr^{-1} from the 1990s (DeFries et al. 2002). Gurney et al. (2002) states, that in general the tropics are either neutral or a small source of carbon to the atmosphere. While consequences of deforestation are unclear, the role intact forests play in releasing carbon from large scale disturbances is less clear (DeFries et al. 2002, Clark 2007).

Likewise, tropical forests can act as *sink*. However, the amount of total carbon stored in living tropical forests, and capacity as a carbon sink, is also uncertain (Houghton et al. 2001, Fearnside and Laurance 2003). Predictions show that tropical forests can act as a major carbon sink in response to global climate change (Phillips et al. 1998, Baker et al. 2004). Tropical forests can store large amounts of terrestrial carbon, even in times of disturbance and land cover change.

Additional examples show trends in which there is an increase in aboveground biomass in tropical forests in recent years and decades (Phillips et al. 1998, Chambers et al. 2001, Baker et al. 2004, Lewis et al. 2004), also seen in temperate forests (McMahon et al. 2010), mostly attributed to increasing CO_2 levels. Chambers et al. (2001) demonstrated that during increases in productivity (increases in CO_2), mature tropical forests accumulate higher amounts of carbon, and these forests can continue to accumulate carbon for a century after increases in CO_2 have stopped, due to large wood storage capacity. Lewis et al. (2004) found widespread evidence of increasing stand-level basal area, stem recruitment, as well as increasing basal area loss, and stem mortality across tropical sites in South America. While all components are increasing, the gain terms (basal area growth and stem recruitments) exceeded the loss terms (basal area loss and stem mortality). Yet the trend of increasing forest stocks and forests acting as a carbon sink is disputed. Other studies show that undisturbed, old-growth forests of the humid neo-tropics are not carbon sinks, and there is not a significant increase in biomass that would affect the global carbon budget (Clark 2002, refuting Phillip et al. 1998).

In addition to forests acting as either carbon sources or sinks, the rate of change (flux) between the two needs to be quantified. There is evidence that flux patterns of autotrophic carbon accumulation, ecosystem level production, and nutrient availability can change temporally and are dynamically altering as a carbon source or sink (Murphy and Lugo 1986a). Patterns in carbon flux can change over time due to environmental stress (Reich and Borchert 1984), land-use change (Prentice et al. 2001, DeFries et al. 2002), climatic variations, and other internal and external factors (fire, drought, insect outbreaks, windstorms). Tropical forests can either be carbon sources, sinks, or in equilibrium depending on age, disturbance, and land use. The Sierra et al. 2007b study found that the natural variation in carbon production from experimental field studies in the Amazon ranges from -4.03 to 2.22 Mg C ha^{-1} yr^{-1}, compared to Seirra's 2007a study which found a range of -1.5 to 1.5 Mg C ha^{-1} yr^{-1} (STANDCARB model) for the same forests. Sierra et al. (2007a) hypothesized there is a natural range of carbon emissions and sequestration, but not enough evidence to state if the forests are in a carbon balance or acting as a significant carbon sink or source.

There is need to clearly understand changes to carbon cycling in tropical forests, due to its high variability. This clarification is important for programs like REDD+ (Reducing Emissions from Deforestation and Degradation). REDD+ is designed to create incentives to protect vital tropical forests by a carbon-payment mechanism (Miles et al. 2008, Canadell and Raupach 2008, Venter et al. 2009). One of REDD+'s goals is to evaluate where carbon is being sequestered and where carbon is being released in tropical forests, an objective addressed by this study. As humans are modifying the Earth's surface and altering the carbon cycle, attention is focused on forests as carbon storage (Cooper 1983, Vargas et al. 2008, McKinley 2011), carbon trading and credit industries (Schlesinger 2006, Laurance 2007, Ebeling and Yasue 2008), and there is a need to define fluxes in carbon budgets for all areas of the world (Steffan et al. 1998, Running et al. 1999, Randerson et al. 2002, Houghton 2005). Climate change is altering the controls over forest production drivers (i.e. temperature, precipitation, soil nutrients, radiation) in both a positive and negative manner (Boisvenue and Running 2006). Countries that hope to use forests as offset for carbon emissions (in accordance with programs like REDD+) run the risk of disturbance, climate change, or land use practices producing offset reversal (i.e. carbon reversal) (Galik and Jackson 2009). This study evaluated the consequences and effects when an indirect forest production driver changes over time in a modeling approach. The indirect forest production driver assessed here is large-scale hurricane disturbances. First the effect of historical hurricanes patterns as a forest production driver were evaluated, followed by increased hurricane events as predicted in climate change scenarios for a subtropical dry forest located in Puerto Rico. To evaluate changes in carbon storage and transfers, this study tracked the changes in components that make up the annual carbon production budget.

4.1.1 Components of annual autotrophic live carbon accumulation (AALCA)

There are many processes that affect and alter the Earth’s carbon cycle. Processes such as plant and microbial respiration, changes to photosynthesis rates, leaching, erosion, or depletion of plant material by harvesting, herbivory, and disturbance all affect the terrestrial carbon cycle and total carbon accumulation into the ecosystem (Woodwell and Whittaker 1968, Woodwell and Botkin 1970. In field experiments, each carbon accumulation component listed above is labor-some to quantify, but upon estimation provides a clearer picture of global carbon cycles (Schlesinger 1997).

This study assesses the changes to annual autotrophic live carbon accumulation (AALCA) with respect to major disturbances in addition to natural gap dynamics. Annual autotrophic live carbon accumulation is a summation of the components making up living aboveground autotrophic components as well as losses due to necromass (defined in detail in methods section), but does not take into account heterotrophic components at the ecosystem level. Annual autotrophic live carbon accumulation is defined as the annual sum of new wood by diameter increment, regeneration, basal-sprouting, new leaf production/growth minus litterfall and necromass for only the aboveground tissues. Litterfall and necromass (or coarse woody debris, CWD) is a major component of AALCA contributing a substantial amount to releasing carbon to the ecosystem, but also vital for ecosystem functioning as described below.

Litterfall in forests is a major source of supplying nutrients back to the forest floor and for cycling of organic matter to be used for forest growth and regeneration (Vitousek 1984, Spain 1984, Jaramillo and Sanford 1995, Chapin 2002). Litterfall is also used as a mechanism to safe guard the health of a tree in drought or stress conditions (Chapin 2002). In addition to providing nutrient supply, litterfall provides ecosystem services such as stopping erosion and assists in soil formation and fertility (Spain 1984). For tropical forests, most of the carbon is located in the vegetation, with little stored in the soils (Kira and Shidei 1967, Odum 1971), and biogeochemical processes are fast corresponding with low amounts of surface litter (Schlesinger 1997). While litterfall is very important in tropical forest systems, knowledge is lacking on the exact process and requires longer periods of field sampling (Stocker et al. 1995), but sampling conditions are difficult in tropical settings due to rapid decay (Brown and Lugo 1982).

There are also many factors that contribute to high variation in annual litterfall (Lonsdale 1988): irregularity of leaf turnover of species, varying reproductive cycles, stress and drought conditions (Reich and Borchert 1984, Wright and Cornejo 1990), and disturbance (Shure and Phillips 1987). There is also a chance that there is low annual variability in litterfall between sites in similar geographic locations (Brasell et al. 1980, Tanner 1980, Proctor et al. 1983), and disturbance does not necessarily contribute to high variation (Herbohn and Congdon 1993).

Coarse woody debris (CWD) is a major component of the carbon cycle in tropical forests, and is often ignored in carbon cycle estimates. In undisturbed Amazonian forests CWD can account for 20% of aboveground stored carbon (Palace et al. 2008). Coarse woody debris has also been estimated to account for 5% to 40% of total carbon in tropical forests (Brown 1997). The current stock of aboveground CWD is balanced by two processes, either production of CWD or decay. The undisturbed Brazilian forests stock of CWD is found to have highly variable ranges between levels of 290 g C m^{-2} (Scott et al. 1992) to 480 g C m^{-2} (Rice et al. 2004). The CWD stock in a dry tropical forest of Jamaica had 600 g C m^{-2} (Tanner 1980). In addition to the stock of CWD being variable within and between locations, the rate of production of new CWD is also inconsistent. Production ranged from 670 g m^{-2} yr^{-1} in an undisturbed plot to 850 g m^{-2} yr^{-1} in a reduced impact logging plot, both in a close location in Brazil, while other studies have found a production of 480 g m^{-2} yr^{-1} in a wet Costa Rican forest (Clark et al. 2002) and 90 g m^{-2} yr^{-1} in an undisturbed dry forest in Mexico (Eaton and Laurence 2006). Production and CWD stock values are considered significant portions of tropical forest carbon stock, but the decay rate is important for the contribution of released carbon to the atmosphere.

Decay of CWD has been found to range between 0.12 – 0.47 yr^{-1} depending on size of CWD (Palace et al. 2008), and due to rapid decay in the tropics CWD can account for 15% of gross CO_2 flux from undisturbed sites. The contribution of carbon from CWD is an essential component in the carbon balance of tropical forests and should not be excluded from calculations, though that has been the trend.

4.1.2 Disturbance, forest productivity, and net carbon accumulation

Annual autotrophic live carbon accumulation (AALCA) can be highly affected by varying degrees of disturbance, with disturbance defined as a relatively discrete event that disrupts the structure of an ecosystem, community, or population and changes resource availability or the physical environment, and limits plant biomass by either partial or total destruction (Pickett and White 1985). This chapter studied the effects of large, infrequent disturbances (i.e. hurricanes) on components of AALCA: four production variables and litterfall and CWD. By way of damage, hurricanes are a type of land cover change.

Hurricanes are biophysical trigger events that have the ability to influence shifts in land-use practices (e.g. farming or grazing practices), due to altering ecosystem structure and functionality after a storm (Turner et al 1995, Kok and Winograd 2002, Lambin et al. 2003). Direct effects of land cover are the removal of litter, stems, branches, and uprooting of whole trees. Furthermore, land cover change (or damage) can indirectly alter two regulating properties that affect the timing of litterfall, which are water-holding capacity of the soil and plant water demand related to biomass (Borchert 1980). Modeling hurricane disturbances in the wet tropical forest of Puerto Rico showed that after repeated hurricanes, forest productivity was enhanced (Sanford et al. 1991), probably due to the enhancement of certain NPP components. O’brien et al. (1992) found that after simulating hurricane effects (ranging from no storms to a storm every year and 100% mortality), and using an earlier version of ZELIG, a range of forest types were possible for the Puerto Rican wet forest, Luquillo. These forest types for the Puerto Rican forest ranged from mature forests to stands never reaching maturity.

Future hurricane predictions, in response to climate change, are still unclear. There is a high discrepancy between whether human-induced climate change will increase the intensity of hurricanes (Emanuel 2005, 2006, IPCC 2007, Bender et al. 2010) or increase frequency of storms (Goldenberg et al. 2001), or even decrease the occurrence of storms (Knutson et al. 2008). Other reports link natural causes to increases in intensity and frequency of storms, such as decadal trends related to La Nina years (Donnelly and Woodruff 2007) and Atlantic Multidecadal Oscillation (Knight 2006), but these changes are not due to human-induced warming (Vecchi and Soden 2007a, 2007b). Due to the large uncertainty in changes to hurricanes, with respect to climate change, an array of hurricane scenarios that matched all predictions were modeled. Simulation modeling was an appropriate tool for predicting changes to individual trees and scaling up to the community and landscape level, from changes due to climate change.

The carbon balance of tropical forests is sensitive to frequency and intensity of storms, and disturbance events can have significant impacts on regional carbon fluxes (Hall et al. 1992, Walker et al. 1991, Scatena et al. 1996, Chambers et al. 2007, Lindroth et al. 2009). Scatena et al. (1996) reported that carbon and nutrients were altered from pre-hurricane levels up to five years after Hurricane Hugo hit Puerto Rico. Estimating that nutrient values in litterfall ranged from 62% - 98% of pre-hurricane levels, with annual litterfall reaching 83% of pre-hurricane levels. Aboveground nutrient pools ranged from 102% - 161% of pre-hurricane levels, because of increased debris and higher nutrients in the regeneration. Through a geographical-hydrological based ecosystem model Hall et al. (1992) discovered that without hurricanes present the Bisley Forest in Puerto Rico acted as a small carbon sink, 100 kg ha^{-1} yr^{-1}, supporting Lugo and Brown (1986) and Odum (1970) predictions that the Luquillo and Bisley Puerto Rican forests are increasing in biomass and are carbon sinks. But with hurricanes present in the model and using empirical data the forest acts as a carbon source to the ocean, 90 kg ha^{-1} yr^{-1}, by means of stream water discharge. Net change in forest carbon varied from positive to negative (sink vs. source) corresponding with changes in magnitude of biomass to necromass versus necromass to decomposition coefficients, but on average disturbances lead to the tropical forest acting as a carbon source to the ocean.

This chapter continues the use of a detailed individual based, forest gap model to determine the effect of large-scale disturbances on forest functionality in terms of carbon losses and gains, for a specific tropical region; Puerto Rico. Individual-based models are an optimal choice to address carbon cycle processes and land cover changes because they have the capability to assess both individual- and ecosystem-level changes due to the incorporation of tree/climate interactions and allowing for each tree to alter the local microenvironment (Whitmore 1982, Brokaw 1985, Silvertown and Smith 1988). In addition, individual-based forest gap models have been successful in simulating vegetation dynamics in response to global change and are appropriate for predicting terrestrial changes in response to climate change (Solomon 1986, Smith and Urban 1988, Smith and Tirpak 1989, Overpeck et al. 1990, Shugart et al. 1992), and have proven to be a good application for the questions addressed in this report. On top of the core mechanisms inherent in gap models, disturbance simulations were applied and forest productivity was monitored within ZELIG-TROP, which enhanced the ability to assess changes to forest functionality in response to a type of land cover change: hurricanes.

The modeling approach will estimate the effects of hurricane disturbances on litterfall, litter production, CWD, in addition to regeneration, basal-sprouting, and new biomass growth components of AALCA in the subtropical dry forest of Puerto Rico. The gap model ZELIG-TROP was used for forest and hurricane simulations. ZELIG-TROP has been validated for the subtropical dry forest (Guanica Forest) in Puerto Rico (chapter 1) and with the addition of a new hurricane routine (chapter 2) successful simulations of damage and recovery processes from multiple hurricane scenarios have occurred.

Another goal of this chapter was to continue to modify the existing gap model ZELIG-TROP so that it will be more realistic and accurately model ecological processes. Including accurate hurricane modeling based on historical data and return intervals has been implemented. Prior to this study, leaf traits were added, such as: deciduousness vs. evergreen, individual leaf senescence, new annual leaf growth on existing leaves, or leaf loss due to water stress or disturbance was not taken into account in the orginial ZELIG or other gap models. This study increased the realism of ZELIG-TROP by adding in monthly and annual leaf traits and calculating AALCA components (g C m^{-2} yr^{-1}) over time.

4.2 Methods

4.2.1 ZELIG-TROP Model and Hurricane Modeling

To achieve the goals in this chapter the methods used in chapter two and chapter three were built upon. Chapter two of this dissertation showed the development and parameterization of ZELIG-TROP, an individual based, gap model that was developed from the latest version of ZELIG (Larocque et al. 2006, 2011). ZELIG was originally developed by Urban (1990), based on the JABOWA, FORET, and FORENA gap models, but has also been later updated and applied to many forest applications (Urban et al. 1991, 1993, Cumming and Burton 1993, Pabst et al. 2008, Urban 2000). ZELIG-TROP is original because it is parameterized and successfully validated for the subtropical dry forest of Puerto Rico for the first time. ZELIG-TROP has been able to accurately reproduce forest structure features such as stem density, basal area, biomass, basal sprouting, height, and LAI comparable with field data. An individually based gap model was chosen to be used in this dissertation because it has the strength to track the progress and fate of each individual tree over its lifetime, and to simulate regeneration, growth, and death of individual trees for very long time periods.

Chapter three of this dissertation developed a hurricane simulation model within ZELIG-TROP which generated hurricane disturbances and corresponding damage to individual trees. Upon successful creation of the disturbance routine within ZELIG-TROP, estimating the response to disturbance at various spatial and time scales (individual, patch scale, and region level, as well as year, decade and century) was achieved. The disturbance routine randomly generated hurricanes based on historical records for the southwestern portion of Puerto Rico, using data from the Hurricane

Database HURDAT. If a hurricane occurred in given year then species-specific damage took place based on probabilities derived from past local measurements in Guanica Forest taken after a hurricane event (Van Bloem 2005). A proportion of randomly selected trees, for each species had the potential of receiving no apparent damage, foliage loss, branch damage, main stem snapping, being uprooted, or dying. The fate and growth of a tree was based on the new tree geometry after a hurricane, and its sustained level of damage or non-damage.

A variety of user-specified hurricane treatments were applied within ZELIG-TROP. The historical number of hurricane occurrences and magnitude were first simulated within the model, labeled as the control. Next, seven assortments of increasing hurricane disturbances in accordance with predictions from human-induced climate change took place. First the intensity of severe storms (wind levels over 178 km/hr) was increased by 25%, 50%, and 100% from the control levels. By choosing to increase the intensity of severe storms only, the occurrences of weaker storms (119-177 km/hr) were proportionally decreased to maintain the historical level of storms per century. Next, the frequency of all storms was increased by 25%, 50%, and 100% from the control levels. Lastly to evaluate the effects of reduced storm events, a decrease in both intensity of severe storms and frequency of all storms by 50% was modeled.

4.2.2 Annual Autotrophic Live Carbon Accumulation (AALCA) Model Additions

In this study annual autotrophic live carbon accumulation (AALCA) was defined as the total amount of carbon that has accumulated into the live autotrophic aboveground components of the forest, minus the loss due to death of the tree or tree parts. Therefore, in this study, a definition of NPP or NEP was not used, but instead production (AALCA) was defined as the sum of carbon into plant parts, or the annual addition of 1) new wood biomass through diameter increment, 2) leaf production and leaf growth, 3) biomass from new basal sprouts, and 4) new saplings during the annual time step minus the autotrophic loss from 1) CWD, and 2) litterfall (all units in g C m^{-2} yr^{-1}). This definition does not include belowground tissue. All earlier versions of ZELIG, prior to the work done here, did not estimate detailed forest carbon values. This research was unique in calculating annual carbon values for each of the tree components listed above for the subtropical dry forest system of Puerto Rico.

Annual autotrophic live carbon accumulation is similar to net primary productivity (NPP) in that it already accounts for maintenance and growth respiration, but with a slight variation: includes the negative components from death/necromass. AALCA is not to be confused with the definition of net ecosystem production (NEP), originally defined by Woodwell and Whittaker (1968). Woodwell and Whittaker (1968) defined NEP as the difference between the amount of organic carbon fixed by photosynthesis in an ecosystem or gross primary production (GPP) and the total ecosystem respiration R_e, with R_e being the sum of autotrophic and heterotrophic respiration. The heterotrophic component was excluded in the definition used here, using only the difference between gross accumulation of carbon by the autotrophic system and autotrophic carbon loss due to natural death and disturbance. The Puerto Rico system was strongly dominated by the autotrophic component, and it was highly difficult to model the heterotrophic contributions. Therefore my method of calculating carbon cycling is using the net rate of carbon production from the autotrophic system (AALCA), not full ecosystem.

While a more all-inclusive equation for carbon accumulation into the ecosystem (NEP or net ecosystem carbon balance, NECB) is appropriate for some ecological questions, it was chosen to only model carbon production from the live autotrophic system, which was more conducive to this study. Incorporating a detailed NEP or NECB would involve using a more detailed approach out of the scope of this study, such as including aboveground and belowground heterotrophic respiration, releases from all disturbance (i.e. burning, grazing), volatile organic compound emissions, and dissolved and particulate carbon losses from leaching (Chapin et al. 2002, Randerson et al. 2002, Bond-Lamberty 2004). Furthermore, there has been conflict between previous studies which have tried to define and simplify NEP. Some studies believe NEP should be defined as its all-encompassing definition: the net ecosystem carbon accumulation rate (Aber and Melillo 1991, Chapin et al. 2002, Randerson et al. 2002). Alternatively, due to the many organic and inorganic fluxes of carbon (such as the ones listed above), other studies have agreed on a similipfied version of NEP as GPP minus E_r, even if solely GPP minus E_r does not account for all carbon fluxes and is not the true net ecosystem carbon accumulation rate (Lovett et al. 2006).

Annual litterfall and new leaf production was tracked through new additions to ZELIG-TROP. Litterfall and leaf production were observed by calculating change in individual leaf area. Prior to my modifications new leaf area within ZELIG-TROP was not updated based on the previous year’s leaf area. Instead leaf area was set to zero at the start of every year and calculated allometrically based on DBH (equation 4.1). Leaf area is a very important component in gap models and is needed to simulate light extinction within the canopy and light competition, and available light influences diameter growth (Botkin et al. 1972).

$$L_a = c*D^2 \qquad \text{(Equation 4.1)}$$

where L_a is leaf area, c is a species specific parameter, and D is diameter at breast height. It was a goal to improve ZELIG-TROP's realism and accuracy; therefore this report updated how leaf area was developed each year. If leaf area is set to zero every year, then it will not take into account the foliage loss from a damaging disturbance event the year prior. Therefore, in the original model a highly damaged tree from a hurricane would still have a crown of full vigor, which is unrealistic. The original Botkin et al. (1972) allometric equation (equation 4.1) was used to calculate leaf area based off of the tree's DBH at each given year, but annual leaf area had the potential to be decreased based on deciduousness, water stress, and disturbance. A marker was set in place to "remember" the reduced leaf area (if reduction even occurred) and the next year's growth and production of new leaf area grew from the reduced value. Leaf production was tracked during all simulated years for each tree and was reported as one of the components of annual AALCA.

The first step to calculating litterfall was to assign if a tree was evergreen or deciduous as a model input. This modification helped the model take into account the utilization of light for each species, depending on evergreen or deciduousness, thus changing growth and regeneration. The input value was labeled as "leaf trait" and given a 2 for evergreen and 1 for deciduous. If a tree was deciduous then it lost half its leaves over the course of the year only during the prominent dry season (December – May), on a per month basis. Evergreen trees were vulnerable to losing a portion of leaves during months of extreme water stress (a low occurrence). When the monthly water level decreased below the wilting point, 30% leaf loss occurred on all trees for that month during the year, a value that is consistent with observed field reports in similar forests (Reich and Borchert 1984, Borchert 1994). These studies looked at litterfall in water stress conditions in the tropical dry forest of Costa Rica. While evergreen tropical tree species are more drought resistant and can maintain higher stem saturation, Borchert (1994) found that some evergreen species could lose enough leaves to stand bare during dry periods. It was typical for leaves on evergreen trees to be exchanged during the early or late periods of the dry season; typically months that could have higher occurrences of extreme water stress.

Leaf loss also occurred during hurricane disturbance events, depending on the severity of the storm, species of tree, and size of tree. For example leaf loss increased with increasing severity of storm congruent with empirical data; leaf loss per species varied depending on that species predisposition based on field measurements, and if a tree was greater than a maximum DBH, (set at 10.0cm) it lost 100% of foliage, otherwise it lost 50% of foliage. The range of litterfall in tropical dry forests is very large. Litterfall in tropical dry forests can range between 150 to 1260 g C m^{-2} yr^{-1} (Table 4.1) depending on environmental conditions (Martinez-Yrizar 1995). Based on multiple years of data collected, litterfall specifically in Guanica Forest can range from 127.75 to 907.18 g C m^{-2} yr^{-1} (Table 4.1), slightly lower due to drier conditions in Guanica (Murphy and Lugo 1986b, Cintron and Lugo 1990). Litterfall in Guanica also has notable deviations from year to year (Van Bloem 2005), as seen in Table 4.1.

Annual diameter increment D_a per tree, and eventually the total amount of carbon from the diameter increment of all individuals (g C m^{-2} yr^{-1}) was tracked in the GROWTH sub-routine within ZELIG-TROP. First the realized diameter increment, D_{inc} (cm) for each individual was tracked, as seen in Equation 4.2:

$$D_{inc} = G_p * G_f \qquad \text{(Equation 4.2)}$$

Where G_p is the optimal growth potential, G_f is the limiting growth factor that retards growth based on environmental constraints, and D_{inc} is the current year's new diameter growth used to calculate new growth biomass. The biomass for each individual's previous year (D_{old}) was calculated based on the tree's DBH (cm) before new diameter growth occurred. The annual, total diameter increment D_a, (g C m^{-2} yr^{-1}) shown in Equation 4.3, was the difference between the current basal size and the previous year's basal size (D_{old}), summed for all individuals, thus recording annual growth for each plot:

$$D_a = \sum((D_{old} + D_{inc}) - D_{old}) \qquad \text{(Equation 4.3)}$$

As a comparison, previous field experiments found that total diameter increment for Guanica Forest was 160 g C m^{-2} yr^{-1} (Lugo and Murphy 1986, Murphy and Lugo 1986, Clark et al. 2001).

The calculation of AALCA took into account the autotrophic carbon loss from litterfall (as explained above) and also from CWD. The assumption that carbon consists of half the tree's biomass (Schlesinger 1997) was used. Therefore using biomass estimations at time of death carbon loss from CWD was tracked for each of the three causes of death separately. A tree could die from natural death (age-related), from suppression or environmental stress (stress-related), or from hurricane disturbances.

In summary, the quantification of autotrophic live carbon accumulation (AALCA) takes into account plant growth, regeneration, and plant losses. The AALCA equation was the sum of: diameter increment, leaf production, new sprouts, new regeneration/saplings during only their first year of growth, minus litterfall and CWD. The live carbon accumulation was reported for each of the nine disturbance treatments, as well as the ratio of woodfall to litterfall, and litterfall to litter production comparisons.

4.3 Results

4.3.1 Litterfall and hurricanes in subtropical dry forests

Annual litterfall (g C m^{-2} yr^{-1}) in a subtropical dry forest was reported for a forest absent of hurricane disturbances, a control setting, and seven manipulated hurricane treatments (Figure 4.1). All results were tabulated once the model reached a stable, mature forest occurring at stand age 200, and from an average of 20 plots. Annual litterfall was lowest (191.17 g C m^{-2} yr^{-1}) during absence of hurricane disturbances in ZELIG-TROP compared to when historical disturbances are present (299.45 g C m^{-2} yr^{-1}). Introducing historical levels of hurricane disturbances (control treatment) into the system generated a 60% increase in litterfall over seasonal causes. Four out of seven hurricane treatments did have an effect on annual litterfall compared to the control. Values for all one-way analysis of variance results can be found in the appendix of this chapter (Appendix 4.1). The three treatments that did *not* have a significant effect on annual litterfall compared to the control where increasing the intensity of severe storms by 25%, 50%, and 100% ($F(_{79,\ 2.7}) = 1.50$, $p=0.221$, $r^2=0.06$). As seen in Table 4.1 there was a decrease in annual litterfall from the control with increasing intensity of storms by 50% and 100% (298.40 and 290.84 g C m^{-2} yr^{-1} respectively), but increasing the intensity of severe storms by 25% did cause a slight increase in litterfall from the control: 300.60 g C m^{-2} yr^{-1}.

Increasing the frequency of storms (increasing the occurrence of storms to hit the forest) had a stronger effect, leading to a greater reduction in annual litterfall. Increasing the frequency of storms by 25%, 50%, and 100% all significantly reduced litterfall from the control ($F_{(79, 2.7)} = 81.5$, $p<0.001$, $r^2=0.76$). An inverse relationship was seen with litterfall and increasing storm frequency. Average annual litterfall became less with each treatment of 25%, 50%, and 100% increase in storm frequency: 291.31, 272.14, and 255.63 g C m^{-2} yr^{-1} respectively. Compared to treatments which increased hurricane intensity or frequency, average litterfall remained highest under the control scenario (with the exception being a very small increase in litterfall seen when increasing storm intensity by 25% causing litterfall to reach 300.60 g C m^{-2} yr^{-1} or 0.4% increase). The only case where litterfall was increased a significant amount was under the treatment which *reduced* hurricane intensity and frequency by 50% ($F_{(39, 4.1)} = 10.22$, $p=0.003$, $r^2=0.21$). A reduction in hurricane disturbances from control levels caused litterfall to increase to 313.95 g C m^{-2} yr^{-1}.

Table 4.1 compares litterfall from three different field studies (dry weight g m^{-2} yr^{-1}) to results from this dissertation (g C m^{-2} yr^{-1}). All field studies were located in Guanica Forest and reported litterfall from 1974 to 2000. Litterfall in subtropical dry forests are highly variable and fluctuate depending on climate and disturbances (Table 4.1). Litterfall measurements have not been conducted every year between 1974 and

2000, but between this time period, litterfall has ranged from 127.75 to 500.00 g m^{-2} yr^{-1} with a standard deviation of 128.82 g m^{-2} yr^{-1}. In September 1998 Hurricane Georges hit Guanica Forest and caused a large increase in litterfall in 1999 to 500 g m^{-2} yr^{-1}. In September, four days before the hurricane hit, the litterfall was 238.7 g m^{-2} yr^{-1}, and in 2000 litterfall was back to 220.0 g m^{-2} yr^{-1} (Van Bloem 2005). The litterfall values reported by ZELIG-TROP were consistent and within the range found in field studies. The similarity between simulated and observed results helped to verify that ZELIG-TROP was functioning accurately. The average annual litterfall reported by ZELIG-TROP for the control simulation over 600 years was 299.45 g C m^{-2} yr^{-1}. ZELIG-TROP does not show the high level of fluctuation that was reported in field observations. The standard deviation between all hurricane treatments was only 18.31 g C m^{-2} yr^{-1} and the standard deviation between the 600 years in the control simulation was 19.47 g C m^{-2} yr^{1}.

Table 4.1. Observed and simulated average annual litterfall (g C m^{-2} yr^{-1}) for a subtropical dry forest in Puerto Rico, Guanica Forest.

Year	Average Litterfall (g/m^2/yr)	Source
1974	127.75	Cintron and Lugo 1990
1975	324.85	Cintron and Lugo 1990
1976	350.40	Cintron and Lugo 1990
1982	433.70	Lugo and Murphy 1986b
Sep. 1998	238.70	Van Bloem 2005
1999	500.00	Van Bloem 2005
2000	220.00	Van Bloem 2005
Hurricane Treatment	**Average Litterfall (g C/m^2/yr)**	**Source**
No Disturbance	191.17	This study
Control	299.45	This study
Intensity + 25%	300.60	This study
Intensity + 50%	298.40	This study
Intensity + 100%	290.84	This study
Frequency + 25%	291.31	This study
Frequency + 50%	272.10	This study
Frequency + 100%	255.63	This study
Decreased - 50%	313.90	This study

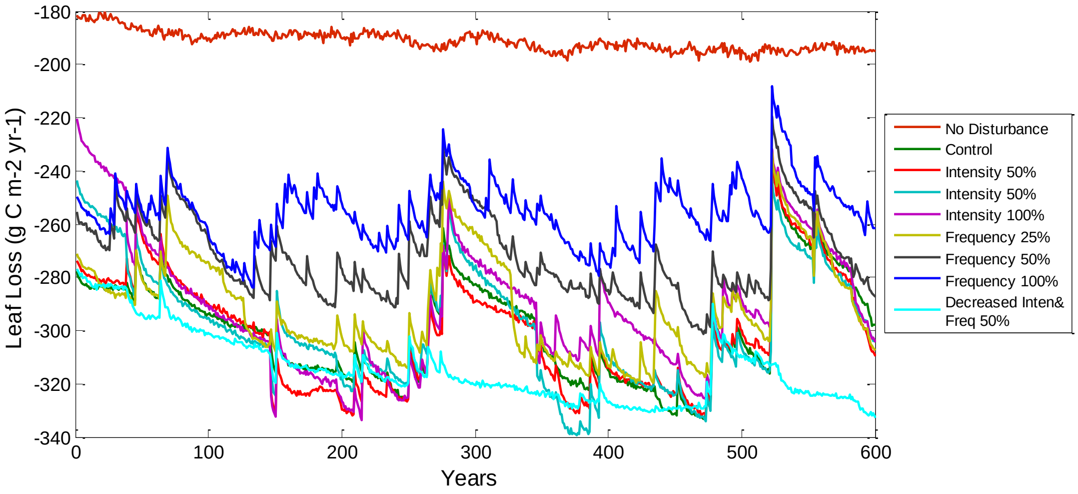


Figure 4.1. Simulated average annual litterfall (g C m^{-2} yr^{-1}) for a subtropical dry forest in Puerto Rico, under scenarios with no disturbance, historical disturbance regime (control), and seven simulated hurricane treatments.

4.3.2 Leaf production and hurricanes in subtropical dry forests

Leaf production in the subtropical dry forest did not mirror litterfall or mimick the same patterns, but instead showed different trends. During all treatments of increased frequency of hurricanes there was a stronger pronounced difference in leaf production over treatments which only increased intensity of storms (Figure 4.2), contrast to what was observed with litterfall. When the forest was in a hurricane disturbance free state, the annual leaf production was very high, averaging 438.56 g C m^{-2} yr^{-1}. During an increase in frequency of hurricanes by 25%, 50%, and 100% high leaf production generally remained high (353.71 to 406.01 g C m^{-2} yr^{-1}, Figure 4.2), but a reduction in leaf production by 7.7% to 21.4 from the disturbance free state. In contrast the average annual leaf production under the control hurricane treatment was 196.13 g C m^{-2} yr^{-1}. Therefore, increasing hurricane frequency leads to a very large significant increase in leaf production over the control F($_{79,\ 2.7}$) = 2007.18, p<0.001, r^2=0.99. The increase in storm frequency accounted for 98.8% of the variation in leaf production for a Puerto Rico forest, due to the variation between treatments.

The annual leaf production during treatments of increased intensity of storms remained very consistent with the control (Figure 4.2). The percent difference only altered by 0.56% and -1.18% around the control, showing only a slight shift in leaf production. An increase in intensity of severe storms by 25%, 50%, and 100% did not lead to a significant change in annual leaf production from the control, (F($_{79,\ 2.7}$) = 0.851, p=0.470, r^2=0.03), and there was small variation between treatments. Increasing the intensity of severe storms by 25%, 50% and 100% produced average leaf production values of 197.22, 197.24, and 193.83 g C m^{-2} yr^{-1} respectively.

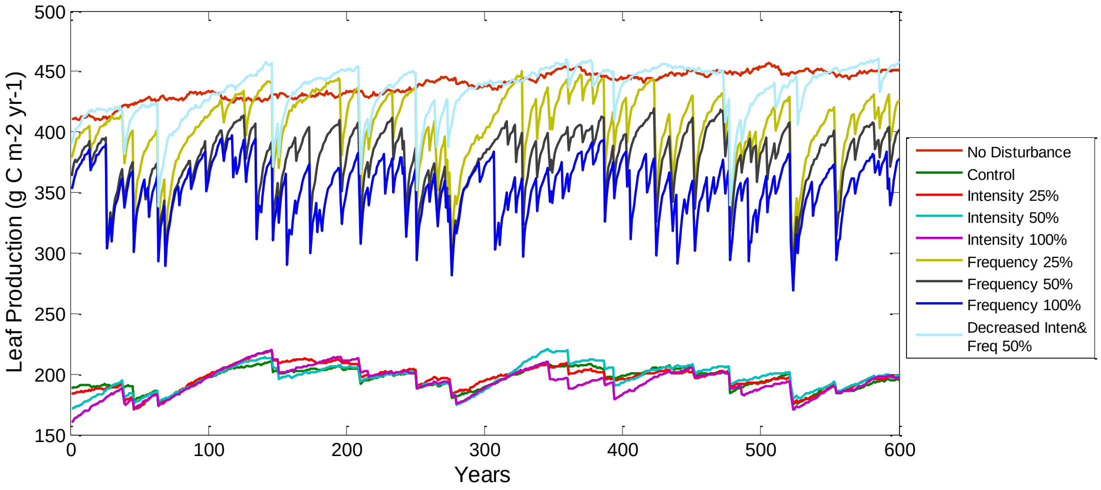


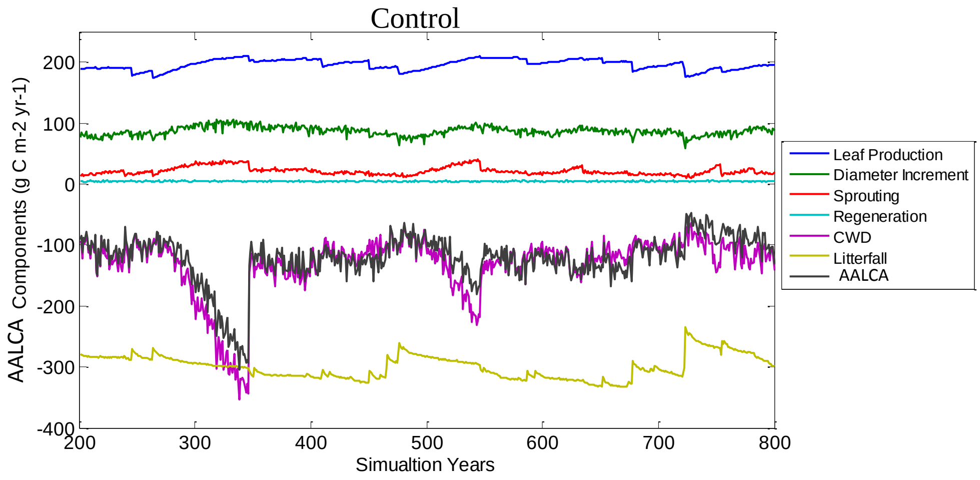
Figure 4.2. Simulated average annual leaf production (g C m^{-2} yr^{-1}) for a subtropical dry forest in Puerto Rico, under scenarios with no disturbance, historical disturbance regime (control), and seven simulated hurricane treatments.

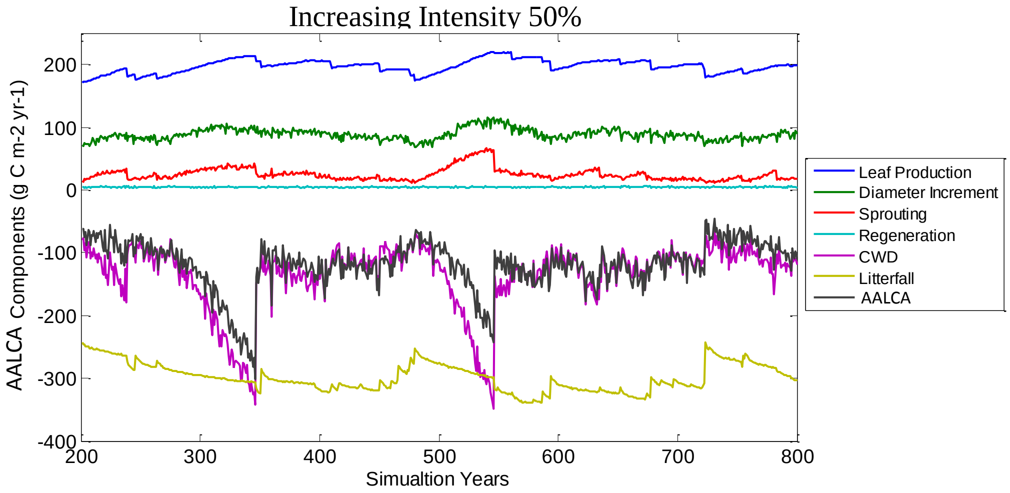
4.3.3 Effects of disturbance on annual autotrophic live carbon accumulation (AALCA)

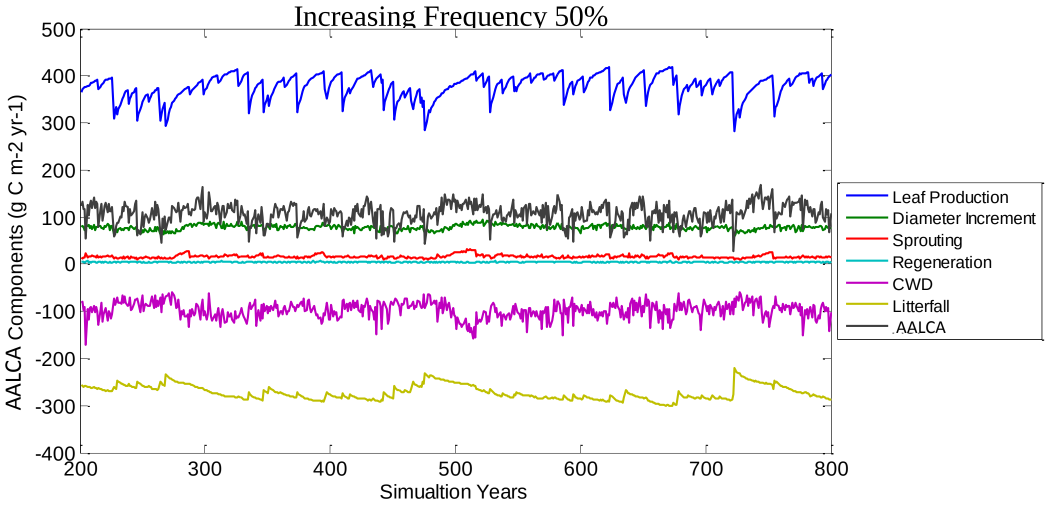
Figure 4.3 illustrates four hurricane treatments and the effect of these large disturbances on AALCA, as well as each of the six individual components used to compute AALCA. The first treatment (Figure 4.3a) was the control scenario and the remaining three treatments alter hurricane intensity or frequency in the intermediate range: 50% increase or decrease in storms. The major dissimilarity I observed between the treatments was that AALCA was negative, therefore the live autotrophic aboveground components were losing carbon, during the control settings as well as when intensity of storms were increasing. Conversely, AALCA was positive and the forest was gaining carbon during treatments which increased the frequency of storms and also decreased the intensity and frequency of storms (Table 4.2, Figure 4.3). In all four hurricane treatments the AALCA component which produced the largest gain in carbon sequestration is annual leaf production, followed by diameter increment, basal-sprouting of new stems, and lastly regeneration of new trees. The AALCA component which produced the largest lost in carbon emissions is leaf litterfall followed by CWD (Figure 4.3 and 4.4).

Two hurricane scenarios: the control and increased hurricane intensity (Figure 4.3a and 4.3b) had individual AALCA components and total AALCA patterns that were very similar to each other. The only variation between the two hurricane scenarios was that during increased storm intensity there was an increase in basal-sprouting by 15.5%, and a slight increase in CWD by 3.9%. Further similarities between the control and treatment with increased intensity of storms were illustrated in Figure 4.4. During the increased storm intensity treatment a slight increase in all six AALCA components over the control was observed, averaged over 600 years of simulations, except for a very small decrease in litterfall (Figure 4.4). The average annual AALCA also increased from -122.1 to -119.6 g C m^{-2} yr^{-1}, only a 2.0% increase, on average transferring 2% less live carbon over 600 years (Table 4.2).

Increased hurricane frequency (Figure 4.3c) and decreased hurricane intensity and frequency (Figure 4.3d) displayed significantly different patterns from the control (Figure 4.3a). There was a significantly larger increase in leaf production, a reduction in CWD, and an increase in overall AALCA. During the increased hurricane frequency treatment, average leaf production exceded the control by 63.4% and 75.5% during the decreased hurricane treatment (Figure 4.4). In these two scenarios the amount of carbon that was lost due to CWD was reduced by 30.0% and 5.0% respectively, from the control. The increase in carbon gain from leaf production and reduction in carbon loss from CWD caused the overall AALCA to increase. Increasing the frequency of storms and decreasing the intensity and frequency of storms were the only treatments that allow the AALCA to remain positive (Figure 4.3c and 4.3d). After reviewing the remaining, individual AALCA components (Figure 4.4) during the treatments of increased frequency of storms and also decreased storms, the diameter increment and basal-sprouting decreased from the control levels, and regeneration slightly increased. The average annual diameter increment dropped to 78.1 and 84.7 g C m^{-2} yr^{-1} (control: 86.7 g C m^{-2} yr^{-1}), and average basal-sprouting dropped to 16.4 and 20.2 7 g C m^{-2} yr^{-1} (control: 21.4 g C m^{-2} yr^{-1}). In general the diameter increment, basal-sprouting, and also regeneration were higher in the treatment which decreased hurricane events compared to the treatment which increased the frequency of storms. However, on average AALCA was the highest during the treatment that increased hurricane frequency (107.9 g C m^{-2} yr^{-1}), as compared to AALCA from the treatment that reduced hurricanes (104.9 g C m^{-2} yr^{-1}).


Control


Increasing Intensity 50%


Increasing Frequency 50%

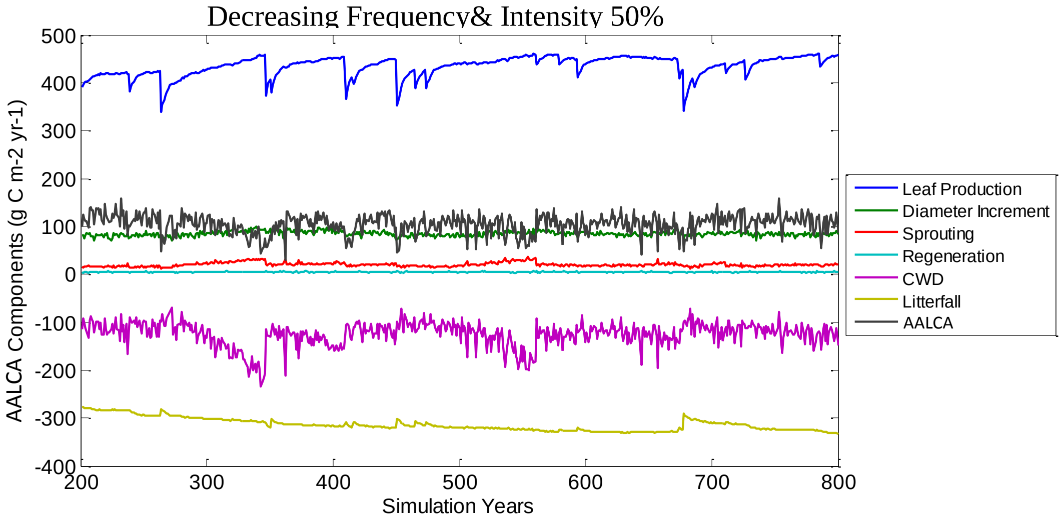


Figure 4.3. Simulated annual autotrophic live carbon accumulation (AALCA), and six components of AALCA for four hurricane treatments, over 600 years. AALCA components are aboveground leaf production, diameter increment, basal-sprouting, regeneration for new saplings, biomass loss to coarse-woody debris, and leaf loss (all in g C m^{-2} yr^{-1}). a) Control treatment, b) Increased hurricane intensity by 50%, c) Increased hurricane frequency by 50%, d) decreased hurricane intensity and frequency by 50%.

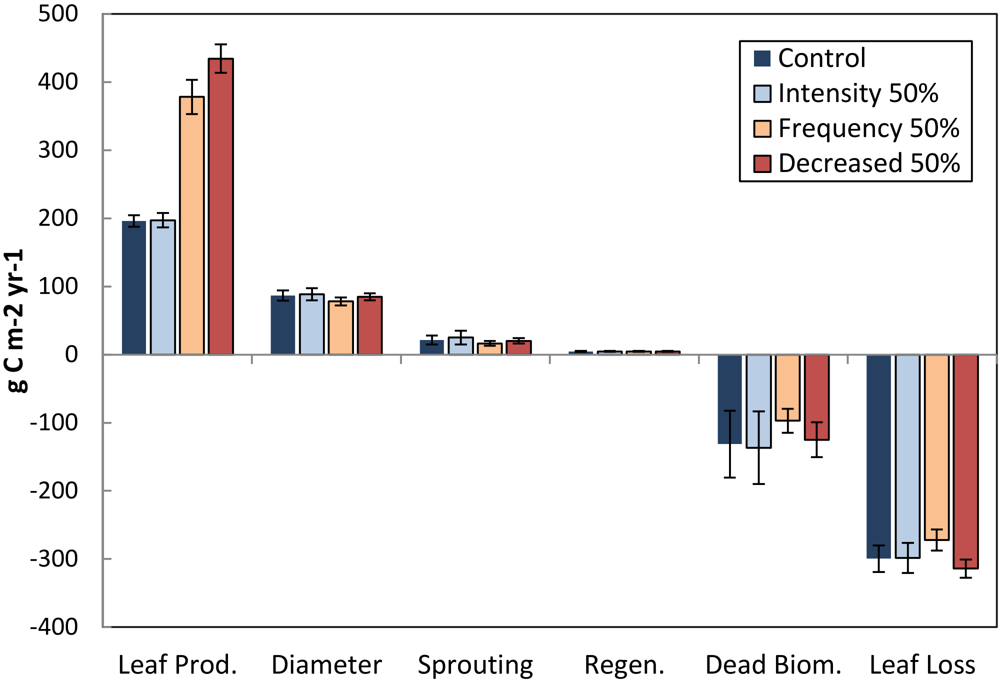


Figure 4.4. Average values that make up the annual autotrophic live carbon accumulation (AALCA) from 600 years of simulation: leaf production, diameter increment, basal-sprouting, regeneration for new saplings, coarse-woody debris, and leaf loss (all in g C m^{-2} yr^{-1}).

Table 4.2. Observed and simulated Net Primary Productivity (NPP), and simulated annual autotrophic live carbon accumulation (AALCA) for a subtropical dry forest in Puerto Rico, Guanica Forest (all units in g C m^{-2} y^{-1}).

Year or Treatment	NPP (g C m^{-2} yr^{-1})	Source	Location
1998	661	Cao and Woodard 1998	Tropical Savanna
1998	759	Cao and Woodard 1998	Tropical Deciduous
2001	450	Clark et al. 2001	Guanica Forest, PR
Control	304.2	This Study	Guanica Forest, PR
Intensity + 50%	310.8	This Study	Guanica Forest, PR
Frequency + 50%	472.7	This Study	Guanica Forest, PR
Decreased – 50%	539.2	This Study	Guanica Forest, PR
Treatment	**AALCA (g C m^{-2} yr^{-1})**	**Source**	**Location**
Control	-122.1	This Study	Guanica Forest, PR
Intensity + 50%	-119.6	This Study	Guanica Forest, PR
Frequency + 50%	107.9	This Study	Guanica Forest, PR
Decreased – 50%	104.9	This Study	Guanica Forest, PR

4.3.4 Relationship between CWD and litterfall

Patterns in coarse woody debris changed notably with each of the four hurricane scenarios: the control treatment and the three treatments which altered hurricane intensity and frequency. Average annual coarse woody debris was low during the treatment which increased storm frequency (97.2 g C m^{-2} yr^{-1}) and higher during the treatment which increased storm intensity (136.6 g C m^{-2} yr^{-1}) (Table 4.3, Figure 4.5). Average annual coarse woody debris made up 11.5% and 18.2% of total AALCA for the treatment which increased storm frequency and the treatment which increased storm intensity respectively.

There were occurrences when carbon contributions from annual CWD were greater than carbon from annual litterfall, as seen in Figure 4.5. These occasions occurred in two out of the four hurricane treatments: the control treatment and when hurricane intensity was increased, but occurrences were rare (18 and 16 years out of the 600 years of simulation). Disregarding these few exceptions, during the majority of simulations years, litterfall was greater than CWD, and was the largest component of carbon loss in all four hurricane treatments. During treatments of increased storm frequency, and decreased intensity and frequency of storms, CWD was never greater than litterfall (Figure 4.5), as seen by zero occurences. During all four hurricane treatments the average carbon component from CWD was always less than half of litterfall (Figure 4.5), calculated by averaging CWD to litterfall ratio for 600 years. The CWD to litterfall ratio was 0.44, 0.46, 0.36, and 0.40 for the control, increasing intensity, increasing frequency, and decreasing intensity and frequency of storms respectively.

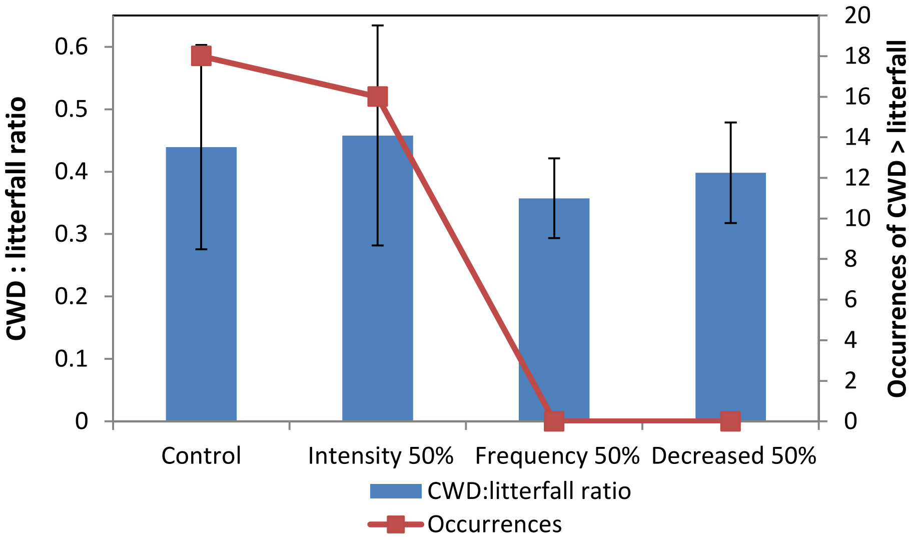


Figure 4.5. Comparison of CWD:litterfall ratio for control and three hurricane disturbance treatments, and number of occurrences when CWD is greater than litterfall over 600 years. On average CWD is always less than half of litterfall.

Table 4.3. Simulated average coarse woody debris (g C m^{-2} yr^{-1}) and percent of total annual autotrophic live carbon accumulation (AALCA) from 600 years of simulation of the control hurricane treatment, and three adjusted hurricane scenarios.

Treatment	CWD (g C m^{-2} yr^{-1})	CWD % of Total AALCA	Location
Control	-131.4	17.8	Guanica Forest, PR
Intensity + 50%	-136.6	18.2	Guanica Forest, PR
Frequency + 50%	-97.2	11.5	Guanica Forest, PR
Decreased – 50%	-125.0	12.7	Guanica Forest, PR

4.4 Discussion

4.4.1 Importance of litterfall, leaf production, and woodfall measurements

This study was able to generate a dynamic process to track leaf area in the crown of each individual tree from year to year, produce annual leaf litterfall from deciduousness, stress, and/or disturbance, and then calculate the new leaf production within a gap model interface. The modifications within ZELIG-TROP to include the process of developing litterfall and leaf production were a new addition to the ZELIG gap model. In the past gap models have taken into account deciduousness into the process of developing total leaf area on each individual tree, but that was the only development.

As previously noted in the introduction there are multiple factors that contribute to high variation in annual litterfall, and to capture this irregularity from season to season requires repeated field measurements. Simulation modeling can both control and limit the variability seen in the field, but also reflect the variation if desired by the user. This study had the ability to account for irregularity of leaf turnover of different species by assigning which species were evergreen vs. deciduous. ZELIG-TROP and gap models also have the ability to control for stress, drought, and disturbance conditions reducing another factor that contributes to litterfall and leaf production variability.

Both litterfall and leaf production were crucial elements of AALCA, making up a large constituent of annual autotrophic carbon. Litterfall was a large component in three out of the four hurricane treatment: the control, an increase in hurricane intensity, and also decrease in hurricane intensity and frequency. During these treatments litterfall accounted for 40%, 40%, and 32% of total AALCA. The similiar conclusion was observed for leaf production. When average annual leaf production was low (during control and increasing intensity of storms treatments) it accounted for 26-27% of total AALCA. When leaf production was high (during treatments which increased the frequency of storms and also decreased storm intensity and frequency) it accounted for 44-45% of total AALCA.

Measuring components of AALCA can be a challenge, especially in tropical terrestrial systems. A major component that is frequently left out or overlooked is the carbon component from dead woodfall. The carbon transfer from large trees once they die can lead to negative AALCA values (a measure of *live* autotrophic accumulation). The carbon contribution from respiring and decomposing woodfall due to death is a hard variable to measure in field studies, but the transfer of live carbon to dead can be monitored in individual based simulation models which track the fate of each tree, and size of biomass is known at the time of death. The methods used here took into account trees dying from stress, age-related death, and disturbance induced. The transfer of carbon (g C m^{-2} yr^{-1}) was only accounted for during the year of death and not spread out over following years, since decomposition rates are highly variable. During the control treatment, or current hurricane disturbance, woodfall accouted for 18% of total AALCA, a significant amount that should be included in more carbon measurements.

Coarse woody debris was high during the control treatment and highest when hurricane intensity was increased, but alternatively CWD was low during the increased hurricane frequency treatment and when hurricane intensity and frequency was decreased. During the hurricane treatment which increased hurricane occurrences (frequency) CWD does not exceed 200 g C m^{-2} yr^{-1}, most likely due to the absence of large sized trees. With increased occurrences of storms repeatedly hitting the dry forest, the size structure of the forest (e.g. total basal area, height) typically remained low, therefore keeping CWD carbon levels low and resulting in a higher AALCA. While CWD contributions were higher during hurricane years, internal gap level disturbances and death of tree parts during non-hurricane years could contribute similiar levels of CWD, indicating the importance to study these forest functioning parameters for carbon flux purposes.

4.4.2 Modeling annual carbon production with disturbances

This report has been successful at separating the components of autotrophic annual carbon production into six measureable values, thus estimating carbon changes within tropical forests at a detailed level. The six components of AALCA, in units of carbon per year, are leaf production, diameter increment in all trees, basal-sprouting, regeneration during the first year of growth, coarse woody debris, and litterfall. Additionally this report predicted the carbon flux in each of these components for different hurricane scenarios with varying levels of storm intensity and frequency.

A main conclusion found in this report was that different hurricane disturbances produce substantial differences in annual litterfall, leaf production, and overall AALCA, followed by milder differences in mortality, basal-sprouting, and regeneration. The largest difference was observed with model simulations that increased the *frequency* of all storms categories by 50%; this treatment showed greater values in almost all categories, as compared to the control. Increasing the frequency of hurricanes produced the highest values in AALCA, greatest decrease in litterfall and CWD, and the second highest increase in new leaf production. When the frequency of hurricanes was increased, the amount of carbon loss due to an increase in disturbances did occur, but overall the carbon sequestration was higher, causing a net gain.

What was the significance of modeling multiple disturbance scenarios? Two drastic results were found with regards to AALCA. In the current, historical hurricane disturbance scenario the average AALCA was negative (-122.1 g C m^{-2} yr^{-1}) and the dry tropical forest of Puerto Rico was losing autotrophic live carbon. This carbon loss was attributed to high woodfall, litterfall, and low leaf production. These conditions remained consistent when intensity of severe disturbances was increased by 50%. In this scenario there was also a negative AALCA (-119.6 g C m^{-2} yr^{-1}). The 2% reduction in carbon transfer to dead components was due to a very small increase in diameter increment and basal-sprouting off existing trees after gaps were opened following a large scale disturbance. There was a large shift in forest dynamics when either hurricane frequencies were increased by 50% and also when hurricanes decreased in both intensity and frequency by 50% from the historical scenario. In both these scenarios there was a positive AALCA, and net gain for carbon. This was estimated to be attributed to less CWD (dying wood) compared to the control as well as a capacity for large increases in leaf production, sequestering up to 63% and 76% more carbon from the control.

Clark et al. (2001) estimated that diameter growth or increment accounted for 10-30% of total NPP for the dry forest in Puerto Rico. This report found diameter increment to account for 16-29% of aboveground NPP depending on hurricane treatment, and accounted for 9-12% of aboveground AALCA. While NPP was not reported in this study, NPP makes up a portion of total AALCA (NPP plus autotrophic death = AALCA).

Previous studies have found that over the past decades tropical forests have growth rates, stem turnover rates, and basal area that are increasing (Lewis et al. 2004) and act as carbon sinks (Phillips et al. 1998, Chambers et al. 2001). One study has shown that after an increase in CO_2 and productivity, mature tropical forests can continue to accumulate carbon for 100 years (Chambers et al. 2001). Other studies show that evidence for tropical forests to act as carbon sinks is undetermined, and this is probably not likely (Clark 2002). The units reported in Lewis et al. (2004) are in absolute values of individuals that are loss and gain (stems ha^{-1} yr^{-1}), and change in area from basal area (m^2 ha^{-1} yr^{-1}), but units in carbon over spatial and temporal scales would show different results. Using rates of change in stem density and mortality to determine if tropical forests are acting as a carbon sink or source should be used with caution. Results should be reported in terms of carbon for each variable, due to the importance of necromass. For example ZELIG-TROP showed evidence that carbon from a large, dead, decomposing stem might be higher than new stem recruits and basal area growth; therefore the gain terms do not exceed the loss terms, reducing the capability for a carbon sink.

4.4.3 Previous methods of determining AALCA components

As noted in the methods section annual autotrophic carbon accumulation is comprised of variables found in both NPP and subsequently NEP equations, but differs because woodfall is not routinely calculated in either. Estimating the components that comprise autotrophic carbon accumulation used here has proven to be difficult in field studies, and in the past, studies have used a large amount of assumptions for estimating components. Older, but still used methods to compute total NPP consist of the following examples.

The Bray and Gorham (1964) method uses the assumption that annual aboveground NPP in tropical forests is three times annual leaf litter, and annual total NPP is 3.3 time annual leaf litterfall, two assumptions that tend to overestimate values of NPP (Clark et al. 2001). The Bray and Gorham (1964) method was also established after reviewing only two sites, in secondary tropical forests. The individual components that make up NEP for tropical forests have only been studied in a few direct field measurements, and the majority has come through estimations. Clark et al. (2001) had reliable data of litterfall and aboveground biomass increment for 13 tropical sites and used a logarithmic relationship between these two variables, with an r^2 of 0.69, to estimate litterfall and biomass increment for an additional 26 sites. There have been previous assumptions that one component of total NEP, coarse root increment, is proportional to aboveground diameter increment. Although, Cains et al. (1997) and Jackson et al. (1997) found a different result that root-to-shoot ratio could range from 0.14 to 0.34, not a 1:1 relationship. In recent years eddy covariance techniques have also been employed to measure NEP. Eddy covariance measurements can estimate the CO_2 exchange above an ecosystem by measuring the vertical net flux of CO_2. While eddy covariance systems are highly sensitive to fluxes in CO_2 there can be inaccuracy, and support for these techniques are costly and difficult.

In Clark et al.’s (2001) review of NPP and NEP components from 39 tropical forest sites, five sites had measurements for leaf herbivory, and no sites had direct measurements for BVOC, organic leachates, losses to non-leaf aboveground consumers, or adequate data for belowground components. A few sites had either coarse root or fine root biomass measurements, but there was not adequate information on coarse or fine root increment, mortality, or loss to heterotrophs making the carbon flux in belowground components near to impossible to estimate. Discrepancies between field measurements in humid tropical sites can exist and lead to inaccurate results (Clark 2002). Phillip et al. (1998) found that old-growth tropical forests are carbon sinks, but Clark (2002) re-analyzed the same data and found that the tropical forests are not carbon sinks due to sampling error and discrepancies.

4.4.4 Advantages to annual autotrophic live carbon accumulation equation

Determining reliable estimates of carbon accumulation in the tropics has been a challenging endeavor mainly based on insufficient or non-existent field data for many components. This is typically due to limited resources, time, and difficult field sampling logistics. Unreliable estimates also arise due to sampling error, as well as strong variation in carbon accumulation across tropical locations, and variation in future controls which determine carbon accumulation values. These examples are a main reason why this report utilized a simplistic method to calculate AALCA. If capabilities exist to calculate all factors needed to estimate a detailed NEP, then those methods should be employed. If the opportunities are not available, the simplistic method used here to calculate AALCA is sufficient, but it is not a substitute for NEP. Apart from belowground processes, AALCA is useful because it uses components which account for the highest levels of aboveground ecosystem productivity and carbon levels, and alleviates hard to obtain variables.

Maintaining annual field data measurements is tedious and logistically hard for certain processes that contribute to ecosystem level production. Modeling AALCA only requires a small amount of input data for initialization and parameterization, and then AALCA can be calculated for multiple years, eliminating the need for repeated field measurements and resources. A main reason AALCA was used is due to the spatial variation between sites, climates, and forest types. As demonstrated in this study, through simulation modeling the question of how carbon accumulation changes over spatial variations can be answered, as long as initial parameterization is known for each site. Temporal variation, from occurrences such as climate change, changes in disturbance, and changes in land cover can cause AALCA to shift. This study is able to evaluate, through individual based simulation modeling how AALCA shifts with fluctuations in disturbances over long time periods.

This report adds to the needed research required to estimate autotrophic carbon accumulation rates in tropical forests of the world, and in particular tropical forests that are routinely hit by disturbances. Carbon fluxes are highly uncertain in tropical forests which are undergoing changes in structure due to disturbance or deforestation (DeFries et al. 2002, Houghton 2005). To create a clear picture of the modern carbon budget, large-scale modeling simulations and techniques like the ones used here should be used. This report aided in reducing the uncertainty in the amount of carbon that is released from tropical forests to the atmosphere during disturbance events, one of the largest concerns related to the carbon budget (Schimel et al. 2001).

There has been a need to research and study as many components of carbon accumulation in terrestrial systems as possible (Lovett et al. 2006), especially for tropical forests (Clark et al. 2001). Clearly, and accurately quantifying carbon accumulation which takes into account carbon loss from death will assist important entities aimed at reducing carbon emissions such as REDD+ (Reducing Emissions from Deforestation and Degradation). Reducing carbon emissions from deforestation and understanding carbon emissions from natural disturbances is very important to tackle climate change issues (Gibbs et al. 2007). This report aids in creating a clearer picture of the modern carbon budget and reduces the uncertainly of carbon flux in terrestrial ecosystems, especially in the tropics.

4.4.5 Management Purposes and Final Conclusions:

In order to track the changes in carbon flux, an initial quantity of carbon or biomass values needs to be known. The individual based modeling tool used here, ZELIG-TROP is able to estimate the current quantities of carbon from the aboveground forest biomass and additions used to quantify components of AALCA. Forests that are used for the main purpose of maximum carbon storage can potentially run higher risks in carbon offset reversal. Techniques can be employed to limit the risk of damage from disturbance, such as changing the structure of forests, age, or composition. Manual or biotically driven thinning (Yoda et al. 1963, Cameron 2002, Mason 2002) as well as increase in frequency of disturbances (Achim et al. 2005) can limit the risk of large scale damage and carbon reversal in forests. It was found that increasing the frequency of disturbance, essentially thinning the forest through increased hurricane occurrences leads to an increase in carbon storage and limits the risk of carbon reversal. Increase in carbon storage is observed through increases in leaf production, decrease in CWD, and slight decreases in litterfall.

There is strong variation in AALCA across tropical forest locations around the globe due to variability from wet to seasonally dry forests and differences in temperature and forest age. Due to difficulties in measuring long-term AALCA in field experiments, this report provided a way for simplistically finding AALCA, using a modeling approach. This study was capable of reporting long term carbon values and detailed functionality parameters, and the methods used here could be employed in additional tropical locations and adds to the knowledge of fluxes in carbon under climate change scenarios.

4.5 Literature Cited

Aber JD and Melillo JM. 1991. Terrestrial ecosystems. Orlando (FL): Saunders College Publishing.

Achim, A., Ruel, J.-C., Gardner, B.A., Laflamme, G., Meunier, S., 2005. Modeling the vulnerability of balsam fir forests to wind damage. Forest Ecology and Management 204, 35–50.

Baker, T. R., O.L. Phillips, Y. Malhi, S. Almeida, L. Arroyo, A. Di Fiore, T. Erwin, N. Higuchi, T. Killeen, S.G. Laurance, W.F. Laurance, S.L. Lewis, A. Monteagudo, D.A. Neill, P. Nunez Vargas, N.C.A. Pitman, J. Natalino M. Silva, R. Vasquez Martinez. 2004. Increasing biomass in Amazonian forest plots. *Phil. Trans. R. Soc.* Lond. B 359: 353–365.

Bender, M.A., T.R. Knutson, R.E. Tuleya, J.J. Sirutis, G.A. Vecchi, S.T. Garner, I.A. Held. 2010. Modeled impact of anthropogenic warming on the frequency of intense Atlantic hurricanes. Science. 327: 454.

Boisvenue, C. and S.W. Running. 2006. Impacts of climate change on natural forest productivity – evidence since the middle of the 20th century. Glob. Chan. Biol. 12: 862-882.

Borchert, R. 1980. Phenology and ecophysiology of tropical trees: *Erythrina poeppigiana* O.F. Cook. Ecology. 61: 1065-1074.

Borchert, R. 1994. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. Ecology. 75: 1437– 1449.

Botkin, D. B., J. F. Janak, and J. R. Wallis. 1972. Some Ecological Consequences of a Computer Model of Forest Growth. J. of Ecology. 60, 849-872.

Bond-Lamberty, B., C. Wang, S.T. Gower. 2004. Net primary production and net ecosystem production of a boreal black spruce wildfire chronosequence. Glob. Chan. Biol. 10: 473-487.

Brasell, H. M., G. L. Unwin, and G. C. Stocker. 1980. The quantity, temporal distribution and mineral element content of litterfall in two forest types at two sites in tropical Australia. J. of Ecology 68: 123-139.

Bray, J. R., and E. Gorham. 1964. Litter production in forests of the world. Advances in Ecological Research 2:101–157.

Brokaw, N. V. L. 1985. Treefalls, regrowth, and community structure in tropical forests. In The Ecology of Natural Disturbances and Patch Dynamics. Eds. S. T. A. Pickett and P. S. White. New York: Academic, pp. 101-108.

Brown, S. and A. E. Lugo. 1982. The storage and production of organic matter in tropical forests and their roles in the global carbon cycle. Biotropica 14: 161-187.

Brown, S. 1997. Estimating biomass and biomass change in tropical forests. A primer. FAO Forestry Paper 134. Food and Agriculture Organization of the United Nations, Rome.

Bryan, J., P. Shearman, J. Ash, J.B. Kirkpatrick. 2010. Estimating rainforest biomass stocks and carbon loss from deforestation and degradation in Papua New Guinea 1972-2002: best estimates, uncertainties, and research needs. J. of Environ. Manage. 91: 995-1001.

Cairns, M. A., S. Brown, E. H. Helmer, and G. A. Baumgardner. 1997. Root biomass allocation in the world’s upland forests. Oecologia 111:1–11.

Cameron, A.D., 2002. Importance of early selective thinning in the development of long-term stand stability and improved log quality: a review. Forestry 75, 25–35.

Canadell, J. G. and M. R. Raupach. 2008. Managing forests for climate change mitigation. Science. 320, 1456-1457.

Cao. M. and F.I. Woodard. 1998. Net primary and ecosystem production and carbon stocks of terrestrial ecosystems and their responses to climate change. Global Change Biology. 4: 185-198.

Chambers, J. Q., Higuchi, N., Tribuzy, E. S. & Trumbore, S. E. 2001. Carbon sink for a century. Nature. 410, 429.

Chambers, J.Q., Fisher, J.I., Zeng, H., Chapman, E.L., Baker, D.B., Hurtt, G.C., 2007. Hurricane Katrina’s carbon footprint on U.S. Gulf Coast forests. Science 318, 1107.

Chapin FS. III, Matson PA, Mooney HA. 2002. Principles of terrestrial ecosystem ecology New York: Springer.

Cintron, B.B. and A.E. Lugo. 1990. Litterfall in a subtropical dry forest: Guanica, Puerto Rico. Acta. Cientifica. 4: 37-49.

Clark, D.A, S. Brown, D.W. Kicklighter, J.Q. Chambers, J.R. Thomlinson, J. Ni, E.A. Holland. 2001. Net primary production in tropical forests: an evaluation and synthesis of existing field data. Ecol. Applications. 11: 371-384.

Clark, D. A. 2002 Are tropical forests an important global carbon sink?: revisiting the evidence from long-term inventory plots. Ecol. Applic. 12, 3–7.

Clark, D. B., Clark, D. A., Brown, S., Oberbauer, S. F. & Veldkamp, E. 2002 Stocks and flows of coarse woody debris across a tropical rain forest nutrient and topography gradient. Forest Ecol. Mngmt 164, 237–248.

Clark, D. A. 2007. Detecting tropical forests’ responses to global climatic an atmospheric change: current challenges and a way forward. Biotropica 39:4–19.

Cooper, C. F. 1983. Carbon storage in managed forests. Can. J. of For. Research 13: 155-166.

Cumming, S. G. and Burton, P. J. 1993. A Programmable Shell and Graphics System for Forest Stand Simulation, Environ. Software. 8, 219-230.

DeFries, R. S., R. A. Houghton, M. C. Hansen, C. B. Field, D. Skole, J. Townshend. 2002. Carbon emissions from tropical deforestation and regrowth based on satellite observations for the 1980s and 1990s. PNAS. 99, 14256-14261.

Donnelly, J.P., and J.D. Woodruff. 2007. Intense hurricane activity over the past 5,000 years controlled by El Niño and the West African monsoon. Nature, 447, 465-468.

Eaton, J. M., and D. Lawrence. 2006. Woody debris stocks and fluxes during succession in a dry tropical forest. For. Ecol. and Manag. 232:46–55.

Ebeling, J. and M. Yasue. 2008. Generating carbon finance through avoided deforestation and its potential to create climatic, conservation and human development benefits. Phil. Trans. R. Soc. B 363: 1917-1924.

Emanuel, K. 2005. Increasing destructiveness of tropical cyclones over the past 30 years. Nature 436:686-688.

Emanuel, K. 2006. Hurricanes: Tempests in a greenhouse. Physics Today 59:74-75.

Emanuel, K. 2007. Environmental factors affecting tropical cyclone power dissipation. J. Climate. 20: 5497-5509.

Fearnside, P. M., and W. E Laurance. 2003. Comment on "Determination of deforestation rates of the world's humid tropical forests." Science. 299:1015a.

Fearnside, P.M. and W.F. Laurance. 2004. Tropical deforestation and greenhouse gas emissions. Ecol. Appl. 14: 982-986.

Galik, C.S. and R.B. Jackson. 2009. Risks to forest carbon offset projects in a changing climate. For. Ecol. and Manage. 257: 2209-2216.

Gibbs, H.K. S. Brown, J.O. Niles, J.A. Foley. 2007. Monitoring and estimating tropical forest carbon stocks: making REDD a reality. Environ. Res. Lett. 2: 045023.

Global Carbon Project (2011) Carbon budget and trends 2010. [www.globalcarbonproject.org/carbonbudget] released on 4 December 2011.

Goldenberg, S.B., C.W. Landsea, A.M. Mestas-Nunez, W.M. Gray. 2010. The recent increase in Atlantic hurricane activity: causes and implications. Science. 293: 474.

Gurney, K. R., Law, R. W., Denning, A. S., Rayner, P. J., Baker, D., Bousquet, P., Bruhwiller, L., Chen, Y.-H., Ciais, P., Fan, S., I.Y. Fung, M. Gloor, M. Heimann, K. Higuchi, J. John, T. Maki, S. Maksyutov, K. Masarie, P. Peylin, M. Prather, B.C. Pak, J. Randerson, J.Sarmiento, S. Taguchi, T. Takahashi, C-W. Yuen. 2002. Towards robust regional estimates of CO2 sources and sinks using atmospheric transport model. *Nature* **415.** 626–629.

Hall, C.A.S, M.R. Taylor & E. Everham. 1992. A Geographically-Based Ecosystem Model and Its Application to the Carbon Balance of the Luquillo Forest, Puerto Rico, Water, Air, and Soil Pollution 64: 385-404.

Herbohn, J. L. and R. A. Congdon. 1993. Ecosystem dynamics at disturbed and undisturbed sites in north Queensland wet tropical rain forest. II. Litterfall. J. of Tropical Ecology 9: 365-380.

Houghton, R. A., Lawrence, K. T., Hackler, J. L. & Brown, S. 2001. The spatial distribution of forest biomass in the Brazilian Amazon: a comparison of estimates. Global Change Biol.7: 731–746.

Houghton, R. A. 2003. Revised estimates of the annual net flux of carbon to the atmosphere from changes in land use and land management. Tellus 55B: 378–390.

Houghton, R. A. 2005. Aboveground forest biomass and global carbon balance. Global Change Biology 11: 945-958.

IPCC. 2007. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I, II, and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Core Writing Team, Pachauri, R.K. and Reisinger, A. (Eds.) IPCC, Geneva Switzerland.

Jackson, R. B., H. A. Mooney, and E.-D. Schulze. 1997. A global budget for fine root biomass, surface area, and nutrient contents. Proceedings of the National Academy of Sciences (USA) 94:7362–7366.

Jaramillo, V. J. and R. L. Sanford. 1995. Nutrient cycling in tropical deciduous forests. In Seasonally Dry Tropical Forests. Eds. H. A. Mooney, S. H. Bullock, and E. Medina. Cambridge University Press, Cambridge, pp. 346-361.

Kira, T. and T. Shidei. 1967. Primary production and turnover of organic matter in different forest ecosystems of the western Pacific. Jap. J. of Ecology. 17: 70-87.

Knight, J.R., C. K. Folland, A. A. Scaife. 2006. Climate impacts of the Atlantic Multidecadal Oscillation. Geo. Research Letters 33: L17706.

Kok, K, and M. Winograd. 2002. Modelling land-use change for Central America, with special reference to the impact of hurricane Mitch. Ecol. Modell. 149: 53-69.

Knutson, T., J.J. Sirutis, S.T. Garner, G.A. Vecchi, I.M. Held 2008. Simulated reduction in Atlantic hurricane frequency under twenty-first-century warming conditions. Nature Geosciences, 1, 359 - 364.

Lambin, E. F., H. J. Geist, and E. Lepers. 2003. Dynamics of land-use and land-cover change in tropical regions. Annu. Rev. Environ. Resour. 28: 205-241.

Larocque, G. R., L. Archambault, and C. Delisle. 2006. Modelling forest succession in two southeastern Canadian mixedwood ecosystem types using the ZELIG model. Ecol. Model. 199, 350-362.

Larocque, G. R., L. Archambault, and C. Delisle. 2011. Development of the gap model ZELIG-CFS to predict the dynamics of North American mixed forest types with complex structures. Ecol. Model. 222: 2570-2583.

Laurance, W. F. 2007. A new initiative to use carbon trading for tropical forest conservation. Biotropica. 39: 20-24.

Lewis SL, O.L Phillips, T.R Baker, J. Lloyd, Y. Malhi, S. Almeida, N. Higuchi, W.F. Laurance, D.A. Neill, J.N.M. Silva, J. Terborgh, A.T. Lezama, R. Vasquez Martinez, S. Brown, J. Chave, C. Kuebler, P. Nunez Vargas, B. Vinceti. 2004. Concerted changes in tropical forest structure and dynamics: Evidence from 50 South American long-term plots. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 359:421–436.

Lindroth, A., Lagergren, F., Grelle, A., Klemedtsson, L., Langvall, O., Weslien, P., Tuulik, J., 2009. Storms can cause Europe-wide reduction in forest carbon sink. Global Change Biology 15, 346–355.

Lonsdale, W. M. 1988. Predicting the amount of litterfall in forests of the world. Annals of Botany 61: 319-324.

Lovett, G.M., J.J. Cole, M.L. Pace. 2006. Is net ecosystem production equal to ecosystem carbon accumulation? Ecosystems 9: 1-4.

Marland, G., Boden, T. A. & Andres, R. J. 2000. In *Trends: A Compendium of Data on Global Change.* Carbon Dioxide Information Analysis Center, Oak Ridge Natl. Lab., U.S. Dept. of Energy, Oak Ridge, TN.

Martinez-Yrizar, A. 1995. Biomass distribution and primary productivity of tropical dry forests. As Bullock, S. H., Mooney H. A., & Medina, A. Seasonally dry tropical forests. Cambridge University Press, Cambridge, UK. pp. 326–345.

Mason, W.L. 2002. Are irregular stands more windfirm? Forestry 75: 347–355.

McKinley, D. C., M. G. Ryan, R. A. Birdsey, C. P. Giardina, M. E. Harmon, L. S. Heath, R. A. Houghton, R. B. Jackson, J. F. Morrison, B. C. Murray, D. E. Pataki, K. E. Skog. 2011. A synthesis of current knowledge on forests and carbon storage in the United States. Ecol. Appl. 21: 1902-1924.

McMahon, S.M., G.G. Parker, D.R. Miller. 2010 Evidence for a recent increase in forest growth. PNAS. 107: 3611-3615.

Miles, L. and V. Kapos. 2008. Reducing greenhouse gas emissions from deforestation and forest degradation: global land-use implication. Science. 320: 1454-1455.

Murphy, P. G. and A. E. Lugo. 1986a. Ecology of tropical dry forest. Annual Review of Ecology and Systematics 17: 67-88.

Murphy, P. G. and A. E. Lugo. 1986b. Structure and Biomass of a Subtropical Dry Forest in Puerto Rico. Biotropica. 18: 89-96.

O'Brien, S.T., B.P. Hayden, H.H. Shugart. 1992. Global change, hurricanes and a tropical Forest. Climatic Change 22: 175-190.

Odum, H. T. 1970. A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico. U.S. Atomic Energy Commission, National Technical Information Service, Springfield, Virginia, USA.

Odum, E. P. 1971. Fundamentals of Ecology (3rd ed) W. B. Saunders Co., Philadelphia. p. 574.

Overpeck, J. T. D. Rind, R. Goldberg. 1990. Climate-induced changes in forest disturbance in vegetation. Nature. 343: 51-53.

Pabst, R.J., M.N. Goslin, S.L. Garman, and T.A. Spies. 2008. Calibrating and testing a gap model for simulating forest management in the Oregon Coast Range. For. Ecol. Manage. 256, 958–972.

Palace, M., M. Keller, H. Silva. 2008. Necromass production: studies in undisturbed and logged Amazon forests. Ecol. Appl. 18: 873-884.

Peters, G.P., G. Marland, C.L. Quere, T. Boden, J.G. Canadell, M.R. Raupach. 2011. Rapid growth in CO_2 emissions after the 2008-2009 global financial crisis. Nature Climate Change. 2: 2-4.

Phillips, O. L., Y. Malhi, N. Higuchi, W.F. Laurance, P.V. Nunez, R.M. Vasquez, S.G. Laurance, L.V. Ferreira, M. Stern, S. Brown, J. Grace. 1998. Changes in the carbon balance of tropical forests: evidence from long-term plots. Science, 282: 439–442.

Pickett, S.T.A., and P.S. White. 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York, NY.

Prentice, I. C. et al. 2001. The carbon cycle and atmospheric carbon dioxide. In *Climate change 2001: the scientific basis* (ed. IPCC). Cambridge University Press. pp 183-197.

Proctor, J., J. M. Anderson, S. C. L. Fogden, and H. W. vallack. 1983. Ecological studies in four contrasting lowland rain forests in Gunung Mulu National park, Sarawak II. Litterfall, litter standing crop and preliminary observations on herbivory. J. of Ecology 71:261-283.

Randerson J.T., Chapin F.S., Harden J.W., Neff J.C., Harmon M.E. 2002. Net ecosystem production: a comprehensive measure of net carbon accumulation by ecosystems. Ecol Appl 12:937–47.

Reich, P. B. and R. Borchert. 1984. Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. J. of Ecology. 72: 61-74.

Rice, A. H., Pyle, E. H., Saleska, S. R., Hutyra, L., de Camargo, P. B., Portilho, K., Marques, D. F. & Wofsy, S. C. 2004. Carbon balance and vegetation dynamics in an oldgrowth Amazonian forest. Ecol. Applic. 14: S55-S71.

Running, S., D. Baldocchi, D. Turner, S. Gower, P. Bakwin, and K. Hibbard. 1999. A global terrestrial monitoring network integrating tower fluxes, flask sampling, ecosystem modeling, and EOS satellite data. Remote Sensing of the Environment 70:108–127.

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

Scatena FN, Moya S, Estrada C, Chinea JD. 1996. The first five years in the reorganization of aboveground biomass and nutrient use following Hurricane Hugo in the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico. Biotropica. 28:424-440.

Schimel DS, J. I. House, K. A. Hibbard, P. Bousquet, P. Ciais, P. Peylin, B. H. Braswell, M. J. Apps, D. Baker, A. Bondeau, J. Canadell, G. Churkina, W. Cramer, A. S. Denning, C. B. Field, P. Friedlingstein, C. Goodale, M. Heimann, R. A. Houghton, J. M. Melillo, B. Moore, III, D. Murdiyarso, I. Noble, S. W. Pacala, I. C. Prentice, M. R. Raupach, P. J. Rayner, R. J. Scholes, W. L. Steffen, C. Wirth. 2001. Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. Nature. 414:169–172.

Schlesinger, W. H. 1997. Biogeochemistry: an analysis of global change. Academic Press, San Diego, California, USA.

Schlesinger, W. H. 2006. Carbon trading. Science 24: p. 1217.

Scott, D. A., J. Proctor, and J. Thompson. 1992. Ecological studies on a lowland evergreen rain forest on Maraca Island, Roraima, Brazil. II. Litter and nutrient cycling. J. of Ecology 80:705–717.

Shugart, H. H., T. M. Smith, W. M. Post. 1992. The potential for application of individual-based simulation models for assessing the effects of global change. Ann. Rev. of Eco. and Systematics. 23: 15-38.

Shure, D.J. and D.L. Phillips. 1987. Litterfall patterns with different-sized disturbance patches in a southern Appalachian mountain forest. Amer. Mid. Nat. 118: 348-357.

Sierra, C.A., M.E. Harmon, F.H. Moreno, S.A. Orrego, J.I.Del Valle. 2007a. Spatial and temporal variability of net ecosystem production in a tropical forest: testing the hypothesis of a significant carbon sink. Glob. Biol. Change. 13: 838-853.

Sierra, C.A., J.I. del Valle, S.A. Orrego, F.H. Moreno, M.E. Harmon, M. Zapata, G.J. Colorado, M.A. Herrera, W. Lara, D.E. Restrepo, L.M. Berrouet, L.M. Loaiza, J.F. Benjumea. 2007b. Total carbon stocks in a tropical forest landscape of the Porce region, Colombia. For. Ecol. and Manage. 243: 299-309.

Silvertown, J. and B. Smith. 1988. Gaps in the canopy: the missing dimension in vegetation dynamics. Vegetatio. 77:57-60.

Smith, J. B., and D. A. Tirpak, 1989. Eds. The potential effects of global climate change on the U.S.: Appendix D – Forest. Off. Policy, Planning Eval. Washington, DC: US Environ. Protection Agency.

Smith, T. M. and D. L. Urban. 1988. Scale and the resolution of forest structural pattern. Vegetatio. 74:143-150.

Solomon, A. M. 1986. Transient response of forests to CO2-induced climate change: Simulations experiments in eastern North America. Oecologia. 68: 567-579.

Spain, A.V. 1984. Litterfall and the standing crop of litter in three tropical Australian rain forests. J. of Ecology. 72: 947-961.

Steffen, W., I. Noble, J. Canadell, M. Apps, E.-D. Schulze, P. G. Jarvis, and the IGBP Terrestrial Carbon Working Group. 1998. The terrestrial carbon cycle: implications for the Kyoto Protocol. Science **280**:1393–1394.

Stocker, G. C. W. A. Thompson, A. K. Irvine, J. D. Fitzsimon, P. R. Thomas. 1995. Annual patterns of litterfall in a lowland and tableland rainforest in tropical Australia. Biotropica. 27: 412-420.

Tanner, E. V. J. 1980. Litterfall in montane rain forests of Jamaica and its relation to climate. J. of Ecology 68: 833-848.

Turner II, B.L., Skole, D.L., Sanderson, S., Fischer, G., Fresco, L.O., Leemans, R. 1995. Land-use and land-cover change. Science/Research Plan. IGBP Report no. 35 and HDP Report No. 7, Stockholm and Geneva, p. 132.

Urban, D.L., 1990. A Versatile Model to Simulate Forest Pattern: A User's Guide to ZELIG Version 1. 0. University of Virginia, Charlottesville, Virginia.

Urban, D.L., 2000. Using model analysis to design monitoring programs for landscape management and impact assessment. Ecol. Appl. 10, 1820–1832.

Urban, D.L., Bonan, G.B., Smith, T.M., Shugart, H.H., 1991. Spatial applications of gap models. Forest Ecol. Manage. 42, 95–110.

Urban, D. L., Harmon, M. R., and Halpern, C. B. 1993. Potential Response of Pacific Northwestern Forests to Climatic Change, Effects of Stand Age and Initial Composition. Clim. Change 23, 247-266.

Van Bloem, S. J., P. G. Murphy, A. E. Lugo, R. Ostertag, R. Rivera Costa, I. Ruiz Bernard, S. Molina Colon, M. Canals Mora. 2005. The influence of hurricane winds on Caribbean dry forest structure and nutrient pools. Biotropica. 37: 571-583.

Vargas, R., M. F. Allen, E. B. Allen. 2008. Biomass and carbon accumulation in a fire chronosequence of a seasonally dry tropical forest. Global Change Biol. 14: 109-124.

Vecchi, G.A. and B.J. Soden. 2007a. Effect of remote sea surface temperature change on tropical cyclone potential intensity. Nature, 450, 1066-1071.

Vecchi, G.A. and B. J. Soden, 2007b. Increased tropical Atlantic wind shear in model projections of global warming. Geophysical Research Letters,

Venter, O., W. F. Laurance, T. Iwamura, K. Wilson, R. A. Fuller, H. P. Possingham. 2009. Harnessing carbon payments to protect biodiversity. Science. 326: 1368.

Vitousek, P. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. Ecology 65: 285-298.

Walker, L. R., D. J. Lodge, N. V. L. Brokaw, and R. B. Waide. 1991. An Introduction to Hurricanes in the Caribbean. Biotropica 23:313-316.

Whitmore, T. C. 1982. On pattern and process in forests. In The Plant Community as a Working Mechanism. Special Publ. No 1, Br. Ecol. Soc. Ed. E. I. Newman. Oxford: Blackwell Sci. pp. 45-59.

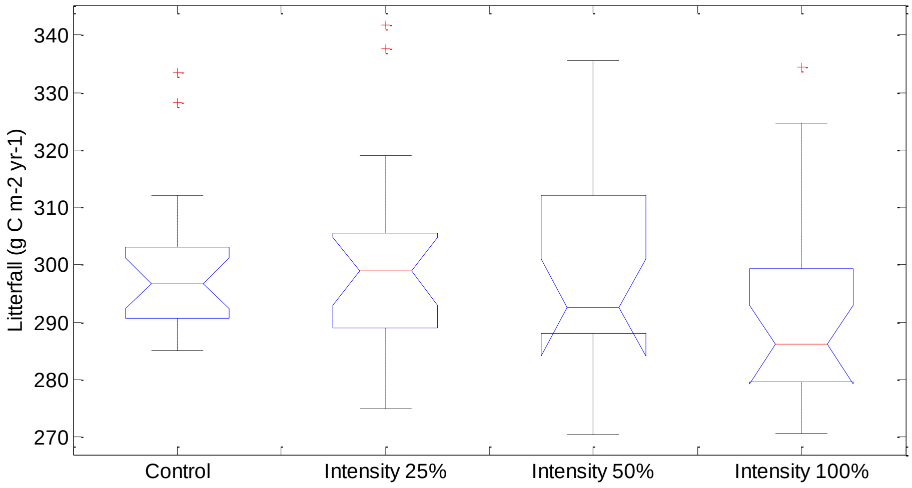
Woodwell, G. M., and D. B. Botkin. 1970. Metabolism of ecosystems by gas exchange techniques. Pages 73–85 in D. E. Reichle, editor. Analysis of temperate forest ecosystems. Springer-Verlag, New York, New York, USA.

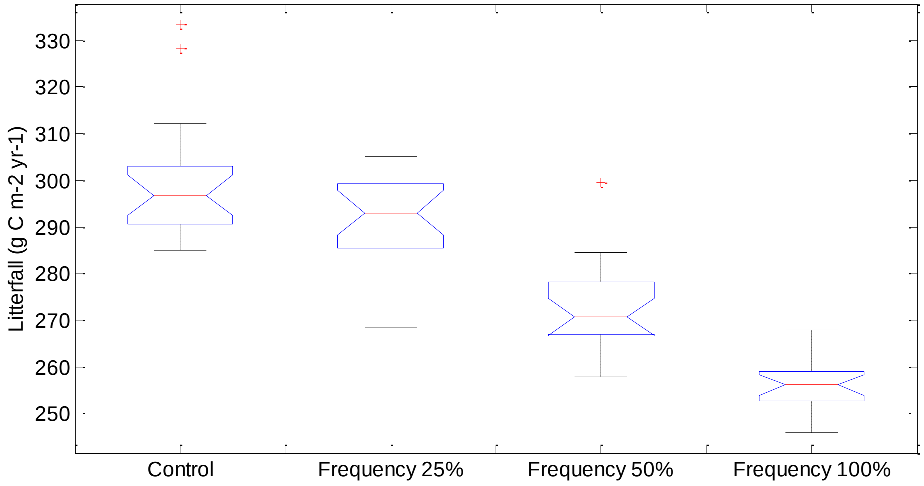
Woodwell, G. M., and R. H. Whittaker. 1968. Primary production in terrestrial ecosystems. American Zoologist 8: 19–30.

Wright, S. J. and F. H. Cornejo. 1990. Seasonal drought and leaf fall in a tropical forest. Ecology. 71: 1165-1175.

Yoda, K., T. Kira, H. Ogawa, and K. Hozumi. 1963. In- traspecific competition among higher plants. XI. Self-thinning in overcrowded pure stands under cultivated and nat- ural conditions. Journal of Biology of Osaka City University 14:107-129.

4.6 Appendix





Appendix 4.1 Sample minimum, lower quartile, median, upper quartile, and largest observations of annual litterfall over 600 years during the control hurricane treatments, and a) increasing hurricane intensity by 25%, 50%, and 100%, and b) also increasing hurricane frequency by 25%, 50%, and 100%.

Appendix 4.2 One-way ANOVA for both litterfall and leaf production. A) ANOVA between control and three treatments of increased intensity (increasing storm intensity by 25%, 50%, and 100%). B) Control and three treatments of increased frequency (increasing storm frequency by 25%, 50%, and 100%). C) Control and one treatment of decreased intensity and frequency by 50%.

	A) Increasing Intensity	
	Litterfall	Leaf Production
p-value	0.221	0.470
F-value	1.500	0.851
F-critical	2.7	2.7
r^2	0.06	0.03
	B) Increasing Frequency	
	Litterfall	Leaf Production
p-value	<0.001	<0.001
F-value	81.50	2007.18
F-critical	2.7	2.7
r^2	0.76	0.99
	C) Decreasing Inten. & Freq.	
	Litterfall	Leaf Production
p-value	0.003	<0.001
F-value	10.22	3053.32
F-critical	4.1	4.1
r^2	0.21	0.99

Chapter 5 Species diversity assessment with varying hurricane disturbances

5.1 Introduction

Biological and ecological diversity has been a main topic of scientific research for some time. Biological diversity can help organisms survive in changing environmental conditions, such as during disease outbreaks or droughts, due to niche specialization (Elton 1927, Grubb 1977, Levine 2010). Biological diversity can also help increase genetic flow (Chase et al. 1996), which in the past has helped to sustain and increase agricultural productivity. Biodiversity provides an array of ecosystem services and maintains ecosystem functions that help to sustain Earth's vital support system (Levine 2010). Examples of such ecosystem services are providing clean water, clean air, pollination, regulating climates, and providing medicines and food (Millennium Ecosystem Assessment 2005).

In general tropical forest ecosystems are categorized as having high vascular plant diversity. Diversity is high due to mechanisms that either stop or limit the competitive exclusion principle, thus allowing for species co-existence (competitive exclusion defined as: interspecific competition among species which will lead to the exclusion of all but one species). For example, the Janzen-Connell theory (Janzen 1970, Connell 1971) illustrates that higher survival of seeds occurs further from the parent trees, thus limiting competitive exclusion and increasing diversity. The negative density dependence theory, similar to the Janzen-Connell theory, describes how nearby conspecifics can impair each other's performance, regulate the population size, and allow for rare, less abundant species to establish (Janzen 1970, Connell 1971, 1984). Niche differences among species will also create more diverse systems (Elton 1927, Grinnell 1917, Grubb 1977, Denslow 1987), due to species having niche specializations or biotic and abiotic differences in resource use. Division and sharing of pollination/seed dispersers, species-specific mutualism, and different timing of flowering and fruiting patterns are examples of niche specializations and lead to species diversity. Gap dynamics and death of individual trees allows for species with different regeneration needs to persist, creating higher diversity due to resources varying in space and time (Oldeman 1978, Hubbell et al. 1999). All these examples lead to higher diversity because they limit the chances for species to be excluded and the development of a single-species environment (Wright 2002).

While there are multiple processes that help to ensure and maintain ecological diversity (e.g. seedling spatial survival, niche specializations, or gap dynamics) external factors such as land use change, increased disturbance, and climate change can limit these natural processes (as well as occasionally enhance processes which maintain diversity). Human land-use change has altered enormous sections of the Earth's biophysical surface and ecological functioning; driven by global forces such as, people's responses to economic opportunity, and national markets, but not necessarily from increases in populations or poverty (Lambin et al. 2001). Land-use change has directly decreased biological diversity (Sala et al. 2000); negatively affecting ecosystem services which benefit humans needs (Vitousek et al. 1997). Pereira et al. (2000) compared scenarios of changes in atmospheric carbon dioxide, climate, vegetation, and land-use change to rank which had the largest negative effect on biodiversity for the year 2100 and predicted that land-use change will have the largest effect on biodiversity.

In addition to land-use change, disturbances have been known to have large effects (negative and positive) on biodiversity. Some disturbances (e.g. landslides, volcanos, logging, intense hurricanes) can result in setting back forests to primary succession while some disturbances (e.g. treefalls, windstorms, fires, shifting cultivation) result in secondary succession (Whitmore and Burslem 1998). Small disturbed sites (at a gap level) can increase species richness within certain plant functional types such that pioneer and liana richness were higher in forest gap sites located in Panama (Schnitzer and Carson 2001). The growth of disturbance ecology has developed over the years, and it is generally accepted that disturbance deters competitive exclusion and is a strong contributor to shaping community structure (Grubb 1977, Connel 1978, Denslow 1987). Despite this knowledge, the effect of disturbance size and frequency of large disturbances on species diversity in additional forest types (e.g. dry tropical forests) still needs to be further examined.

5.1.1 Hurricane Disturbances and Species Diversity

The Caribbean region is prone to hurricane disturbances more than other tropical locations, and evaluating how these large, but infrequent events alter or maintain species diversity needs to be further examined. Vandermeer et al. (1996) found that a catastrophic category-4 storm did aid in reducing competitive dominance and preserved species diversity in Nicaragua. They also determined that if hurricane disturbances are density dependent or density independent they can set back competitive exclusion, but quasi-dependent storms cannot, with quasi-dependent being a disturbance that randomly destroys stems (independent), but recruitment and surviving stems are correlated with the original species (dependent).

In the wet tropical forest of Puerto Rico, after a category 4 hurricane, Zimmerman et al. (2004) determined that pioneer species suffered higher stem breakage and mortality, and had a low capacity to sprout new branches while non-pioneer species had branch damage and sprouted new branches, but lower main stem breakage and mortality. Therefore non-pioneers dominate early in recovery. This produces evidence that hurricane effects do maintain species diversity through species-specific damage and response. In the same forest Sheils et al. (2010) found different species response following a manually manipulated hurricane impact. After manually simulating a hurricane by opening canopy gaps and adding detritus inputs to the forest floor, they found that increased canopy openness was the main factor that increased densities of seedlings and stems, in particular pioneer species, with the most pronounced change occurring 1-2 years following hurricane treatments.

Further reports from Puerto Rico and the Caribbean forests, and specifically the subtropical dry forests of Puerto Rico (Van Bloem et al. 2005, 2007) conclude that hurricane disturbances did not drastically decrease species composition, but aided in supporting diversity (Brokaw and Walker 1991, Frangi and Lugo 1991). A previous modeling study from Puerto Rico, which simulates consecutive disturbances similar to this study, concluded that hurricanes act as an aid in maintaining forest composition and produce shifts in community composition that are likely (O’Brien et al. 1992, Uriarte et al. 2009), but at the extreme end of increased hurricanes, composition was negatively affected (O’Brien et al. 1992). At a highly damaged site in Puerto Rico there was differential production of new leaves among species, low mortality, increased sprouting which aided in closing canopy gaps, all leading to low changes in species composition (Walker 1991). But there needs to be further examination on the effect of increased hurricane disturbances (increases in intensity and frequency) on long-term species diversity (Brokaw and Walker 1991). Additional research should be conducted because some studies state that the human-induced increase in greenhouse gases and warming has caused an increase in tropical cyclone intensity (Goldenberg et al. 2001, Emanuel 2005, 2006, Knight 2006, Mann and Emanuel 2006, IPCC 2007, Bender et al. 2010). Emanuel (2006) stated that the destructiveness of cyclones has doubled over the past 30 years and attributes it to human induced warming and increased sea-surface temperatures (SSTs) (Emanuel 2005).

This study evaluated the effect of multiple and varying hurricane disturbances on species diversity in the subtropical dry forest of Puerto Rico. A computer forest simulator was used to simulate long-term forest regeneration, forest growth, species diversity, and mortality in response to simulated repeated hurricane disturbances. Hurricanes are a major contributor to species diversity, as it has also been known that disturbances play a role in structuring natural communities (White 1979, Sousa 1984). In summary, tropical forests are positively influenced by multiple types of disturbance, such that advanced regeneration (Uhl et al. 1988), diversity maintenance, and seedling regeneration (Guzman-Grajales and Walker 1991) are supported, if disturbances occur at appropriate intervals and magnitudes. But, due to the likelihood that hurricanes will vary in intensity, frequency, and timing, the future direction of hurricanes might alter the maintenance of species diversity.

5.1.2 Intermediate Disturbance Hypothesis

Simulation modeling has advantages for testing the Intermediate Disturbance Hypothesis (IDH), such as the ability to report patterns of vegetation abundance and distribution as a function of disturbance patterns over time. As stated by Connell (1978) the Intermediate Disturbance Hypothesis suggests that the highest diversity is maintained at intermediate scales of disturbance. For example the highest level of diversity is found when one, or a combination, of the following is observed: 1) intermediate frequency of disturbance, 2) intermediate time since the last disturbance, or 3) intermediate intensity of disturbance.

The IDH further states that, when there are a frequent amount of disturbances, typically colonizing species are only present, lowering the diversity. Colonizing species, or ruderals, are fast growing, do well in high levels of sunlight, are opportunistic in recruitment, and are typically species type with a shorter life span (also known as early successional species). When disturbance is infrequent then the ecosystem is dominated by climax or competitive species. Long time periods between disturbance events creates opportunities for competitors that are most efficient at utilizing resources to eliminate other species that are not as capable at exploiting resources, thus lowering diversity.

The IDH has been shown to apply to ecosystems affected by hurricanes, such as tropical dry forests (Bongers et al. 2009). Subtropical forests in the Caribbean are hit by hurricanes at varying frequent and infrequent intervals. It is assumed that these ecosystems are prone to disturbances by hurricanes (with an average return time of hurricanes around 10-15 years). There is evidence that the IDH is currently occurring in subtropical dry forests of the Caribbean which contain species that are early, mid, and late successional. These subtropical forests are mixed and effectively show communities that are going through different parts of succession. Some species are increasing, while dominant species are decreasing which promotes a higher level of diversity, possibly due to hurricane disturbances. Mixed species vs. single species ecosystems need to be studied to address on-going debate on ecosystem stability, productivity, and sustainability as a function of species diversity (Tilman et al. 1997, Johnson et al. 1996). There is the assumption that more diverse systems are more stable (Elton 1927, Tilman et al. 1997). The diversity-stability concept in general states that communities or ecosystems that contain more species will vary less over time when there is increase in competition, ecological stress, or disturbance. The community will not be subject to large shifts in ecosystem function when encountered with different environmental variables. Validating if the highest level of diversity is seen with an intermediate level of disturbance is a primary goal, but additionally a main goal is to test when species diversity levels become low for management purposes. This chapter will address which combinations of disturbances regimes and hurricane effects will lead to a high diversity, low diverse, or potential single species system.

5.2 Methods

5.2.1 ZELIG-TROP Model and Hurricane Modeling

Similar to chapter four of this dissertation, to achieve the goals in this chapter the methods used in chapter two and chapter three were built upon. The individual-based gap model ZELIG-TROP (described in Chapter 2) was developed to simulate the effects of hurricane disturbances on subtropical dry forests (results in Chapter 3). The original model ZELIG has been used to model many forested locations and for different applications (Urban 1990, 2000, Urban et al. 1991, 1993, Cumming and Burton 1993, Larocque et al. 2006, Pabst et al. 2008). ZELIG-TROP was parameterized with species and site-specific parameters for the Guanica Dry Forest, in southwestern Puerto Rico, and validated by directly comparing model results to observed field data (computing correlation coefficients and percent differences), and reproducing a similar modeled forest structure to existing forests (Holm et al. in press). ZELIG-TROP uses functional relationships for annual computations of tree establishment, growth, survival, and death. Also, the crown interaction algorithm developed in ZELIG-CFS was integrated into ZELIG-TROP (Larocque et al. 2011).

The processes of each individual tree were modeled as functions of environmental constraints (i.e. available light, soil moisture, soil fertility resources, and temperature). Tree growth and regeneration grew as a function of tree size, site specific climate, available light, soil moisture, temperature, and competition. Tree mortality was a function of age (1.5% of trees being able to survive to their maximum age), stress (site/environmental stress or suppression), or disturbance (hurricane events).

Detailed methods describing hurricane modeling can be found in chapter 3 of this dissertation. Detailed methods of how historical hurricane records from HURDAT were obtained, development of a new disturbance module within ZELIG-TROP, species-specific damage from hurricane effects, and alterations to hurricane intensity and frequency were explained (Chapter 3). Six of the hurricane treatments as found in the previous chapters were used to examine changes in community composition in response to increased hurricanes. The six treatments were increasing hurricane intensity and separately increasing hurricane frequency by 25%, 50%, and 100% from historical records (defined as the control).

5.2.2 *Species diversity assessment*

A relative importance value (RIV) index was used to calculate species composition. The relative importance value used a combination of species dominance (basal area, m^2 ha^{-1}) and species abundance (stem density, stems ha^{-1}), which allows for a better representation of species presence in Guanica Forest, Puerto Rico (eq. 5.1).

$$\text{RIV} = \left(\left(\frac{d_s}{d_t} * 100 \right) + \left(\frac{b_s}{b_t} * 100 \right) \right) / 2.0 \qquad \text{Equation 5.1}$$

Where RIV is relative importance value for each species, d_s is stem density for each species, d_t is the total stem density, b_s is basal area for each species, and b_t is the total basal area. In the dry forest of Puerto Rico, tree species tend to have small DBH and the forest is very dense, so by using RIV one trait (such as basal area contribution) did not out-weigh the actual presence of species. The average RIV for each of the 18 species across 20 plots (8000 m^2) for 800 years of simulation was calcualted. If a species was not present during a given year it was assigned a RIV of zero. These procedures were followed for seven hurricane treatments. The first hurricane treatment was the control treatment (historical hurricane regime), then additionally adding six treatments which separately increased the hurricane intensity and frequency by 25%, 50%, and 100%.

To further evaluate species diversity a percent difference in RIV for each hurricane treatment from the control was calculated and a Shannon Diversity Index (Shannon 1948) was used (eq. 5.2).

$$H = -\sum_{i=1}^{S}\left(P_i * \ln P_i\right) \qquad \text{Equation 5.2}$$

where H is the Shannon Diversity Index, S is the total number of species (18 in this study), P_i is the relative abundance of each species calculated as n_i/N, in which n_i is the number of individuals of species i and N is the total number of all individuals. The Shannon Diversity index takes into account the number of individuals present of each species and species evenness, so that the index increases with unique species. The typical range for the Shannon Diversity Index is 1.5 to 3.5. The maximum value (H_{max}) for this study is equal to 2.89 as found by equation 5.3.

$$H_{max} = \ln(S) \qquad \text{Equation 5.3}$$

In addition to the six hurricane treatments that evaluated community composition (separately increasing hurricane intensity and frequency by 25%, 50%, and 100% above the control), three additional hurricane treatments were added to evaluate species diversity and test the Intermediate Disturbance Hypothesis (Figure 5.1). These three additional treatments created a spectrum of hurricane occurrences that ranged from zero per year to a hurricane occurring every 2.6 years, which is the maximum for this region (Goldenberg et al. 2001). Therefore, the model can achieve a larger representation of possible hurricane affects.

The historical annual hurricane return frequency for southwestern Puerto Rico is 0.077. This is the equivalent of one hurricane passing over the forest once every thirteen years (arrow in Figure 5.1). Three additional treatments were added to the model. The first two additional treatments reduced hurricane intensity and frequency, with the first treatment reducing intensity and frequency of hurricanes entirely by removing them from the simulations (0% hurricane occurrence). The second treatment reduced hurricanes by 50% from the control. This second treatment produced a 0.038 annual return frequency, or one hurricane passing over every 26 years. The final treatment increased hurricane frequency from the the control and represented the maximum hurricane level as predicted by Goldenberg et .al. (2001). This produced an annual hurricane return frequency of 0.385, or one hurricane every 2.6 years. This larger distribution of hurricane disturbances ranging from 0% to the maximum amount typical for this area (100%), will aid in testing the IDH.

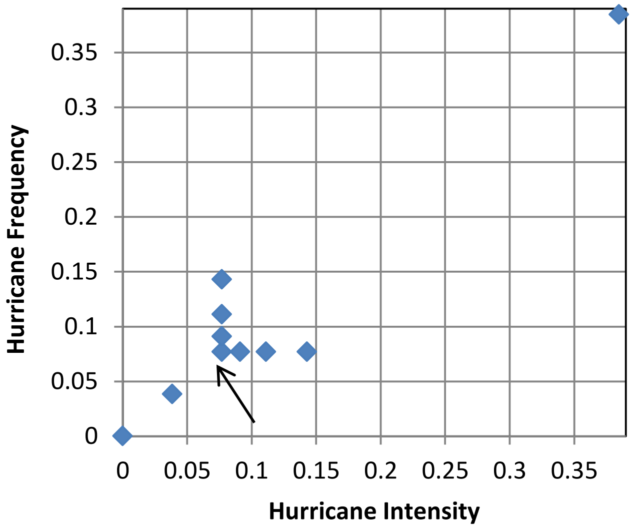


Figure 5.1. Location of ten hurricane model runs in hurricane intensity by frequency space. A frequency of 0.0 indicates no hurricanes, and a frequency and intensity of 0.385 indicates

the potential maximum hurricane disturbance for southwestern Puerto Rico (one storm every 2.6 years). The arrow indicates the location of return frequency and intensity of 0.077, which represents the historical hurricane scenario for Guanica, Puerto Rico.

5.3 Results

After repeated, simulated hurricane disturbances in the control setting, species diversity and community composition remained at a constant level over 600 years. The same consistency in community composition was also observed during treatments in which hurricane disturbances were increased in either intensity or frequency above the control. In general there was not a large shift in community composition with moderate to strong increases in hurricane events from the control setting. The six hurricane treatments showed a strong correlation in RIV with the control treatment; r^2 ranging from 0.944 to 0.992 (Table 5.1).

In all seven hurricane treatments *Gymnanthes lucida* and *Coccoloba diversifolia* remained the first and second highest ranked species (Figure 5.2). In the control treatment *Bourreria succulent* was the third highest ranked species, but after running treatments with increased intensity or frequency of storms *Bourreria succulent* dropped to a ranking of 4th or 5th depending on hurricane treatment. During increased storm scenarios the third highest ranked species was always *Coccoloba microstachya* in all six hurricane treatments. *Coccoloba microstachya* was ranked 4th in the control treatment and second highest in the 1999 observed values (Van Bloem 2005, using importance values). Species ranking and relative importance values averaged over 600 years of simulation (after the model has reached an initial spin up of 200 years) from an area of 8,000 m^2 can be found in the appendix for each of the seven hurricane treatments (Appendix 5.1 – 5.7).

5.3.1 Species composition shifts in response to increased hurricanes

Figure 5.2 displays the RIV (%) of each of the 18 tree species, for the control hurricane scenario and six treatments of increased hurricane intensity or frequency. All of the 18 species remained present during the increased hurricane simulations, and none went absent for a long period of time from the community. As seen from Figure 5.2, in general there was not a substantially large shift in species RIV, and species composition did not experience dramatic alterations, but some species were more affected by hurricane occurrences than others (species code found in Table 5.2).

The same species would respond differently to either an increase in storm intensity or an increase in storm frequency, with regards to relative dominance and abundance (RIV). Species that were more sensitive to increased intensity of hurricanes were *Bucida bucerus* decreasing in RIV by 24% to 57% depending on hurricane treatment, followed by *Bursera simaruba* which decreased in RIV by 31% to 49% depending on hurricane treatment (Figure 5.3). A species that was positively affected by increased intensity of hurricanes was *Coccoloba microstachya*, a late successional species, increasing in RIV by 8% to 17% depending on hurricane treatment. *Eugenia foetida*, which is a rare species in the canopy, also was positively affected and increased in RIV by 22% and 39% with increased storm intensity of 25% and 50%, respectively. The third highest ranking species to increase in RIV with increased storm intensity was the pioneer species *Exostema caribaeum*, followed by the pioneer species *Pictetia aculeate* which increased in RIV by 10% and 16% with increased storm intensity of 50% and 100%, respectively.

There was a different species response after applying the treatment which increased storm frequency, or increased storm occurrence by 25%, 50%, and 100%. The species that were more sensitive to increases in hurricane frequency were *Bursera simaruba,* the early successional species, which decreased in RIV by 16% to 34% and *Erithroxylon rotundifolium* which decreased in RIV by 8% to 32% depending on treatment (Figure 5.3 and Appendix 5.5-5.7). The late successional species, and 2nd most common species, *Coccoloba diversifolia* was also sensitive to increases in hurricane frequency (but not increases to hurricane intensity), decreasing in RIV by 7% to 24% depending on treatment. A higher number of species were affected positively, and increased in RIV when hurricane frequency was increased as compared to increased hurricane intensity. For example 12 out of the 18 tree species generally saw some level of increase in RIV with increased hurricane frequency. The species that increased the most in RIV was *Eugenia foetida,* ranging from 33% to 50%, followed by *Erithalis fruticosa* (13% to 34% increase in RIV), then *Amyris elemifera* (11% to 32% increase in RIV), and *Exostema caribaeum, Coccoloba microstachya, and Pictetia aculeate* all increased in very similar levels of RIV to each other (10% to 22% increase in RIV).

Table 5.1. Relationship of community composition in terms of relative importance value (RIV) between the control and six hurricane treatments, expressed using a linear regression and coefficient of determination (R^2).

	r^2 to Control (All Species)	Linear Equation
Intensity 25%	0.985	y=1.017x
Intensity 50%	0.978	y=1.014x
Intensity 100%	0.981	y=1.022x
Frequency 25%	0.992	y=0.992x
Frequency 50%	0.980	y=0.970x
Frequency 100%	0.944	y=0.944x

Table 5.2. Species code and full species name for the 18 tree species used in ZELIG-TROP, representing the common species found in the subtropical dry forest in Puerto Rico.

Species Code	Species
GYL	*Gymnanthes lucida*
COD	*Coccoloba diversifolia*
BOS	*Bourreria succulenta*
COM	*Coccoloba microstachya*
KRF	*Krugiodendron ferreum*
PIA	*Pictetia aculeate*
PII	*Pisonia albida*
EXC	*Exostema caribaeum*
CAX	*Cassine xylocarpa*
BUS	*Bursera simaruba*
JAB	*Jacquinia berteroi*
BUB	*Bucida bucerus*
AME	*Amyris elemifera*
CRR	*Crossopetalum rhacoma*
ERI	*Erythroxylon rotundifolium*
ERF	*Erithalis fruticosa*
GUK	*Guettarda krugii*
EUF	*Eugenia foetida*

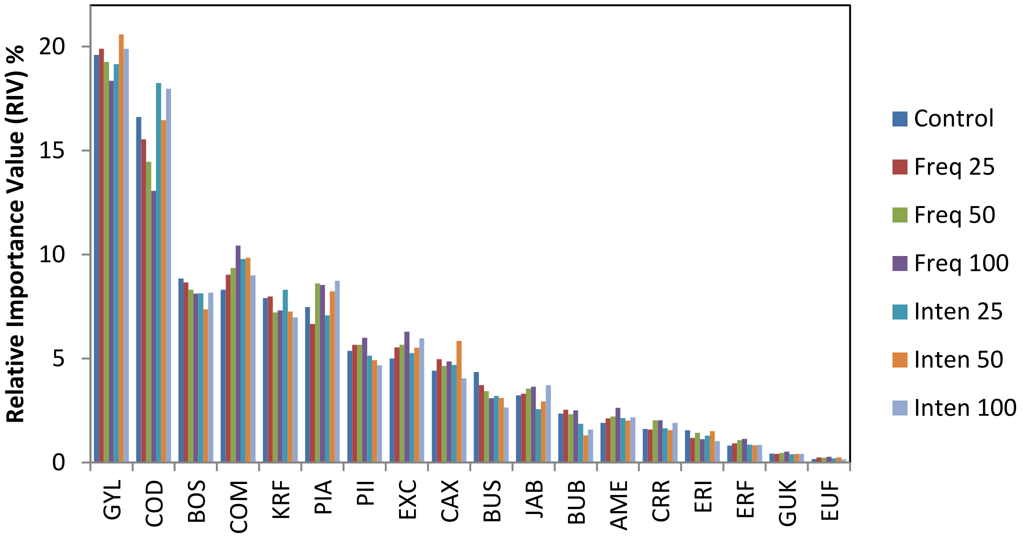


Figure 5.2. Relative importance value (RIV, %) for all 18 tree species used in the ZELIG-TROP model which simulates the subtropical dry forest located in Puerto Rico, averaged over 600 years of simualtions. RIV calculated for seven hurricane treatments; the control scenario and six treatments of increasing either hurricanes intensity or frequency. *Gymnanthes lucida* has the highest RIV during all seven hurricane simulations.

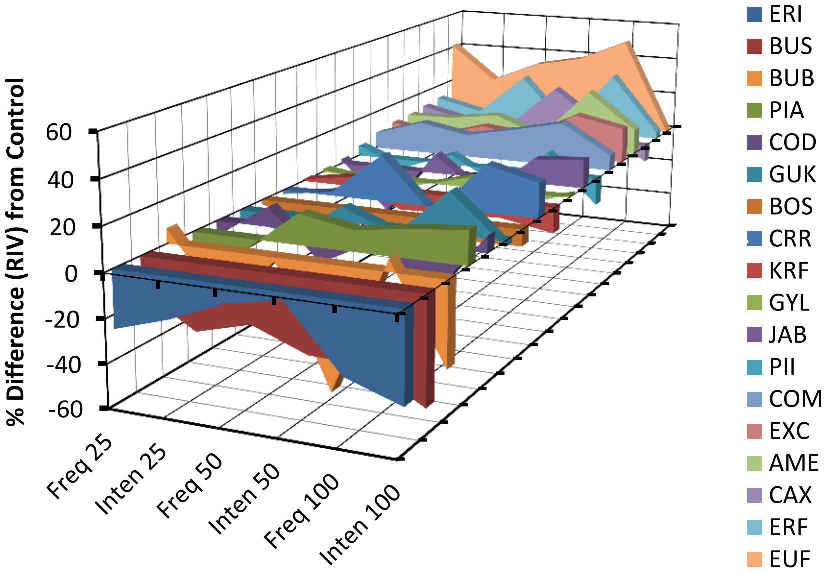


Figure 5.3. Percent difference in RIV from the control scenario for all 18 tree species used in the ZELIG-TROP model, averaged over 600 years of simualtions. Percent difference in

RIV calculated for six treatments of increasing either hurricane intensity or frequency by 25%, 50%, or 100%.

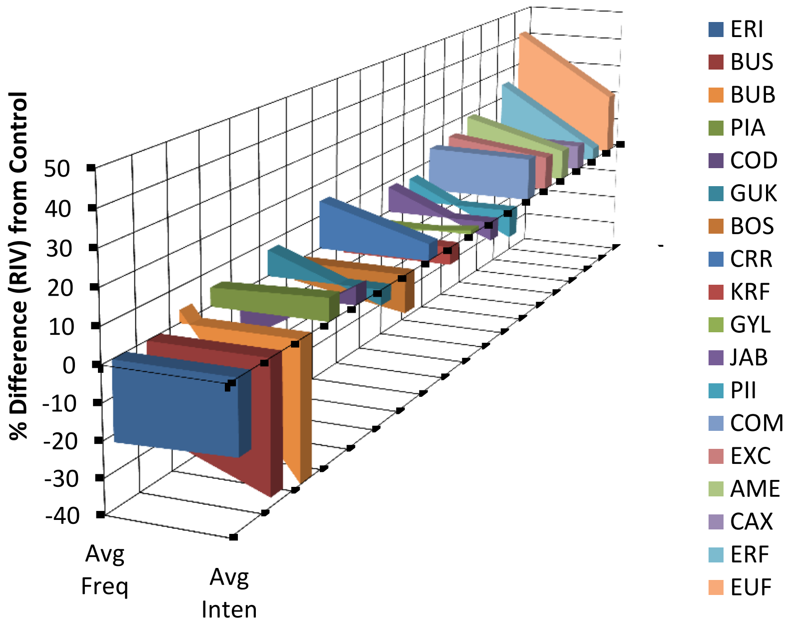


Figure 5.4. Percent difference in RIV from the control scenario for all 18 tree species used in the ZELIG-TROP model, averaged over 600 years of simualtion and averaged between the three treatments which increase hurricane frequency by 25%, 50%, and 100% and three treatments of increasing hurricane intensity by 25%, 50%, and 100%.

5.3.2 Successional traits in response to increased hurricanes

After examining all 18 tree species together at once, some trends became clear. In Table 5.3 when there was an increase in intensity of storms, there was a decrease in overall RIV (averaged over 18 species). Alternatively when there was an increase in the frequency of storms, there was an increase in overall RIV (averaged over 18 species).

Upon separating the early successional and late successional species from the group of total 18 species, additional trends became clear. Increasing hurricanes over the control (both increased intensity and increased frequency) decreased RIV of early successional, or pioneer species, a trend that was more apparent during the treatment which increased the intensity of severe storms (Table 5.3). Early successional species responded negatively to increased intensity of severe storms. However after individually evaluating the five known early successional species (Figure 5.5a), not all early successional species were decreasing in RIV. The average decrease in RIV was probably low due to the stronger contribution from *Bursera simaruba* and *Bourreria succulent.* Figure 5.5 showed that *Exostema caribaeum* increased in RIV in all six hurricane scenarios, and *Pictetia aculeate* increased in RIV in four out of the six hurricane treatments.

Late successional species were shown to behave in the opposite manner. Increasing hurricanes over the control, especially increasing intensity of storms, caused late successional species to increase in RIV (Table 5.3). But after examining five of the common late successional species individually (Figure 5.5b), some discrepancies at the individual level were observed, such that not all late successional species increased in RIV, though the average RIV increased. *Coccoloba microstachya* responded positively to all hurricane treatments, while the remaining three late successional species showed a mix of positive and negative RIV reponses depending on hurricane treatment.

Table 5.3. Percent difference in relative importance value (RIV) for six hurricane simualtion treatments from the control treatment (historical hurricane scenario) for all 18 species uesed in the model, early successional species, and late successional species. A negative percent difference is a decrease in RIV.

	% Difference in RIV from Control		
Treatment	All Species	Early Successional	Late Successional
Intensity 25%	-2.3	-8.7	7.9
Intensity 50%	-1.7	-8.1	3.5
Intensity 100%	-4.2	-7.3	3.6
Frequency 25%	2.4	-2.7	2.9
Frequency 50%	5.6	0.4	0.3
Frequency 100%	8.0	1.0	3.2

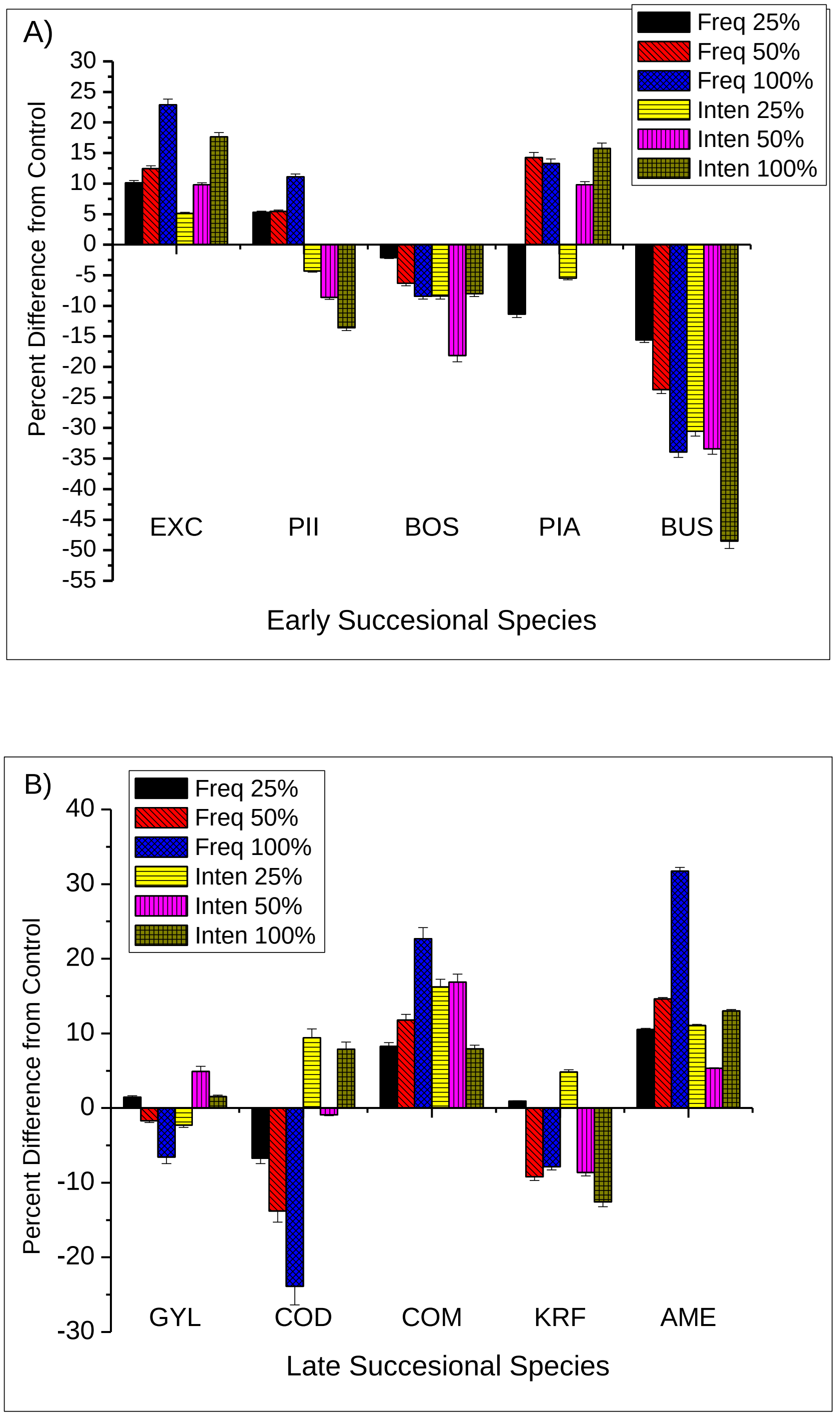


Figure 5.5. Percent difference in RIV from the control treatment (historical hurricane scenario) for A) the early successional species (*Exostema caribaeu, Pisonia albida, Bourreria succulent, Pictetia aculeate,* and *Bursera simaruba*) and B) the common late successional

species (*Gymnanthes lucida, Coccoloba diversifolia, Coccoloba microstachya, Krugiodendron ferreum*) for six hurricane simualtion treatments.

5.3.3 Diversity analysis with hurricane disturbances

A disturbance regime of 0%, or an absence of hurricane disturbances, generated the lowest average Shannon Diversity value: 1.98 (secondary axis: Figure 5.6). The remaining nine treatments that included hurricane simulations had significantly higher diversity values than the treatment with no disturbances. After calculating differences in diversity for each of the ten hurricane treatments used in this section, increasing the *frequency* of hurricane events caused the largest increase in diversity, as shown by the largest values in the Shannon Diversity Index (Figure 5.6 and 5.7). The largest increase in diversity occurs during the maximum increase in storm frequency and intensity for the southwestern Puerto Rican region: a return interval of 0.385, or one storm every 2.6 years (Figure 5.7). This treatment increased the diversity index from an average of 2.48 (control) to 2.56. The next highest diversity levels were seen when hurricane frequency was increased by 100%, 50%, and then 25%. All of these scenarios that increased the frequency of storms produced a Shannon Diversity Index larger than the control scenario (Figure 5.6 and Figure 5.7), but was not significant ($F_{(71,2.7)}$ =0.006, p=0.999).

Increasing the intensity of hurricanes by 25%, 50%, and 100% produced a decrease in species diversity from the control scenario at each intensity, but was also not significant ($F_{(71,2.7)}$ =0.002, p=0.999). While all three scenarios of increasing hurricane intensity produced similar diversity results, the largest increase in hurricane intensity

(100%) generated the lowest diversity levels over the 600 years of simulation out of any of the ten hurricane treatments (Figure 5.6).

From the diversity analysis conducted in this report, evidence was found that the Intermediate Disturbance Hypothesis (IDH) could be refuted for the subtropical dry forest in Puerto Rico. This was due to the fact that increasing storms by a five-fold increase over the control (once every 2.6 years), or increasing disturbance occurrences by 100% generated the highest level of diversity. The highest species diversity was not seen at the intermediate storm level (50%). Increasing the occurrences of disturbance by any amount over the control produced a more diverse forest, again showing that higher diversity in these forests might be found at higher *frequencies* of disturbances (Figure 5.7). Different results were found when hurricane intensity was increased. When only comparing the three levels of increased hurricane intensity against the control, the species diversity decreased (Figure 5.7). Upon decreasing the amount of hurricane disturbances (a 50% reduction in storm intensity and frequency from the control), the species diversity dropped slightly from the control. This indicates that for this forest type, species diversity lowers when hurricane disturbance are decreased from the intermediate range (control) along the 0% to 100% storm spectrum.

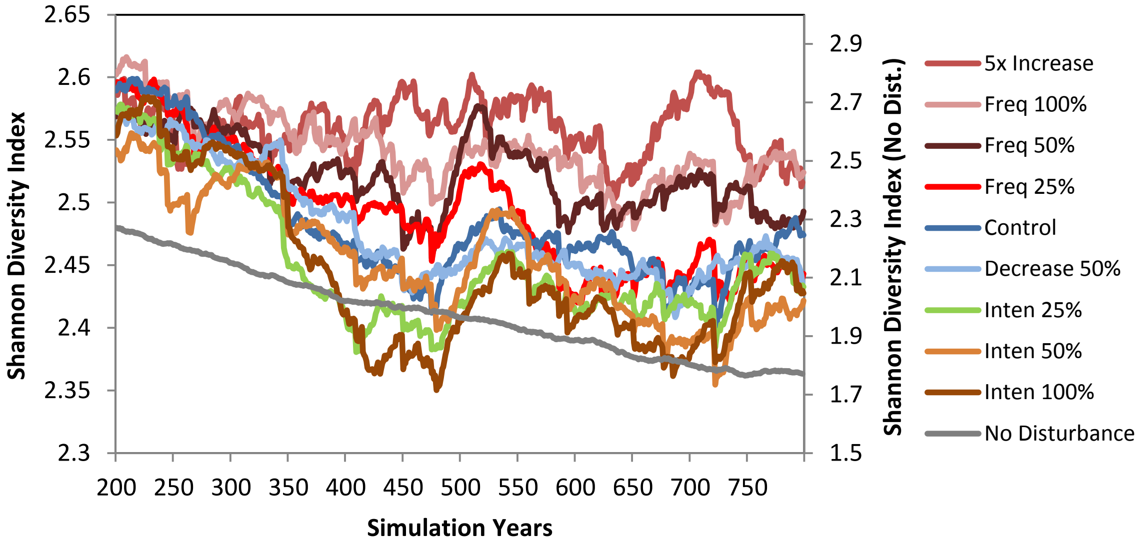


Figure 5.6. Shannon Diversity Index values for the simulated Puerto Rican subtropical dry forest over 600 years and for six hurricane simulation treatments (increasing hurricane intensity or frequency by 25%, 50%, and 100%) and the control treatment (historical hurricane scenario).

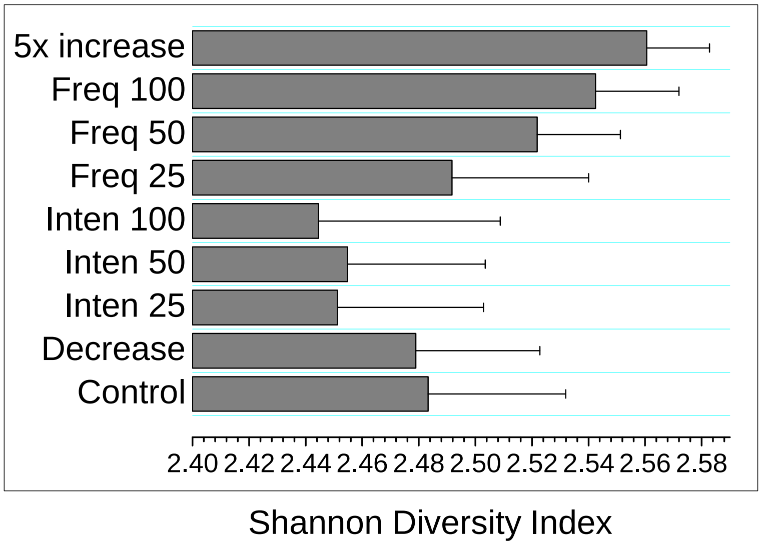


Figure 5.7. Average Shannon Diversity Index values for the simulated Puerto Rican subtropical dry forest over 600 years and for nine hurricane simulation treatments (decreasing hurricane intensity and frequency by 50%, increasing hurricane intensity or

frequency by 25%, 50%, and 100%, increasing hurricane intensity and frequency by a five-fold increase over the control) and the control treatment (historical hurricane scenario).

5.4 Discussion

Although large hurricanes can remove a large portion of the aboveground biomass (chapter 3), and a substantial part of the canopy (chapter 4), species composition did not drastically alter with the inclusion of increasing hurricane intensity and frequency from 25%-100% above the control. None of the 18 species modeled over the 600 year time span went extinct or dropped to critically low abundance levels, relative to their orginial abundance (control scenario). The species that suffered the greatest decrease in RIV was *Bursera simaruba,* dropping in RIV by 15% to 48% depending on the hurricane treatment. This species is typically an early successional, fast growing species, does well in high light environments, and has a large trunk and thick spreading branches. The species that flourished and increased the most in RIV was *Eugenia foetida,* increasing in RIV by 22% to 49% depending on the treatment (except for the treatment which increased intensity of storms by 100%, this led to a decrease in RIV by 0.4%). *Eugenia foetida* is characterized as a late successional, understory tree that does not become large, abundant during the sapling stage, and adapted for many landscapes. Overall, it was found that over long time periods (decades and centuries) late successional species thrive and increase in abundance over early successional species, when hurricanes were increased from the control settings. This agrees with results found by Zimmerman et al. (1994) which determined that non-pioneer species dominated in hurricane recovery over pioneer species. This dominance is likely due to increased branch damage leading to increased sprouting, and less likelihood of mortality (but this study was found for the wet forest of Puerto Rico and comparison should be cautioned).

There was also evidence that scenarios that increased only hurricane *frequency* created a larger effect on the community composition and species diversity. Treatments with increased frequency of disturbances reduced the dominance of the two species that contributed the greatest to basal area and abundance, and in turn increased the dominance of rarer, less frequent species. During treatments that increased the frequency of storms, both late successional and early successional species had a small increase in RIV from the control. During treatments that increased the intensity of storms, the late successional species still increased in RIV, but the early successional species decreased in RIV from the control.

Increasing the frequency of hurricanes by 25%, 50%, and 100% allowed for species diversity to increase. However increasing the frequency of storms by 500% over the control (return interval of 0.385, or one storm every 2.6 years) produced the highest Shannon Diversity value. While more testing should be investigated, it is predicted that the Intermediate Disturbance Hypothesis could be rejected for the subtropical dry forests of Puerto Rico. Bonger et al. (2009) analyzed a very large dataset of tropical forests sites and found that disturbances are more important in dry forests than wet or moist forests, with disturbances explaining more variation in diversity. Compared to wet and moist forests, there was a stronger uni-modal species richness response to disturbances in dry forests (Bongers et al. 2009). The simulation modeling employed here showed that the absence of hurricane disturbances led to a forest with lower diversity compared to a forest with hurricane disturbances. Furthermore, species diversity was seen to gradually decrease over 600 years of forest succession during an absence of storm disturbances. This is possibly due to dominant species having higher presence in the forest and reducing species which thrive in a disturbance setting.

Overall species diversity of the subtropical dry forest in Puerto Rico could be controlled by a combination of the hurricane treatment and the successional status of the tree species. Additionally, it is important to note that each species responds differently to hurricane disturbances (Walker 1991), in the amount of survival and presence in the dry forest (Figure 5.3). Understanding how the community composition of a dry forest might change depending on which of the six different hurricane trajectories occur is important for understanding the future direction of these forests. If Caribbean islands incur more intense or more frequent storms it is useful to know that community composition will not drastically shift and become dominated by a few species, that species respond differently to hurricanes, and late successional species tend to increase in abundance and size over pioneer species (likely due to sprouting ability).

5.5 Literature Cited

Bender, M.A., T.R. Knutson, R.E. Tuleya, J.J. Sirutis, G.A. Vecchi, S.T. Garner, I.A. Held. 2010. Modeled impact of anthropogenic warming on the frequency of intense Atlantic hurricanes. Science. 327: 454.

Bongers, F. L. Poorter, W.D. Hawthorne, D. Sheil. 2009. The interemediate disturbance hypothesis applies to tropical forests, but disturbance contributes little to tree diversity. Ecol. Lett. 12: 798-805.

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

Chase, M.R., C. Moller, R. Kesseli & K. S. Bawa. 1996. Distant gene flow in tropical trees. Nature. 383: 398-399.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science. 199: 1302-1310.

Connell JH, Tracey JG, Webb LJ. 1984. Compensatory recruitment, growth, and mortality as factors maintaining rain forest tree diversity. Ecol Monogr 54:141–164.

Cumming, S. G. and Burton, P. J. 1993. A Programmable Shell and Graphics System for Forest Stand Simulation, Environ. Software. 8, 219-230.

Denslow J.S. 1987. Tropical rainforest gaps and tree species diversity. Annu. Rev. Ecol. Syst. 18: 431–451.

Elton, C.S. 1927. Animal Ecology. Macmillian, New York.

Emanuel, K. 2005. Increasing destructiveness of tropical cyclones over the past 30 years. Nature 436:686-688.

Emanuel, K. 2006. Hurricanes: Tempests in a greenhouse. Physics Today 59:74-75.

Frangi J.L. and Lugo AE. 1991. Hurricane damage to a flood plain forest in the Luquillo Mountains of Puerto Rico. Biotropica. 23:324-335.

Goldenberg, S. B., et al., 2001. The recent increase in Atlantic hurricane activity: causes and implications. Science, 293, 474-479.

Grinnell, J. 1917. The niche-relationships of the California Thrasher. Auk 34: 427–433.

Grubb P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol. Rev. 52: 107–145.

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

Holm, J.A., H.H. Shugart, S.J. Van Bloem, G. R. Larocque. In press. Gap model development, validation, and application to succession of secondary subtropical dry forests of Puerto Rico. Ecol. Model.

Hubbell SP, Foster RB, O’Brien ST, Harms KE, Condit R, Weschler B, Wright SJ, Loo de Lao S. 1999. Light gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. Science 283: 554–557.

IPCC. 2007. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I, II, and III to the Fourth Assessment Report of the Intergovernmental Panel on

Climate Change. Core Writing Team, Pachauri, R.K. and Reisinger, A. (Eds.) IPCC, Geneva Switzerland.

Janzen D.H. 1970. Herbivores and the number of tree species in tropical forests. Am Nat 104: 501–528.

Janzen, D. 1988. Tropical dry forests. The most endangered major tropical ecosystem. Biodiversity (ed. By E.O. Wilson), pp. 13-137. National Academy of Sciences/Smithsonian Institution, Washington DC.

Johnson, K.H., K.A. Vogt, H.J. Clark, O.J. Schmitz, D.J. Vogt. 1996. Biodiversity and the productivity and stability of ecosystems. Tree. 11: 372-377.

Knight, J.R., C. K. Folland, A. A. Scaife. 2006. Climate impacts of the Atlantic Multidecadal Oscillation. Geo. Research Letters 33: L17706.

Lambin, E.F., B.L. Turner, H.J. Geist, S.B. Agbola, A. Angelsen, J.W. Bruce, O.T. Coomes, R. Dirzo, G. Fischer, C. Folke, P.S. George, K. Homewood, J. Imbernon, R. Leemans, X. Li, E.F. Moran, M. Mortimore, P.S. Ramakrishnan, J.F. Richards, H. Skanes, W. Steffen, G.D. Stone, U. Svedin, T.A. Veldkamp, C. Vogel, J. Xu. 2001. The causes of land-use and land-cover change: moving beyond the myths. Glob. Environ. Change. 11: 261-269.

Larocque, G. R., L. Archambault, and C. Delisle. 2006. Modelling forest succession in two southeastern Canadian mixedwood ecosystem types using the ZELIG model. Ecol. Model. 199, 350-362.

Larocque, G. R., L. Archambault, and C. Delisle. 2011. Development of the gap model ZELIG-CFS to predict the dynamics of North American mixed forest types with complex structures. Ecol. Model. In press.

Levine, J. M. and J. HilleRisLambers. 2010. The Maintenance of Species Diversity. Nature Education Knowledge 1: 67.

Mann, M.E. and K.A. Emanuel. 2006. Atlantic hurricane trends linked to climate change. EOS. 87: 233-244.

Millennium Ecosystem Assessment. 2005. Ecosystems and Human Well-Being: Full Report. Washington, DC: Island Press.

O'Brien, S.T., B.P. Hayden, H.H. Shugart. 1992. Global change, hurricanes and a tropical Forest. Climatic Change 22: 175-190.

Oldeman, R.A.A. 1978. Architecture and energy exchange of dicotyledonous tree in the forest. *In* P.B. Tomlinson and M:H. Zimmermann, ed., Tropical Trees as Living Systems. pp. 535-560. Cambridge Univ. Press, London.

Pabst, R.J., M.N. Goslin, S.L. Garman, and T.A. Spies. 2008. Calibrating and testing a gap model for simulating forest management in the Oregon Coast Range. For. Ecol. Manage. 256, 958–972.

Pereira, H.M., P.W. Leadley, V. Proenca, R. Alkemade, J.P.W. Scharlemann, J.F. Fernandez-Manjarrés, M.B. Araújo, P. Balvanera, R. Biggs, W.W.L. Cheung, L. Chini, H.D. Cooper, E.L. Gilman, S. Guénette, G.C. Hurtt, H.P. Huntington, G.M. Mace, T. Oberdorff, C. Revenga, P. Rodrigues, R.J. Scholes, U.R. Sumaili, M. Walpole. 2000. Global biodiversity scenarios for the year 2100. Science. 287: 1770-1774.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H. 2000. Biodiversity:global biodiversity scenarios for the year 2100. Science 287, 1770–1774.

Schnitzer, S.A. and W.P. Carson. 2001. Treefall gaps and the maintenance of the species diversity in a tropical forest. Ecology. 82: 913-919.

Shannon, C.E. 1948. A mathematical theory of communication. Bell System Technical Journal 27: 379–423.

Sheils, A.B., J.K. Zimmerman, D.C. Garcia-Montiel, I. Jonckheere, J.A. Holm, D. Horton, N. Brokaw. 2010. Plant response to simulated hurricane impacts in a subtropical wet forest, Puerto Rico. J. of Ecology. 98: 659-673.

Sousa, W. P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15:353–391.

Tilman, D. J. Knops, D. Wedin, P. Reich, M. Ritchie, E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. Science. 277: 1300-1302.

Uhl, C., K. Clark, N. Dezzeo, and P. Maquirino. 1988. Vegetation dynamics in Amazonian treefall gaps. Ecology. 69: 751-763.

Urban, D.L., 1990. A Versatile Model to Simulate Forest Pattern: A User’s Guide to ZELIG Version 1. 0. University of Virginia, Charlottesville, Virginia.

Urban, D.L., 2000. Using model analysis to design monitoring programs for landscape management and impact assessment. Ecol. Appl. 10, 1820–1832.

Urban, D.L., Bonan, G.B., Smith, T.M., Shugart, H.H., 1991. Spatial applications of gap models. Forest Ecol. Manage. 42, 95–110.

Urban, D. L., Harmon, M. R., and Halpern, C. B. 1993. Potential Response of Pacific Northwestern Forests to Climatic Change, Effects of Stand Age and Initial Composition. Clim. Change 23, 247-266.

Uriarte, M., C. D. Canham, J.Thompson, J. K. Zimmerman, L. Murphy, A. M. Sabat, N. Fetcher, and B. L. Haines. 2009. Understanding natural disturbances and human land use as determinants of tree community dynamics in a subtropical wet forest: results from a forest simulator. Ecological Monographs. 79, 423-443.

Van Bloem, S. J., P. G. Murphy, A. E. Lugo, R. Ostertag, R. Rivera Costa, I. Ruiz Bernard, S. Molina Colon, M. Canals Mora. 2005. The influence of hurricane winds on Caribbean dry forest structure and nutrient pools. Biotropica. 37: 571-583.

Van Bloem. S. J., P. G. Murphy, A. E. Lugo. 2007. A link between hurricane-induced tree sprouting, high stem density and short canopy in tropical dry forest. Tree Physiology. 27: 475-480.

Vandermeer, J., D. Boucher, I. Perfecto, I. Granzow de la Cerda. 1996. A theory of disturbance and species diversity: evidence from Nicaragua after Hurricane Joan. Biotropica. 28: 600-613.

Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human domination of earth’s ecosystems. Science 277: 494–499.

Walker, L.R. 1991. Tree damage and recovery from Hurricane Lugo in Luquillo Experimental Forest, Puerto Rico. Biotropica 23: 513-521.

White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. The Botanical Review 45:229–299.

Whitmore, T. C. and D. F. R. P. Burslem. 1998. Major disturbances in tropical rainforests. Pages 549–565 in D. M. Newbery, H. H. T. Prins, and N. D. Brown, editors. Dynamics of tropical communities. Blackwell Science, Oxford, UK.

Wright, J. S. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. Oecologia. 130: 1-14.

Zimmerman, J.K., E.M. Everham III, R.B. Waide, D. Jean Lodge, C.M. Taylor, N.V.L. Brokaw. 1994. Responses of tree species to hurricane winds in subtropical wet forests in Puerto Rico. J. of Ecology. 82: 911-922.

5.6 Appendix

Appendix 5.1. Observed species ranking from 1999, simulated species ranking, and relative importance value for 18 species in the control hurricane treatment.

	Control		
1999 Observed Rank	Control Rank	Species	RIV
1	1	GymLuc	19.61
8	2	CocDiv	16.62
7	3	BouSuc	8.85
2	4	CocMic	8.32
11	5	KruFer	7.92
4	6	PisAlb	7.47
3	7	PicAcu	5.37
5	8	ExoCar	5.01
10	9	CasXyl	4.42
6	10	BurSim	4.36
12	11	JacBer	3.23
?	12	BUB	2.36
14	13	AmyEle	1.91
15	14	CroRha	1.61
16	15	EriRot	1.56
9	16	EriFru	0.81
13	17	GueKru	0.43
17	18	EugFoe	0.16

Appendix 5.2. Species ranking, relative importance value, and percent difference in RIV between the control and hurricane treatment with increased intensity of storms by 25% for 18 species.

	Intensity + 25%			
Control Rank	Inten. 25% Rank	Species	RIV	% Diff from control
1	1	GymLuc	19.16	-2.28
2	2	CocDiv	18.26	9.43
4	3	CocMic	9.78	10.02
5	4	KruFer	8.31	-0.06
3	5	BouSuc	8.14	2.71
6	6	PisAlb	7.08	-5.45
8	7	ExoCar	5.27	-1.91
7	8	PicAcu	5.14	2.69
9	9	CasXyl	4.69	6.05
10	10	BurSim	3.20	-30.52
11	11	JacBer	2.56	-22.85
13	12	AmyEle	2.13	-10.24
12	13	BUB	1.86	-2.54
14	14	CroRha	1.64	1.94
15	15	EriRot	1.29	-18.72
16	16	EriFru	0.87	6.96
17	17	GueKru	0.40	-8.37
18	18	EugFoe	0.20	22.31

Appendix 5.3. Species ranking, relative importance value, and percent difference in RIV between the control and hurricane treatment with increased intensity of storms by 50% for 18 species.

	Intensity + 50%			
Control Rank	Inten. 50% Rank	Species	RIV	% Diff from control
1	1	GymLuc	20.59	4.91
2	2	CocDiv	16.46	-0.91
4	3	CocMic	9.85	10.69
6	4	PisAlb	8.24	-0.89
3	5	BouSuc	7.38	-7.07
5	6	KruFer	7.26	-2.84
9	7	CasXyl	5.84	8.44
8	8	ExoCar	5.52	9.79
7	9	PicAcu	4.92	10.82
10	10	BurSim	3.11	-33.43
11	11	JacBer	2.94	-9.23
13	12	AmyEle	2.01	-15.97
14	13	CroRha	1.56	-20.43
15	14	EriRot	1.51	-6.78
12	15	BUB	1.31	-17.07
16	16	EriFru	0.83	1.85
17	17	GueKru	0.42	-2.85
18	18	EugFoe	0.24	38.55

Appendix 5.4. Species ranking, relative importance value, and percent difference in RIV between the control and hurricane treatment with increased intensity of storms by 100% for 18 species.

	Intensity + 100%			
Control Rank	Inten. 100% Rank	Species	RIV	% Diff from control
1	1	GymLuc	19.91	1.53
2	2	CocDiv	17.98	7.87
4	3	CocMic	9.00	1.71
6	4	PisAlb	8.75	5.09
3	5	BouSuc	8.17	3.10
5	6	KruFer	6.98	-6.79
8	7	ExoCar	5.97	10.66
7	8	PicAcu	4.69	-6.57
9	9	CasXyl	4.04	-8.89
11	10	JacBer	3.72	-15.69
10	11	BurSim	2.65	-19.42
13	12	AmyEle	2.18	-8.29
14	13	CroRha	1.91	0.04
12	14	BUB	1.59	-1.24
15	15	EriRot	1.03	-40.34
16	16	EriFru	0.84	3.44
17	17	GueKru	0.42	-2.67
18	18	EugFoe	0.16	-0.45

Appendix 5.5. Species ranking, relative importance value, and percent difference in RIV between the control and hurricane treatment with increased frequency of storms by 25% for 18 species.

	Frequency + 25%			
Control Rank	Freq. 25% Rank	Species	RIV	% Diff from control
1	1	GymLuc	19.89	1.46
2	2	CocDiv	15.54	-6.70
4	3	CocMic	9.03	2.06
3	4	BouSuc	8.66	4.07
5	5	KruFer	7.99	0.91
6	6	PisAlb	6.67	-11.35
7	7	PicAcu	5.66	5.29
8	8	ExoCar	5.54	10.14
9	9	CasXyl	4.97	11.70
10	10	BurSim	3.73	-15.57
11	11	JacBer	3.30	2.37
12	12	BUB	2.54	7.02
13	13	AmyEle	2.12	10.53
14	14	CroRha	1.58	-1.99
15	15	EriRot	1.19	-26.40
16	16	EriFru	0.92	12.81
17	17	GueKru	0.41	-4.47
18	18	EugFoe	0.25	41.22

Appendix 5.6. Species ranking, relative importance value, and percent difference in RIV between the control and hurricane treatment with increased frequency of storms by 50% for 18 species.

	Frequency + 50%			
Control Rank	Freq. 50% Rank	Species	RIV	% Diff from control
1	1	GymLuc	19.27	-1.71
2	2	CocDiv	14.47	-13.78
4	3	CocMic	9.36	5.60
6	4	PisAlb	8.62	3.63
3	5	BouSuc	8.31	4.79
5	6	KruFer	7.22	-3.43
8	7	ExoCar	5.67	5.45
7	8	PicAcu	5.67	12.45
9	9	CasXyl	4.65	5.06
11	10	JacBer	3.56	-20.22
10	11	BurSim	3.43	6.18
12	12	BUB	2.32	-1.82
13	13	AmyEle	2.21	14.61
14	14	CroRha	2.03	22.69
15	15	EriRot	1.43	-8.13
16	16	EriFru	1.08	28.71
17	17	GueKru	0.46	7.24
18	18	EugFoe	0.23	33.39

Appendix 5.7. Species ranking, relative importance value, and percent difference in RIV between the control and hurricane treatment with increased frequency of storms by 100% for 18 species.

	Frequency + 100 %			
Control Rank	Freq. 100% Rank	Species	RIV	% Diff from control
1	1	GymLuc	18.36	-6.56
2	2	CocDiv	13.07	-23.86
4	3	CocMic	10.44	16.53
6	4	PisAlb	8.54	2.62
3	5	BouSuc	8.13	2.69
5	6	KruFer	7.32	-2.10
8	7	ExoCar	6.30	15.95
7	8	PicAcu	6.00	18.10
9	9	CasXyl	4.86	9.47
11	10	JacBer	3.65	-17.72
10	11	BurSim	3.09	-4.22
13	12	AmyEle	2.63	10.67
12	13	BUB	2.50	26.88
14	14	CroRha	2.03	23.15
15	15	EriRot	1.14	-30.99
16	16	EriFru	1.13	32.81
17	17	GueKru	0.53	20.29
18	18	EugFoe	0.27	49.72