FLORIDA INTERNATIONAL UNIVERSITY

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THE SUCCESSIONAL DYNAMICS OF LIGHTNING-INITIATED CANOPY GAPS IN THE MANGROVE FORESTS OF SHARK RIVER, EVERGLADES NATIONAL PARK, USA

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Kevin Richard Terrence Whelan
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To: Interim Dean Mark Szuchman
College of Arts and Sciences

This dissertation, written by Kevin Richard Terrence Whelan, and entitled The Successional Dynamics of Lightning-initiated Canopy Gaps in the Mangrove Forests of Shark River, Everglades National Park, USA, having been approved in respect to style and intellectual content, is referred to you for judgment.

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DEDICATION

I dedicate this dissertation to my family. My wife, Tina, who has read so many versions of this work, helped me in the field, and listened to me rant about life. She was always there for a push in the right direction or a hug, whichever was needed. This work would not have happened without her constant encouragement. To my daughter, Josie, who will be charged to have wise stewardship over this planet using our limited and flawed knowledge. To my father, Michael Whelan, who encouraged me to get a good education and always wondered how I had a job that allowed me to play in the woods. To my mother, Donna Whelan, who early on dragged me out to the garden, exposing me to the wonders of nature. She always encouraged me to do what I enjoyed. To my brother, Mike Whelan, with whom I experienced numerous explorations of nature, during our inquisitive youth, fishing, swimming, and camping in the Everglades. He always had the courage to try new things, towing me along with him. To the loving memory of my grandmother and mother$_2$, Betty Jephson and Nancy Ugarte, two grand ladies, who taught me to love life and family the most. Finally, this dissertation is dedicated to the resilience of the Everglades. Specifically to a forest that has been logged, repeatedly impacted by hurricanes, starved for water or excessively flooded, ignored and violated yet remains wild, beautiful and always educating the curious souls that wander through it.

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Mention of trade names does not constitute endorsement by the US Government. The author takes full responsibility for any errors or oversights in this manuscript.

ABSTRACT OF THE DISSERTATION

THE SUCCESSIONAL DYNAMICS OF LIGHTNING-INITIATED CANOPY GAPS IN THE MANGROVE FORESTS OF SHARK RIVER, EVERGLADES NATIONAL PARK, USA

by

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Gap succession is a significant determinant of structure and development in most forest communities. Lightning strikes are an important source of canopy gaps in the mangrove forest of Everglades National Park. I investigated the successional dynamics of lightning-initiated canopy gaps to determine their influence on forest stand structure of the mixed mangrove forests (*Rhizophora mangle*, *Laguncularia racemosa*, and *Avicennia germinans*) of the Shark River. I measured gap size, gap shape, light environment, soil characteristics, woody debris, and fiddler crab abundance. I additionally measured the vegetative composition in a chronosequences of gap successional stages (new, recruiting, and growing gaps). I recorded survivorship, recruitment, growth and soil elevation dynamics within a subset of new and growing gaps. I determined the relationship between intact forest soil elevation and site hydrology in order to interpret the effects of lightning disturbance on soil elevation dynamics.

Gap size averaged 289 ± 20 m^2 (± 1SE) and light transmittance decreased exponentially as gaps filled with saplings. Fine woody debris was highest in recruiting gaps. Soil strength was lower in the gaps than in the forest. The abundance of large and medium fiddler crab burrows increased linearly with total seedling abundance. Soil surface elevation declined in newly formed lightning gaps; this loss was due to a combination of superficial erosion (8.5 mm) and subsidence (60.9 mm). A distinct two-cohort recruitment pattern was evident in the seedling/sapling surveys, suggesting a partitioning of the succession between individuals present before and after lightning strike. In new gaps, the seedling recruitment rate was twice as high as in forest and the sapling population increased. At the growing gap stage, *R. mangle* seedling mortality was 10 times greater and sapling mortality was 13 times greater than recruitment. Growing gaps had reduced seedling stem elongation, sapling growth and adult growth. However, a few individuals (*R. mangle* saplings) were able to recruit into the adult life stage. In conclusion, the high density of *R. mangle* seedlings and saplings imply that lightning strike disturbances in these mangrove forests favor their recruitment over that of *A. germinans* and *L. racemosa*.

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Chapter I

Introduction

Lightning gaps are a common disturbance in mangroves throughout the world, including Papua New Guinea (Paijmans and Rollet 1977), Panama (Smith 1992, Sousa and Mitchell 1999), Dominican Republic (Sherman et al. 2000), and the United States of America (Odum et al. 1982; Smith et al. 1994). Lightning strikes within the mangrove canopy create a relatively circular to elliptical clearing from the top to the bottom of the forest canopy (Duke 2001, Sherman et al. 2000). These strikes kill several trees, instead of just one or two as is often seen in upland terrestrial forests (Anderson 1966). The mechanism by which lightning strikes kill multiple trees is not well understood, but it occurs in many ecosystems (Peace 1940, Anderson 1964, Brunig 1964, 1972, Paijmans and Rollet 1977, Magnusson et al. 1996, Sherman et al. 2000, Duke 2001). Florida, in particular, has one of the highest rates of cloud to ground lightning strikes in the United States (Changnon 1989). Lightning gaps are common in the mangrove forest of Everglades National Park due to the high rate of strikes (7 to 9 flashes/km^2 yr^{-1}, Huffines and Orville 1999).

Mangroves comprise an extensive expanse at the junction of the terrestrial forest and nearshore marine ecosystems in the tropics. Mangroves are generally highly productive ecosystems, which have extremely stressful environmental conditions (i.e. high salinity, high temperatures, extreme tidal flooding, anaerobic soils, etc. Odum et al. 1982). Mangrove forests worldwide are noted for a sparse understory and few sapling-size individuals (Janzen 1985, Corlett 1986, Lugo

1986, Tomlinson 1986). There have been numerous studies to determine how the mangrove forests develop. Classical mangrove investigations have reported species-specific zonation patterns to the forest (Davis 1940, Lugo and Snedaker 1974, Chapman 1976). These zonation patterns have typically been linked to environmental stressors that may facilitate specific species at the expense of others. Evidence for and against species sorting has been reported (Rabinowitz 1978, Clarke and Allaway 1993, Smith 1992, Smith et al 1994, Chen and Twilley 1999, Clarke and Kerrigan 2000). More recently, mangroves have been being investigated to determining the role disturbance (hurricanes/typhoons, tidal waves/Tsunamis, hydrological diversions) plays in the forest dynamics (Smith et al. 1994, Duke 2001, Cahoon et al. 2003, Baldwin et al. 2001).

Observations of numerous small gaps and a meager understory within closed canopy forest have inspired investigations to determine the role gaps play in mangrove community structure and diversity by applying concepts from upland terrestrial systems to mangrove forest dynamics (Smith 1992, Feller and McKee 1999, Clarke and Kerrigan 2000, Sherman et al. 2000, Duke 2001, Ellison 2002). Gaps provide an altered environment both above and below ground. Typically gaps have increased light (quantity), temperature, humidity, soil temperatures (Fetcher et al. 1985), soil water (Denslow et al. 1987, Becker et al. 1988), and change the quality of light, and decreased root formation (Denslow et al. 1987). Despite the importance of soil processes during succession, most canopy gap investigations have concentrated on only aboveground effects. Specifically, mangrove canopy gaps have been found to alter several physical factors and processes important for mangrove regeneration: humidity, evapotranspiration, light levels, and soil properties (salinity, temperatures, and nutrients) (Smith 1987a, Smith 1992). These changes can also lead to modifications in the crab community (Osborne and Smith 1990, Smith 1987b). Crabs play a key role in these ecosystems; their burrows increase soil aeration, reduce sulfides and ammonium, and increase mangrove sapling productivity (Smith et al. 1991). Mangrove forest structure and productivity have also been found to influence fiddler crab size (Colpo and Negreiros-Fransozo 2004). Thus the relationship between crab and mangrove population structure is a complex feedback that will likely change during gap succession.

The physical environment within the gaps may facilitate favorable conditions that can shift species-specific survivorship, recruitment, and growth of the flora and fauna both among and within a species across life stages (Brokaw 1985, Denslow 1987, Hubbell et al. 1999). Additionally, as succession progresses within the gap the environmental conditions will change which may allow a specific species to have favorable conditions only at certain stages during the successional trajectory. The regenerative processes within lightning-initiated gaps can potentially drive mangrove forest diversity and structure in South Florida. Chapman (1976) suggested the idea of “cyclical succession” with mangrove forest oscillating between two stages of development due to physical disturbances. Lugo (1980) argued for the “arrested succession” of mangroves due to physical disturbances such as hurricanes, winds, waves, fire, etc. Finally, Duke (2001) hypothesized that recruitment within small canopy gaps can prevent mangroves from reaching a senescence stage. The conditions within these lightning gaps may facilitate recruitment of certain species at the expense of others.

A comprehensive understanding of the dynamics of this mangrove forest is of considerable importance. The forest is located in the Shark River estuary, downstream of the Shark River Slough, and receives freshwater inputs from the greater Everglades drainage and thus is under the influence of upstream water management practices of the Greater Everglades. The Everglades drainage is currently undergoing an ecosystem restoration concentrating on modifying water deliveries to mimic pre-drainage flows. In addition to the changing freshwater flows linked to restoration, this mangrove forest is impacted by sea level rise. The hydrological conditions of a site are known to substantially affect soil processes including sedimentation, erosion, and the shrink and swell of soil materials. Additionally, soil elevation and surface flooding have been identified as important factors in mangrove species recruitment and survival (McKee 1993, 1995, Ellison and Farnsworth 1993, Rabinowitz 1978ab, McMillan 1971). For example, under more flooded conditions survival of *Rhizophora mangle* is greater than that of *Avicennia germinans* and *Laguncularia racemosa* (McKee 1993). Therefore, a comprehensive understanding of the successional dynamics of lightning initiated gap in the mangrove forest of Shark River must take into account current and future hydrological conditions.

Overall dissertation objective:

The overall objective of this dissertation is to address the role that lightning gaps play in community structure and composition in the mangrove forest of Shark River. To understand the underlying basis for that role, detailed studies of lightning gap forest composition and structural changes through time along with assessments of the physical and biological interactions are needed. Specifically, one needs to have insight into the following questions. Do recruitment, survivorship, or growth dynamics change allowing a particular mangrove species to prevail at a particular life stage? How does gap succession affect the constituent fiddler crab population? Does lightning gap disturbance affect soil surface elevation? To interpret the change in soil elevation through time, one needs to determine the relationship of hydrology to soil elevation. What will be the affect of Everglades Restoration on lightning gap succession?

Finally, to comprehend the role lightning gap disturbance has on the mangrove forest a basic awareness of the closed canopy forest structure and composition is needed, including the life history parameters of recruitment and mortality rate, survivorship, and growth by life stage class (propagule, seedling, sapling and adult) in the intact forest. There will be approximately 8 billion dollars spent on Everglades Restoration, these basic life stage parameters in closed mangrove canopy forest are critically needed for proper parameterization of mangrove forest development models used by the land managers.

Specific research objectives covered in the dissertation:

Chapter II provides a quantitative understanding of the dynamics of lightning-initiated gaps as they progress towards a closed canopy condition in the South Florida mangrove ecosystem. I accomplished this by comparing gaps at three stages of development among themselves and with surrounding intact forest. The two main objectives were to assess physical characteristics of gaps (gap size and shape, light environment, woody debris, soil strength and crab fauna) and quantify the vegetation at different stages of successional development at three regions of the Shark River.

The objective of **Chapter III** was to determine how survival (mortality), growth, and recruitment (both as density and specific rates) varied across three successional stages of mangrove forest development (newly initiated lightning gaps, closing gaps, and intact forest) for the four dominate life phases (propagules, seedlings, saplings, and adult) of the three mangrove species (*Avicennia germinans, Laguncularia racemosa, Rhizophora mangle)*. In this way I was able to follow change in density of stems but also change in population structure at these different successional stages as gaps progress to closed canopy condition.

Chapter IV determines the impact of lightning strike disturbance on the soil elevation. I believed that this loss in soil surface elevation in a peat-dominated substrate might be a result of root death of lightning killed trees. Root mortality may lead to a decrease in the cohesiveness of the soil allowing the soil surface to erode, resulting in a decline in surface elevation. Additionally root mortality may lead to a collapse or subsidence of the peat layer, which would also result in a decline of the soil surface elevation. I determined the impact of lightning disturbance by monitoring soil elevation of both the shallow soil zone and the entire soil profile and measured amount of live and dead roots, soil strength (bulk density, torsion, and compaction) and accretion.

To understand the changes in soil elevation I needed to understand how hydrology affects the soil elevation pattern. It is possible to partition the change in soil elevation into its component processes of surface accretion, and subsurface expansion or compaction using the surface elevation table – marker horizon approach. In **Chapter V**, I studied the soil elevation dynamics in the lower Shark River drainage that extends over the entire soil profile and distinguishes between three depths within the soil profile; the 0-0.35 m, 0-4 m, and 0-6 m. My objective was to investigate the relationship among changes in soil surface elevation and changes in the hydrological parameters of river stage and groundwater piezometric head pressure at the site over the three depths. Additionally, I wanted to determine the relative contribution to soil elevation by each of the four components of the soil profile: surface (i.e., accretion), shallow zone (active root zone; 0 – 0.35 m), middle zone (0.35 – 4 m), and bottom zone (4 – 6 m).

Chapter VI provides an overall synthesis of the dissertation, in which the lightning successional process is described as well as changes in the life stage parameters. Finally, I discuss the role proposed Everglades hydrological restoration may play on the gap successional process.

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Chapter II

Succession of lightning-initiated canopy gaps in a Neo-subtropical mangrove forest.

Abstract

Lightning strikes are a important disturbance mechanism in the mangrove forest of Everglades National Park. I studied the successional dynamics of lightning-initiated gaps to determine their influence on mangrove forest stand structure and community dynamics. I determined the environmental characteristics of gap size, gap shape, light environment, soil bulk density, soil torsion, soil compaction, and fiddler crab (*Uca thayeri*) abundance. I additionally determined the vegetative composition in a chronosequence of gap stages (new, recruiting, and growing gaps, closed canopy intact forest). Canopy opening size averaged 202 ± 16 m^2 (± 1SE) and expanded gap size averaged 289 ± 20 m^2 (± 1SE) (*sensu* Runkle). As gaps filled with saplings, light transmittance at seedling height (1.3 m) decreased exponentially. Gaps had greater fine woody debris but less coarse woody debris than the surrounding forest. Soil torsion and soil compaction were lower in the gaps than the forest. The abundance of fiddler crab burrows decreased with distance upstream from the Gulf of Mexico, and large and medium burrow abundance increased linearly with total seedling abundance. A distinct two-cohort recruitment pattern was evident in the seedling/sapling surveys, suggesting a partitioning of the succession between individuals present pre-lightning strike and individuals recruited post-strike. High densities of *Rhizophora mangle* imply that lightning strike disturbances in these mangroves

favors their recruitment and does not favor *Avicennia germinans* and *Laguncularia racemosa*. However, average *A. germinans* seedling height was found to increase in later gap stages, suggesting an increase in the transition probability from seedling to sapling stage, perhaps related to gap successional development. This study does not support *L. racemosa* pioneering status in the mangrove forest as has been suggested in the literature. Overall, vegetative dynamics in lightning-initiated canopy gaps indicate that this disturbance may maintain South Florida mangroves in a cyclical or arrested successional state of development.

Introduction

Florida has one of the highest levels of cloud to ground lightning strikes in the United States (Changnon 1989). Lightning gaps are common in the mangrove forest due to the high frequency of strikes (7 to 9 flashes km^{-2} yr^{-1}, Huffines and Orville 1999). Lightning strikes influence all the major ecosystems of South Florida (Craighead 1971), and in the mangroves are readily apparent as circular gaps. The regenerative processes within these lightning-initiated gaps potentially drive mangrove forest diversity and structure in South Florida. Chapman (1976) suggested the idea of “cyclical succession” with mangrove forest oscillating between stages of development due to physical disturbances. Lugo (1980) argued for the “arrested succession” of mangroves due to physical disturbances such as hurricanes, winds, waves, fire, etc. Finally, Duke (2001) hypothesized that recruitment within small canopy gaps can prevent mangroves from reaching a senescence stage. The conditions within these lightning gaps may facilitate recruitment of certain species at the expense of others.

Lightning gaps are a common disturbance in mangroves throughout the world, including Papua New Guinea (Paijmans and Rollet 1977), Panama (Smith 1992, Sousa and Mitchell 1999), Dominican Republic (Sherman et al. 2000), as well as those in Florida, Untied States of America (Odum et al. 1982; Smith et al. 1994). Lightning strikes within the mangrove canopy create a relatively circular to elliptical clearing from the top to the bottom of the forest canopy (Duke 2001, Sherman 2000). These strikes kill several trees, instead of just one or two as is often seen in upland terrestrial forests (Anderson 1966). The mechanism by which lightning strikes kill multiple trees is not well understood, but it occurs in many ecosystems (Peace 1940, Anderson 1964, Brunig 1964, 1972, Paijmans and Rollet 1977, Magnusson et al. 1996, Sherman et al. 2000, Duke 2001).

Mangrove forests worldwide are also noted for a sparse understory and few sapling-size individuals (Janzen 1985, Corlett 1986, Lugo 1986, Tomlinson 1986). Observations of numerous small gaps and a meager understory within closed canopy forest have inspired investigations to determine the role gaps play in mangrove community structure and diversity. The few studies of naturally occurring small-scale mangrove canopy gaps provide conflicting results. Two studies found no difference in the relative species composition between gaps and the surrounding forest (Clarke and Kerrigan 2000, Feller and Mckee 1999). Two other studies found preferential facilitation of specific species saplings (*Rhizophora mangle*, *Avicennia marina*) in the gaps as opposed to the surrounding forest (Sherman 2000, Smith 1987a). Such conflicting results are perhaps understandable because differing types of disturbance in the mangrove ecosystem change physical and biotic factors and their interactions in a complex manner.

Duke (2001) observed that the dead tree trunks in the mangrove canopy gaps comprised of multiple stems (lightning mortality) remain standing for years. This may prolong the disturbance period, as these trunks rain down on the recruiting individuals. In mangroves, as well as in other forest types, woody debris is important as a prolonged nutrient source and sink (Harmon and Hua 1991, Romero et al. 2005). It can promote sedimentation (Krauss et al. 2003), and has been implicated in seedling growth (Allen et al. 2000, Clark and Clark 2001). Mangrove canopy gaps have been found to alter several physical factors and processes: humidity, evapotranspiration, light levels, and soil properties (salinity, temperatures, and nutrients) (Smith 1987a, Smith 1992). These changes may lead to modifications in the crab community (Osborne and Smith 1990, Smith 1987b). Crabs play a key role in these ecosystems; their burrows increase soil aeration, reduce sulfides and ammonium, and increase mangrove sapling productivity (Smith et al. 1991). Both fiddler and grapsid crab (Ocypodidae and Grapsidae) burrow density in turn has been associated with soil physical composition (Frusher et al. 1994, Mouton and Felder 1996). Mangrove forest structure and productivity have also been found to influence fiddler crab size (Colpo and Negreiros-Fransozo 2004). Thus the relationship between crab and mangrove population structure is a complex feedback that will likely change with gap development. To address the role that lightning gaps play in mangrove community structure and composition and to understand the underlying basis for that role, detailed studies of lightning gap forest composition and structural changes through time along with assessments of the physical and biological interactions are needed.

The purpose of this study was to provide a quantitative understanding of the dynamics of lightning-initiated gaps as they progress towards closed canopy condition in the South Florida mangrove ecosystem. I accomplished this by comparing gaps at three stages of development among themselves and with surrounding intact forest. The two main objectives were to assess environmental characteristics and quantify the vegetation and crab fauna at different stages of successional development. Specifically, I accomplished this by determining (1) the gap size, shape, and light conditions of lightning-initiated canopy gaps; (2) the amount of woody debris and soil strength; (3) the relative fiddler crab burrow abundance and relative abundance of trees at each life stage; (4) species specific density differences at each life stages. Additionally, at this forest there is a strong influence of river position (a proxy for salinity), upstream vs. downstream relative to the Gulf of Mexico on the mangrove community dynamics. From other research at this forest it has been found that tree height, soil nutrients, soil pore water, woody debris, decomposition, and species composition vary along the Shark River (Chen and Twilley 1998, Chen and Twilley 1999, Krauss et al 2005, Romero et al. 2005). To take this into account I studied gaps at three locations along the Shark River drainage.

Methods

Study area

My study examined the mangroves on the southwest coast of Florida, in Everglades National Park, (25ºN - 26ºN). This area encompasses approximately 60,000 ha of mangrove forest (Fig.1). These mangroves form a continuous band along the coast varying in width from 0.1 to 15 km (Smith et al. 1994). Tree height generally declines with distance from the coast towards the freshwater marshes (Chen & Twilley 1999). The climate is subtropical with an average annual maximum temperature above 27 °C. Precipitation has a distinct dry and wet season, and it varied from 86 cm to 224 cm over a 10-year period (Duever 1994). Tidal amplitude fluctuates from 10 to 60 cm. Three mangrove species, *Rhizophora mangle* L. (red mangrove), *Laguncularia racemosa* (L.) Gaertn. (white mangrove), and *Avicennia germinans* (L.) Stearn (black mangrove), grow in this area, varying from heterogeneous mixed stands to single species dominated forests. Hurricane disturbance is common in this region, with catastrophic hurricanes occurring approximately every thirty years (Doyle 1997). The 1935 “Labor Day” Hurricane, Hurricane Donna (1960) and Hurricane Andrew (1992) all strongly impacted the Everglades region.

Gap definition

Gaps have been defined in several different ways. In this study, I follow the definition set forth by Runkle (1982) for canopy and expanded gap area. Canopy gap area is the area directly under the canopy opening. The expanded gap area includes the area directly under the canopy opening and the area out to the base of canopy trees bordering the gap. Expanded gap area can be measured with more precision in the field and removes some of the ambiguity of defining the edge of the surrounding forest canopy (Meer 1995). The expanded gap definition is particularly useful when evaluating the indirect effect of gaps on seedling and sapling dynamics, especially when there is interest on the edge effect (Meer 1995).

Site Selection and sampling design

To determine gap size and shape, 75 lighting-initiated gaps were haphazardly located by boat and by helicopter surveys in the lower Shark River region, Whitewater Bay, and Coot Bay area from 1999 to 2004. To assess the light environment, I acquired hemispherical photographs in the winter of 2004 at 29 locations, of which 20 were gaps. These gaps were a subset of the above 75 gaps. In 2004, at 52 sites of which 39 were lightning gaps, I determined the average canopy height by randomly measuring six dominant canopy trees. At all 39-gap locations I determined the average sapling canopy height by measuring the height of six dominant saplings. I defined relative gap fullness (RGF) as the ratio (reported as %) of the canopy height of colonizing saplings within the gap to the height of the surrounding intact forest canopy.

To determine the environmental successional characteristics (woody debris, soil strength and crab burrow abundance) and the vegetative successional dynamics of lightning-initiated gaps in the mangrove ecosystem, I studied a second subset of the 75 gaps. These gaps (n=31) were located in three regions along the Shark River in order to span a known salinity and nutrient gradient (Chen and Twilley 1998, 1999; Table 1). This sampling was conducted from 2002 to 2004. Additionally, these gaps were chosen to represent a time series of succession from new gap to closed forest. The gaps were grouped into three ages: (1) new gaps, sites that varied in age from a recent lightning strike (sometimes witnessed in the field) up to one year old; (2) recruiting gaps, approximately five years in age that contained a noticeable layer of seedlings and; (3) growing gaps, estimated to be approximately 10 yrs old that had a very dense sapling layer. These categories correspond to the following stages within Duke's (2000) small gap mangrove conceptual model: gap initiation and gap opening combined, gap recruitment, and gap filling, respectively. These categories were assigned based on a set of gaps of known approximate age (pers. obs. K. Whelan). To compare the community attributes of the lightning-initiated gaps with the surrounding intact forest, I established 9 intact forest sites (Table 1). In this paper I define comparisons of "forest stage" to include new, recruiting and growing gaps plus intact forest locations where comparison among "gap phase" only refers to new, recruiting and growing gaps.

For the 31 gaps and 9 forest locations, all possible efforts were made to find groupings of a time series of gaps within a relatively small area. Thus, at the majority of locations, groups were comprised of one new gap, one recruiting gap, one growing gap and one intact forest location in close proximity, and for all group locations, all gaps of the time series were within 300 m of each other.

Gap environmental characteristics

Size and shape of lightning gaps

For each of the 75 gaps, I measured the major and minor axis (perpendicular to the major axis) along with the direction of the major axis. I used the formula for an ellipse (Area = $(\pi)(\text{length}_{(\text{major axis})}/2)^{*}(\text{length}_{(\text{minor axis})}/2)$) to determine the area of the gap. For each gap I calculated the eccentricity to determine if the gap was circular or elliptical. Eccentricity was calculated as the $(\text{length}_{(\text{major axis})})/(\text{length}_{(\text{minor axis})})$; for a circle the value is 1 (Battles and Fahey 1996).

Gap and forest light environments

I used hemispherical photography to estimate canopy openness, light transmittance of Photosynthetically Active Radiation (PAR) (as percent transmittance of total, direct and diffuse PAR) and leaf area index (LAI) in the intact mangrove forest (Mitchell and Whitmore 2001). Photographs were taken in the center of the site (gap) with a Coolpix 990 digital camera with a Nikon FC-E8 0.21x Fisheye converter lens (Nikon, Inc., www.nikonusa.com). All photographs were taken from a tripod, at 1.4 m height, under uniform gray cloudy skies. Photographic analysis was performed with Gap Light Analyzer (GLA) software version 2.2 (Fazer et al. 1999). The same individual analyzed all photos. The image threshold (set by the used in GLA) was independently set three times per picture and the mean value was used for analysis.

Woody Debris

I surveyed the mass of fine and coarse woody debris in the gaps and the surrounding intact forest. I using a line-intercept methodology (Van Wagner 1968, Allen et al. 2000, Krauss et al. 2005). At each site I established two 15 m transects parallel to each other and parallel to the major axis direction of the gap or in a random direction at intact forest sites. Additionally, at each site I established two transects in the immediate surrounding forest approximately 30 m from the edge of the gap (transects on opposites sides of the gap and in the same direction as the transects established within the gap). All coarse wood debris (≥7.5 cm diameter) intercepted by the transect was measured for diameter and assigned to a decomposition status (sound, intermediate, or rotten). Fine woody debris (1-7.5 cm) was surveyed in a 3 m subsection (3 to 6 m or 9 to 12 m) of the 15 m transect. A further 1.5 m sub-section of the 3 m sub-section (3 to 4.5 m or 9 to 10.5 m) was surveyed for fine woody debris <1 cm. Fine woody debris was grouped into three diameter size classes (<1, 1-2.5 and 2.5-7.5 cm). The volume of woody debris was determined in each size class using the equation, $v = \pi^2 \Sigma d^2 / 8L$, where v is the volume (m^3), d is the diameter of the piece (m) and L is the length of the sampling transect (m) (Van Wagner 1968). Calculation of wood mass from wood volume was accomplished using the conversion factors of 0.5 tons m^{-3} for fine woody debris, 0.5, 0.35 and 0.20 tons m^{-3} for sound, intermediate, and rotten wood respectively (Robertson and Daniel 1989).

Soil bulk density, torsion and compaction

I sampled soil bulk density, soil torsion, and soil compaction at all treatment sites. Cores were taken to determine bulk density. Core locations were haphazardly located within a six-meter radius of the center of the gap or forest location. At each location, for each sampling event I took three soil bulk density cores. Bulk density cores were extracted with a 140 cc syringe (3.7 cm diameter) with the end removed and sharpened. Due to compaction of peat soils, the hole depth (resulting from core removal) was measured three times and averaged (values ranged from 7 to 13 cm). Soil samples were oven dried at 50° C for 7 days. At each bulk density core collection location I took three paired samples of soil torsion and compaction. Maximum soil surface shear strength was sampled under field-saturated conditions with the Torsional Vane Shear Tester with the 2.5 kg cm^{-2} vane adapter (Forestry Suppliers, Inc; Jackson MS). I used a pocket penetrometer with the 2.5 cm adapter foot (Forestry Suppliers, Inc, Jackson MS) to sample soil compaction in these peat soils. Additionally, at every site I repeated the above procedures to collect three samples from the immediate surrounding intact forest. These three forest samples were haphazardly located at equal spacing surrounding the site. Two hundred forty bulk density samples and 720 surface soil torsion and soil compaction values were averaged to 40 site values of which nine were intact-forest sites and 31 were gaps of varying age. At all locations, samples were averaged for one in gap value and one surrounding forest value.

Crabs

I investigated mangrove fiddler crab [*Uca thayeri* Rathbun (Ocypodidae)] population structure by surveying the abundance and size of fiddler crab burrows. Burrow size has been found to reflect resident fiddler crab size (Mouton and Felder 1996, Brietfuss 2004). Therefore, I used a three-size categorization for the burrow diameters (small <1.4 cm, medium 1.4-2.2 cm, large > 2.2 cm, size gauges used during field data collection) to estimate relative abundance of fiddler crab population size class structure. All burrows present in eight 1 m^2 plots were quantified per site except for one location in which only four 1 m^2 was censused (Three locations did not have crabs censused). Each 1 m^2 plot was subdivided into four 0.25 m^2 plots to aid in counting accuracy. Independent observers were cross-calibrated in initial plots to standardize detection. I censused crab burrows at 37 sites (28 gaps and 9 forest sites) for a total of 292 m^2 of which 220 m^2 were in gaps and 72 m^2 were in intact forest sites.

Vegetation composition

A circular plot (radius six or eight m) was established in the center of each gap (site). The specific plot size was chosen to confine sampling within the canopy gap area. All stems were identified to species and a physical condition status was assigned. I used the size class definition of Koch (1997) and Chen and Twilley (1998) to ensure comparability of my work with previous studies. Adults were defined as all stems greater than 1.4 m in height and ≥ 4 cm in diameter at breast height (dbh). Saplings were defined as all stems > 1.4 m and

< 4 cm in dbh. Seedlings were defined as height > 0.3 m to < 1.4 m. Propagules were established (rooted, i.e. not in a dispersal phase) up to 0.3 m in height. I used the species-specific allometric formulas of Smith and Whelan (in review) to convert dbh to living biomass. Saplings, seedlings, and propagules were counted in four 4 m plots, nested within the circular plot.

Data analysis

Normality plots were used to assess normality for parametric tests. I used half normality probability plots to assess normality for the linear regressions. Count data was $\sqrt{x+3/8}$ transformed or rank-transformed in order to meet normality assumptions. Non-parametric tests were used when the normality assumption could not be meet. I used the Kolmogorov-Smirnov test to determine differences in frequency distributions of gap size and shape metrics. The Wilcoxon matched paired test was used to determine difference in light conditions due to gap stage. Linear regression was used to determine relationship between gap characteristics and light conditions. A minimum sapling height within the gap of 0.5 m was required for inclusion in the investigation of relationship between RGF and transmittance of PAR.

I used a one-way Analysis of Variance (ANOVA) to determine if fine, coarse, or total woody debris volume (or mass) differed by river location using averages of the surrounding forest transects at each site (n = 39). I used a Wilcoxon matched paired test to test for differences between gaps and surrounding forest volume and mass of fine, coarse and total woody debris (n=30). To determine if woody debris differed by forest stage, I calculated the difference between site and the surrounding intact forest (d = site value - surrounding forest) and used a Kruskal-Wallis non-parametric ANOVA to evaluate differences in d. A post-hoc comparison test was run on the rank values at an $\alpha = 0.05$.

I used a two-way ANOVA to determine if river location or forest stage was different for the surrounding forest soil samples taken at each site (n = 40). I used a paired t-test to determine differences between gaps and surrounding forest samples (n=31). To determine the forest stage in which difference in soil cohesiveness was greatest when compared to the paired surrounding forest sample, I calculated the difference (d_1 = surrounding forest – site value). Kruskal-Wallis non-parametric ANOVA was used to test for differences in d_1. A post-hoc comparison test was performed on the rank values at an $\alpha = 0.05$.

I used a Multivariate Analysis of Variance (MANOVA) to analyze differences in crab burrow abundance. The main factors were forest stage (new, recruiting, growing, intact forest) and river position (downstream, mid-stream, and upstream). I nested plots (n=8 per site) within site. With the MANOVA I was able to investigate changes in crab burrow abundance by size class without increasing the likelihood of a Type I error and accounted for correlation among the multiple variables (abundance of small burrows and medium burrows were slightly correlated r = 0.48, Zar 1999).

Abundance of stems within vegetative size classes (count data) was standardized to 500 m^2 to ensure comparability of my work with a previous gap study and to be at a relative scale similar to the actual size of area sampled (Chen and Twilley 1998). This count data was $\sqrt{x+3/8}$ transformed or rank-transformed followed with a parametric two-way ANOVA (Quinn and Keough 2002, Zar 1999).

All analyses were performed using STATISTICA 5.0 (Statsoft, Inc., 1996) and Statistix for windows (96 Analytical Software, Inc). Unless otherwise noted, I used Tukey's Honestly Significant Difference test for unequal sample sizes for posthoc comparison.

Results

Gap environmental characteristics

Size and shape of lightning gaps

In the 75 lightning-formed canopy gaps, multiple trees, rather than one or two, were killed. In most instances, some saplings and seedlings survived the lightning strike. Canopy gap size (*sensu* Runkle, 1982) ranged from 38 to 640 m^2 with an average size of 202 ± 16 m^2 (± 1SE). Length of the major axis ranged from 7.5 to 33.4 m and averaged 17.5 m. The expanded gap size (*sensu* Runkle) for the 75 gaps ranged from 70 to 940 m^2 and averaged 289 ± 20 m^2 (± 1SE). The length of the major axis ranged from 10.0 to 36.4 m and averaged 20.9 m. The frequency distributions of the canopy gap and expanded gap area were different (Kolmogorov-Smirnov D = -0.29 $p<0.01$ Fig. 2). I compared the frequency distribution of the subset of gaps chosen for further study (n=31) to that of the other 44 gaps that comprised the entire 75 gaps studied. The frequency distribution of the two groups were not different (Kolmogorov-Smirnov D = -0.08 n.s., Fig. 3). Therefore, the focal subset of gaps was representative of the range of gaps from this area.

Gaps were circular to elliptical in shape. Average eccentricity using the canopy gap definition was 1.36 ± 0.35 and 1.31 ± 0.33 for the expanded gap definition. A few gaps were extremely elongated in shape (2.50) instead of the more common circular shape (1.10). There was no difference in the frequency distribution of the shapes of the gap using either gap definition (Kolmogorov-Smirnov D = -0.03 n.s. Fig. 4). There was a linear relationship between average canopy height and expanded gap area for all gaps surveyed (R^2 = 0.13, p = 0.001, n = 73, two gaps missing surrounding tree height data) and the 51 gaps along the Shark River (R^2 = 0.11, p = 0.02), this variation explained by average canopy height increased when I limited the gaps to the lower Shark River (R^2 = 0.35, p = 0.01, n = 22).

Gap and forest light environments

Analysis of hemispherical photographs showed that new lightning gaps had greater canopy openness and transmitted significantly more total, direct and diffuse PAR than the surrounding intact forest (Z = 2.8, 2.7, 2.8, 2.8, respectively, for all p < .01, n= 10, Table 2). Recruiting gaps had the greatest percent canopy openness and percent transmittance of total PAR. However, this difference was not significant because of the low sample size (n=4). Intact forest and growing gaps had similar light environments {canopy openness, Leaf Area Index, percent transmittance (total, direct and diffuse PAR)(Wilcoxon matched paired test n.s., Table 2}.

There was a linear relationship (adj. $R^2 = 0.67$) between gap size and percent canopy openness for the new gaps (Fig. 5). As the size of the gap increased the amount of openness increased. A similar trend (adj. $R^2 = 0.50$, $F = 10.2$, $p<0.02$) was found for percent transmittance of PAR and size of new gaps. As the gaps filled with saplings the transmittance of PAR at 1.4 m decreased exponentially (adj. $R^2 = 0.65$, Fig. 6). Gaps with a well-developed sapling canopy, RGF > 65%, had transmittance levels of 12 %, which was similar to that of the intact forest.

Woody Debris

Overall, the forest floor contained, on average, 33.9 m^3 ha^{-1} of woody debris that had an average mass of 12.4 tons ha^{-1} (only surrounding forest transects). Most of the woody debris was coarse woody debris (64%), but the woody debris mass was approximately equally divided between fine and coarse (49% and 51%, respectively). For the intact forest transects (n=39) coarse wood debris volume and mass decreased towards upstream locations. There was no other river location trend in fine or total wood debris volume or mass (Table 3).

Gaps on average had greater fine and total woody debris volume than the surrounding forest (Table 4). However, gaps had less coarse woody debris volume than the surrounding forest. Mass of woody debris showed a similar trend. The differences in total woody debris volume and mass were a result of the fine woody debris component, which was twice as large in gaps as in the surrounding forest (Table 4). Recruiting gaps had more fine woody debris material than the intact forest sites by both volume and mass (Table 5). No other significant differences in fine woody debris volume and mass among the gap ages were found. Additionally, there was no difference between the intact forest sites and the new and growing gaps in fine woody debris volume or mass (Table 5). Both coarse and total woody debris volume did not differ among forest stages a similar result was found for mass (Table 5).

Soil bulk density, torsion and compaction

Comparing the surrounding forest samples at all sites, I found a river position effect on bulk density, maximum soil surface shear strength and compaction ($F_{(2,28)} = 13.5$, $p < 0.001$, $F_{(2,28)} = 8.9$, $p < 0.001$, $F_{(2,28)} = 10.0$, $p < 0.001$, Table 6). Bulk density was greatest at the downstream location, probably a result of marine deposits in the samples. The soil surface torsion and soil surface compaction were greatest at the upstream location. Torsion was lowest midstream (Table 6). Soil compaction did not differ between downstream and midstream positions (Table 6). The surrounding forest samples at a given river position were similar. In the pairwise comparison between gaps and the surrounding forest (n=31), there was no difference in bulk density (Table 7). However, soil torsion and soil compaction were lower in the gaps than the forest (Table 7). I found that torsion and compaction were lowest in recruiting gaps followed by growing gaps, new gaps, and intact forest when expressed as the difference from the immediate surrounding forest (Table 8).

Crabs

Small burrows comprised 53.9% (10,116), medium burrows 27.6% (5,168) and large burrows 18.5% (3,471) of the total count of crab burrows (18,755). The mean density of total crab burrows was 64.2 per m^2, with the densities varying from 6 to 183 burrows m^{-2} (Table 9). Downstream locations had the most burrows (101.2 burrows m^{-2}), followed by the mid-stream (53.8 burrows m^{-2}), then upstream (36.2 burrows m^{-2}). This reduction in burrow abundance towards the upstream location occurred in all three-burrow size classes (Rao's $R_{(6, 388)} = 45.6$, $p<0.001$). Medium burrows declined the most in the transition from downstream to the upstream position. The decline in small burrows occurred mostly between the downstream and midstream locations. The large burrows were most abundant in the midstream location, followed by the downstream, and the upstream location (Table 9).

The abundance of crab burrows also changed depending on forest stage (Rao's $R_{(9, 472)} = 6.0$, $p<0.001$). Summed across the three river positions but within each burrow size class, I found the largest change in burrow abundance was a reduction of small burrows in growing gaps (Table 9). Large burrow abundance was lowest in recruiting gaps when summed across the river positions (Table 9).

There was a strong interaction effect between river location and forest stage on burrow density (Rao's R $_{(18,\ 549)}$ = 2.1, $p<0.004$, Fig. 7). At the downstream river location the number of small crab burrows was affected by forest stage. Growing gaps (37.3 burrows m^{-2}) had fewer small burrows than recruiting gaps (61.8 burrows m^{-2}); no other differences in the small burrows were found among the forest stage (Fig. 7, Table 9). At the downstream location, the number of large burrows in the growing gaps (8.5 burrows m^{-2}) and the intact forest (4.4 burrows m^{-2}) differed significantly. At the midstream location the recruiting gaps (4.2 burrows m^{-2}) had significantly fewer large burrows than the new (8.7 burrows m^{-2}) and the growing sites (9.2 burrows m^{-2}, Fig. 7, Table 9). There were no differences within burrow size classes at the upstream location (Fig. 7, Table 9).

Vegetation composition

Overall, the distribution of density and biomass of tree size classes differed across gap age and intact forest when summed for all species (Fig. 8, Table 10, 11, 13). The intact forest had greater adult density compared to gaps of all stages (Table 10,13). The number of saplings was similar in the forest and the new gaps, and both had substantially less than recruiting and growing gaps (Table 10, 13). Sapling density was greatest in the growing gaps and was significantly greater than that in recruiting gaps. The interaction of river position and forest stage explained a 20 % of variation in sapling density (Table 13). This interaction was clearly evident in the sapling density at the growing gaps (Table 10). Growing gaps at midstream region had the greatest sapling density followed by the upstream location, but not significantly so. The downstream growing gaps had the fewest number of saplings among the growing gaps. At the downstream location, recruiting gaps had the most saplings compared to growing and new gaps. At the midstream and upstream locations, the highest density was in the growing gaps, followed by recruiting and new gaps (Table 10, 13).

Seedling and propagule density varied with river position with the lowest density of seedlings and propagules occurring at the downstream location (Table 11). Gaps had more seedlings than the forest (Table 12, 13). Although recruiting gaps had the greatest number of seedlings, but not significantly more than new or growing gaps (Table 12, 13).

Adult and sapling biomass combined was consistently greater in the forest than in all of the gap stages (Table 11, 14). This difference was due to the high biomass of living adult trees. Recruiting and growing gaps had greater sapling biomass compared to new gaps and the intact forest (436, 905, 131, and 132 kg 500 m^{-2}, respectively, Table 14). Basal area increment for nine intact forest varied from 29 to 50 m^2 hec $^{-1}$. The mean (± 1 se) basal area increment was 31.09 ± 1.95, 40.77 ± 4.58, and 30.95 ± 3.92 from upstream to the downstream river location, respectively.

Species-specific density and biomass

I found that 12 to 41 canopy trees were killed (mean 26.3) in the 10 new lightning gaps. The immediate adult and sapling biomass killed by lightning at the ten new gaps varied from 26% to 95%, with a mean of 67% of the live stems pre-lightning strike. The mortality was not species-specific, with mean mortality of 61% of *A. germinans*, 76% of *L. racemosa*, and 68% *R. mangle* ($F_{2,23} = 0.6$ n.s.). The mean adult and sapling biomass damaged by lightning strikes was 22% and varied from 4% to 58%. The mean total biomass impacted by the lightning strike was 90% and varied from 75% to 99% (Table 12).

Among forest stage the results differed for the three species that comprised this forest. For *A. germinans* there was no difference among the forest stage for adult, sapling, seedling, and propagule density (Fig. 9, Table 10, 11, 13). *Avicennia germinans* biomass was lowest in the new gaps but not different in recruiting gaps, growing gaps, and intact forest sites. Mean seedling height of *A. germinans* was greatest in growing gaps compared to the other forest stages (Table 15, Fig. 10). Adult density of *A. germinans* was greater at the downstream location than the other two river positions (Table 10). *A. germinans* adult and sapling biomass were not affected by river position (Table 12, 14).

Biomass of *L. racemosa* was greater at the midstream and downstream locations compared to the upstream sites (Table 12, 14). As might be expected the adult abundance of *L. racemosa* was greater in the forest compared to gaps (Fig. 9, Table 10), as was L*. racemosa* adult and sapling biomass (Table 12, 14).

The mean seedling height of *L. racemosa* was greatest in the forest compared to the gap sites (Table 15, Fig. 10). The abundance of *L. racemosa* propagules was lower at the downstream location compared to the midstream and upstream locations (Table 11, 13).

Rhizophora mangle accounted for a majority of the summed-across-species general findings (Fig. 9). Saplings and seedlings were more common in gaps than the forest. However, mean seedling height was not different across the gap stages and the forest (Table 15, Fig. 10). Sapling density was greatest in growing gaps followed by recruiting gaps, however, both were significantly different from new gaps and intact forest (Table 10, 11, 13). Adult abundance of *R. mangle* was greatest in the forest (Table 10). Biomass of *R. mangle* saplings and adults combined was greater in the forest compared to the gaps. Separately, *R. mangle* sapling biomass was greatest in recruiting and growing gaps; there was no difference between new gaps and the forest (Table 11, 14). River position did not affect *R. mangle* sapling biomass (Table 11, 14). Upstream *R. mangle* sapling biomass was greatest but not different from midstream locations; however, downstream locations had the lowest biomass (Table 11, 14). River position interacted with gap phase for sapling density (accounting for 21 % of the variance); sapling density downstream was greatest in recruiting gaps as opposed to growing gaps (Table 10, 13).

The frequency distribution of seedlings and saplings heights (binned into 10 cm height classes) differed by forest stage and by species (Fig. 11). New gaps and intact forest had a large number of very small seedlings and few individuals of the large size classes. In recruiting gaps, the distribution was shifted to the right, presumably due to growth of the seedlings and saplings as the site has aged. A distinct two-peak distribution was evident in growing gaps. One peak at approximately 1 meter was presumably due to primary growth of the seedlings and saplings that either existed at the site pre-disturbance or established at the site shortly after gap creation. A second peak centered at 0.4 m height appears to be a second wave of recruiting seedlings (Fig. 11). This two-peak pattern was evident and driven by *R. mangle*; as were the distributions for the new, recruiting, and intact forest stages. These distribution patterns were not evident for *L. racemosa*. There was an increased frequency of small seedlings in new gaps but this disappeared in the other forest stages (Fig. 11). *Avicennia germinans* distributions were similar to the general seedling and sapling height frequency distribution pattern; however, the distribution in growing gaps had a peak at 1.9 m and two smaller peaks at 1.2 and 0.8 m in height (Fig. 11).

Discussion

Characteristics of gap successional stages

The average expanded gap size of lightning-initiated gaps in the mangroves of Everglades National Park was smaller (289 m^2) than has been reported for lightning-initiated gaps in mangrove forest of the Dominican Republic (Sherman et. al. 2000, average expanded gap size of 724 m^2 (n=52), tree height 24-30m), Panama (Sousa and Mitchell 1999, gap size 601 m^2 (n=9)), and Papua

New Guinea (Paijmans and Rollet 1977, gap size 530 m^2 calculated from reported average diameter of 20-30m, tree height 35m), and for the cursory initial Everglades mangrove survey (Chen 1996, gap size 502 m^2 (n=1)). Gap area was also smaller compared to lightning-caused gaps in other forest types (average gap size 1861 m^2, n = 106 for the year 1947; 2671 m^2, n = 175, for the year 1961, *Shorea albida* forest, Sarawak, tree height 45 m, Brunig 1964, 520 m^2, n = 3, Tropical Rainforest in Amazonia, Brazil, Magnusson et al. 1996). The smaller size of the lightning gaps found in my study, may be related to the total canopy height. The canopy height in this mangrove forest is at maximum 20m, which is shorter than the canopy height reported in the other lighting gap studies (all >24 m, see above). Additionally, I found a linear relationship between gap size and surrounding canopy height, suggesting that tree height may partially explain the size of the gaps. The lightning gaps in this study had a similar elliptical shape (1.31 ± 0.33) to those reported in the Dominican Republic study (1.3 ± 0.04, Sherman et al. 2000).

I found that fine branches did not drop from the lightning-killed trees within the first year, and my results imply that it can take up to 5 years for these trees to drop to the forest floor (recruiting gap stage). Consequently, there was twice as much fine woody debris in the gaps compared to the surrounding forest, with the greatest amount in the recruiting gaps. Decomposition of small branches in the mangrove environment is slow, taking up to 2.5 years for a 50% reduction in the mass (Robertson and Daniel 1986). Presumably, the numerous seedlings and saplings of the recruiting and growing gaps added to the fine woody material pool preferentially, as their diameter precluded them from the coarse woody debris size class. A reduction in the coarse woody debris amounts in recruiting and growing gaps as compared to the forest can be accounted for by the reduced productivity of these locations due to large canopy tree mortality. Robertson and Daniel (1986) found that coarse woody debris amount was related to mangrove forest productivity. Coarse woody debris amounts have been associated with intensity of hurricane disturbance in this mangrove forest (Krauss et al. 2005). Krauss et al. (2005) suggested that at some stage of gap succession there should be an increase in coarse woody debris compared to the forest, but I did not observe this among the gaps in this study. Presumably the extended period of time associated with trunks toppling at the sites prevented rapid accumulation of coarse woody debris this is in contrast to the short period of intense trunk drop associated with Hurricane disturbance. Or the methodology I used to survey woody debris within the gaps may not have been able to detect this increase in coarse woody debris.

The slow toppling of the long-standing dead tree trunks may prolong the disturbance event. It is unclear how the falling of the tree trunks affects the survivorship of the saplings. However, we found that 15 % (362 of the 2450 live saplings) of the living saplings in recruiting and growing gaps had either been hit by debris, bent under debris, or had broken stems from debris. Additionally, I found that 8 % of all dead saplings in recruiting and growing gaps were due to either having been hit by debris, bent under debris, or had broken stems from debris. The adult size class of the three species that make up this mangrove forest has been found to have species specific response to breakage based on the ability of epicormic buds to resprout (Duke 2001, Baldwin 2001). Additionally, in terrestrial tropical forests, damage from falling debris has been found to substantially affect sapling growth (Clark and Clark 2001) and presumably survivorship. Taken together the falling of branches and tree trunks may affect long-term regeneration within these lightning gaps.

The soil surface strength (difference between gaps and surrounding forest) varied across the gap stages. The new gaps, growing gaps, and the forest soil strength were not different when compared to immediate surrounding forest. The recruiting gaps had weaker soils than the surrounding forest. In these peat soils much of the strength is a result of the live root constituent (Cahoon et al. 2003). As the roots of the lightning killed trees decompose, which has been found to be quite slow (Middleton and Mckee 2001), the soil torsion and compaction decreased until the site reaches the recruiting gap stage. A reduction in soil torsion was found post hurricane for a mangrove peat site in Honduras (Cahoon et al. 2003). The high density of seedlings and saplings (and presumably their roots) may explain the increased soil strength of the growing gaps.

Crab burrow abundance has been associated with plant cover, soil properties, and modifying hydrological infiltration rates (Mouton and Felder 1996, Hughes et al 1998). In this study, the fiddler crab burrow abundance was strongly affected by the position along the Shark River (presumably due to salinity). Overall, burrow abundance declined with distance upstream. This type of reduction in fiddler crab abundance with landward distance has been reported elsewhere (Mouton and Felder 1996). Soil metrics (bulk density or strength) and burrow abundance were not correlated, even though soil strength changed with gap successional stage. Frusher et al. (1994) found a correlation between soil parameters and crab abundance. The physical composition (% clay, sand, organic matter) of the soil material in their study changed between habitats. In this study, I did not sample constituent material. However, my field observations indicated the soil has composed primarily of peat with little variation within and between river positions. This was a similar finding that Cohen (1968) reported "superficial *R. mangle* peat with minimal marine carbonate inputs" for the Shark River region as a whole (cores 1 and 10). I would suggest that the physical composition of the soil did not vary greatly across the three river locations.

Differences in crab burrow abundance associated with forest stages were most evident at the downstream locations. At the downstream position, burrow abundance, medium and large burrows only, was linearly related to total seedling abundance (R^2=0.55). There was no relationship between small burrow abundance and seedlings. These differences may be explained by constant recruitment of the small fiddler crabs into all locations regardless of successional stage, and as the gap fills with seedlings, the site is more favorable to medium and large fiddler crabs. I would suggest that increased seedling abundance may lead to a more complex habitat and this may reduce risk of predation making the site more favorable to middle and large size fiddle crabs. Wilson (1989) found variation in crab predation depending on microhabitat within the mangroves of

South Florida. She found increased rates of predation on the sediment surface compared to mangrove roots. I suggest that increased seedling abundance may reduce fiddle crab predation by fishes feeding during high tidal infiltration events. Therefore these sites maybe favored by medium and large crabs to the detriment of the small crabs.

The effect of the crab burrows on mangrove sapling productivity was associated with the amount of surface area comprised of burrow openings (Smith et al. 1991), which presumably increases surface infiltration rates (Clarke and Hannon 1967). At the downstream locations, crab burrows comprised 1.5 % (mean) of the soil surface area and declined to 0.5 % at the upstream locations. Total tree trunk surface area (basal area of saplings and adults) ranged 0.3 to 0.5 % of the soil surface area. Crab burrow surface area was up to 5 times greater than tree trunk surface area for intact forest locations and up to 25 times greater in some of the new gaps sites, emphasizing the importance of burrow in mangrove ecosystem.

The majority (~ 85.0 %) of the crab burrow surface area was comprised of medium and large burrows at all river locations. In general, differences in relative abundance of burrow size class were greater when converted to the proportion of crab burrow surface area. Therefore, at the downstream location there was a positive linear relationship of increasing total burrow surface area with increasing seedling abundance (R^2=0.55). These findings suggest a complex interdependent relationship between fiddler crab abundance and the mangrove habitat. Other researchers have found this type of complex association (see review Lee 1999, Colpo and Negreiros-Fransozo 2004).

Compiling a conceptual model of lightning gap succession

Based on the results of this study, I suggest the following conceptual model of lightning gap succession from newly formed gaps through recruiting and growing gap successional stages. In newly formed lightning gaps; the trees completely defoliated within three months post-strike. However, the numerous fine branches persisted in the canopies of the new gaps. These fine branches affect the light environment in new gaps, with the canopy openness and transmittance levels higher than the intact forest but lower than the recruiting gaps. New gaps had more fine woody debris mass and volume than the surrounding forest, but had less than the recruiting gaps. The soil strength properties and fiddler crab burrow density did not differ from those of the forest for new gaps.

By the recruiting gap stage, fine branches had fallen to the ground; however, the majority of the dead trunks were still standing. The recruiting gaps had the most open canopies with the most transmittance (not statistically significant due to low sample size). These gaps had the greatest amount of fine woody debris compared to the other gaps and the forest. Recruiting gaps had the lowest soil strength. Small crab burrow density was highest in these gaps (only at the downstream location). The recruiting gaps had the greatest seedling density. The majority of the recruiting seedlings were comprised of *R. mangle*.

By the growing gap stage the dead trunks have started to fall. The canopy openness and transmittance in growing gaps were not greater than the intact forest, and the leaf area index was similar (Table 2). The amount of coarse woody debris in growing gaps was not different from the forest. At this stage the fine woody debris volume and mass were similar to the surrounding forest. Soil strength was not different from the forest. Small crab burrow density decreased and large crab burrow density increased (at the downstream river location). Sapling density was greatest at this stage. As saplings filled the gap from below, the light environment changed drastically. Consequently transmittance of PAR decreased exponentially in these gaps (Fig. 6). This led to a low light environment, with reduced likelihood of seedlings surviving to the sapling recruitment stage and saplings to recruiting to the adult stage. Of all saplings that were found dead in growing gaps 89 % were classified a mortality due to suppression. This categorization was assigned to dead saplings with no other obvious forms of mortality (characterized by: stems attached and intact, typically in low light environment, overtopped by other saplings, no evidence of insect damage).

Implications of lightning gaps on mangrove forest structure

I found that the saplings and seedlings in new gaps survived the lightning strike and that, most likely, the majority of the propagules censused (propagules in this study were defined as attached to the substrate) were present at the site before the strike. This judgment is based on the short time between the lightning strike and the census, and that there were no differences in sapling, seedling, and propagule densities between new gaps and intact forest. Here I am providing the first published evidence that in a mangrove forest a large amount of the non-canopy trees present before the lightning strike survive (Table 10, 11, 12). Similar observations have been reported in *Shorea albida* forest in Sarawak (Anderson 1964), mangroves in Papua New Guinea (Paijmans and Rollet 1977), and mangroves in Panama (Sousa, pers. comm. 2000).

These remaining seedlings and saplings are significant in the successional dynamics of this forest. The seedling and sapling height distributions suggest that there is a distinct two-cohort regeneration. The first cohort consists of the propagules and seedlings present at the site pre-strike and individuals recruiting very soon after the canopy is removed. The second group recruits into the site some number of years post strike (Fig. 11). The large mean height of *A. germinans* seedlings in the growing gaps suggests that in the long-term, gap dynamics may favor *A. germinans* seedlings to recruit into the sapling stage (Fig. 10). However, as the gaps develop, recruitment at the seedling stage for recruiting gaps and at the sapling stage for growing gaps was dominated by *R. mangle* (based on densities, Fig. 11). Curiously, L. racemosa characterized as the most pioneer-like of the three species was not an important factor in the gap successional stages.

The results from this study suggest that lightning strike disturbance in these mangroves favors *R. mangle* recruitment based on densities and does not favor *A. germinans* and *L. racemosa*. Seedling and sapling density of *R. mangle* was higher in gaps than in the closed forest. *R. mangle* domination in lightning gaps was also found in the one other mangrove lightning strike study; however, their findings were conditional on surrounding forest composition (Sherman et al. 2000). My research suggests that *R. mangle* recruitment into the sapling stages was favored by lightning disturbance. The results of these studies support the hypothesizes forwarded by Duke (2000) and others (Lugo 1980, Chapman 1976) that these small gap disturbances have the potential to stop mangrove forest from succeeding to a senescence state of development (“arrest succession”) which in this forest is one dominated by large *A. germinans* (Craighead 1971). However, the full implication of *A. germinans* enhanced seedling height development (Fig. 10 and 11) is not considered in this type of survey. An understanding of long-term recruitment and survivorship is needed to determine the role these gaps play in long-term stand development.

Ball (1980) argued that the breaks in the mangrove forest canopy in South Florida allowed species whose seedlings do not compete well in shade, such as *L. racemosa*, to become established as saplings, at least temporarily, within solid zones of *R. mangle*. The results from this study indicate there is not an increased recruitment of *L. racemosa* in lightning gaps with around one sapling per 170 m^2 for both the intact forest and the gaps. Additionally, the mean heights of L. racemosa seedlings are much lower in the gaps compared to the intact forest. This may suggest that the benefits of the increased light environment maybe counteracted by changes in other environmental characteristics (i.e. temperature, hydrology, etc.). In the intact forest there was one *A. germinans* sapling per 50 m^2 but values varied greatly from a mean of one sapling per 500 m^2 to one per 3 m^2 at the growing gaps at the midstream river position. This extreme value was due to one growing gap that was surrounded by a few large *A. germinans* able to produce numerous propagules for recruitment. Located at the edge of this gap was a 92 cm dbh *A. germinans,* a rare giant in this forest.

The present study is located in a region regularly impacted by hurricanes. Smith et al. (1994) observed that post hurricane survival of individuals growing in pre-existing canopy gaps was greater than for individuals growing in the surrounding closed canopy. These authors argued that preexisting gaps could provide an important seed source for re-colonization of forest after large-scale disturbances, such as hurricanes and typhoons. The results of my current study indicate that *R. mangle* would probably have an enhanced recruitment opportunity from the preexisting lightning gap post hurricane disturbance. The role these gaps play in maintaining diversity and community dynamics of the mangrove ecosystem needs to be further examined with long-term survivorship of individuals within the growing gap phase. As with other studies of gap dynamics, the major shortcoming of surveying gaps of different successional stages and using these results to project the final influence on forest structure lies in the inability to locate and adequately sample sites of former gaps that are covered by closed intact canopies. The saplings and young adults are still presumably in a state of extreme light and nutrient competition. In other words, when does the recovery from gap disturbance reach a point that closed canopy forest dynamics drive the structure and diversity? This can only be adequately determined with long-term census sampling.

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Table 1. Sample size of gaps investigated for successional characteristics.

River position	New	Recruiting	Growing	Intact Forest Sites	Total
Downstream	4	5	4	3	16
Midstream	3	3	3	3	12
Upstream	3	3	3	3	12

Table 2. Photosynthetic Active Radiation (PAR) light environments of lightning gaps. Percent canopy openness, Leaf area index, and Percent transmittance of total, direct, and diffuse PAR [mean (±1 SE)].

Stage	N	Canopy Openness	Leaf Area Index (LAI)	Total Light	Direct Light	Diffuse Light
New	10	16.1 (1.4)	--	29.9 (2.7)	32.7 (3.4)	27.1 (2.3)
Recruiting	4	17.4 (3.8)	--	32.8 (7.2)	37.1 (8.6)	28.4 (5.8)
Growing	6	9.4 (0.7)	2.9 (0.1)	16.9 (1.8)	18.5 (12.2)	15.4 (1.4)
Intact Forest	9	9.7 (0.6)	2.6 (0.1)	16.1 (1.0)	17.7 (6.0)	14.7 (0.7)

Table 3. Volume and mass of fine, coarse, and total woody debris for the three river locations using the surrounding forest (n = 39) average of the two transect values. One-way ANOVA log (+0.5) transformed data. I report the Mean (±1 SE). Mean values within a size class followed by similar letters were not significantly different at a α = 0.05. (Tukey's HSD for unequal samples sizes on transformed data).

Size class	Downstream (n=15)	Midstream (n=12)	Upstream (n=12)	$F_{(2,36)}$	p
		Volume (m^3 ha^{-1})			
Fine (≤ 7.5 cm)	11.26 (2.12)	12.32 (1.04)	13.45 (1.96)	1.69	n.s.
Coarse (>7.5 cm)	27.73 (6.62) a	22.62 (2.94) a	13.15 (1.57) b	5.02	0.01
Total	38.99 (6.97)	34.93 (3.73)	26.59 (2.19)	1.38	n.s.
		Mass (tons ha^{-1})			
Fine (≤ 7.5 cm)	5.63 (1.06)	6.16 (0.52)	6.72 (0.98)	1.69	n.s.
Coarse (>7.5 cm)	7.98 (1.38) a	6.69 (1.27) a	3.75 (0.46) b	7.03	0.002
Total	13.61 (1.78)	12.85 (1.68)	10.47 (1.07)	0.93	n.s.

Table 4. Volume and mass of fine coarse, and total woody debris in gaps compared to surrounding forest (n=30). Mean (±1 Std. Error) Wilcoxon matched pair test.

Parameter	Gap	Surrounding forest	T
		Volume (m^3 ha^{-1})	
Fine (≤ 7.5 cm)	24.68 (2.37)	12.48 (1.28)	68.0 $p < 0.001$
Coarse (>7.5 cm)	18.41 (2.05)	23.68 (3.50)	110.0 $p < 0.001$
Total	43.09 (3.29)	36.16 (3.81)	157.0 $p < 0.001$
		Mass (tons ha^{-1})	
Fine (≤ 7.5 cm)	12.34 (1.19)	6.24 (0.64)	68.0 $p < 0.001$
Coarse (>7.5 cm)	5.58 (0.70)	6.70 (0.89)	135.0 $p < 0.04$
Total	17.92 (1.46)	12.94 (1.14)	115.0 $p < 0.02$

Table 5. Mean difference between site values and surrounding forest for fine, coarse, and total woody debris by volume and by mass. Post-hoc test performed on ranks at $\alpha = 0.05$. (Difference = site value - surrounding forest). Positive values indicate more material within the gap (site) than the surrounding forest.

	Volume (m^3 hec^{-1})			Mass (tons hec^{-1})		
Forest stage	Fine (≤ 7.5 cm)	Coarse (>7.5 cm)	Total	Fine (≤ 7.5 cm)	Coarse (>7.5 cm)	Total
New (10)	13.8 ab	-2.0	11.8	6.9 ab	0.1	6.9
Recruiting (10)	20.2 a	-10.1	10.0	10.0 a	-2.7	7.4
Growing (10)	2.6 ab	-3.6	-1.0	1.3 ab	-0.7	0.6
Intact Forest (9)	-2.0b	-2.0	-4.3	-1.0 b	-0.9	-1.9
Kruskal Wallis	11.2	0.78	4.47	11.2	1.36	7.3
p-value	0.01	n.s.	n.s.	0.01	n.s.	0.05

Table 6. Bulk density, soil torsion, and soil compaction of the surrounding forest samples (n=40). Mean (±1 Std. Error) followed by similar letters were not different (Tukeys HSD for unequal samples sizes).

River position	Bulk density g cm^{-3}	Maximal torsional shear strength kg cm^{-2} X 10^{-3}	Soil compaction kg cm^{-2} X 10^{-2}
Downstream (16)	0.18 (0.01) a	5.6 (0.7) ab	10.1 (1.0) a
Midstream (12)	0.12 (0.01) b	3.9 (0.3) a	8.1 (0.9) a
Upstream (12)	0.13 (0.01) b	7.2 (0.4) b	13.6 (0.8) b

Table 7. Bulk density, soil torsion, and compaction in gaps compared to surrounding forest. Mean (±1 Std. Error)

Parameter	n	Gap	Surrounding forest	T
Bulk density g cm^{-3}	31	0.16 (0.01)	0.15 (0.01)	0.87 n.s.
Maximal torsional shear strength kg cm^{-2} X 10^{-3}	31	4.8 (0.4)	5.7 (0.4)	-4.21 $p < 0.001$
Soil compaction kg cm^{-2} X 10^{-2}	31	8.6 (0.7)	10.6 (0.8)	-4.15 $p < 0.001$

Table 8. Mean difference between surrounding forest and site values for bulk density, soil torsion, and soil compaction. Kruskal- Wallis non-parametric ANOVA (kw = 6.2 ns, kw = 8.0 $p < 0.05$, kw = 7.7 $p < 0.05$, Respectively) Post-hoc test performed on ranks at $\alpha = 0.05$. (Difference = surrounding forest – site value).

Stage (n)	Difference in Bulk Density X 10^{-3}	Difference in Soil Torsion X 10^{-4}	Difference in Soil Compaction X 10^{-2}
New (10)	-6.5	4.7 ab	1.3 ab
Recruiting (11)	1.7	13.5 a	2.9 a
Growing (10)	-12.1	8.7 ab	1.7 ab
Intact Forest (9)	-1.9	0.0 b	0.1 b

Table 9. Number of plots counted for crab burrows (each plot was 1 m^2). Mean abundance (±1 Std. Error) of crab burrow by size class, forest stage, and river location.

1) Forest stage [Mean abundance by burrow size class across river position followed by similar superscript number was not different].

2) River position [Mean abundance by burrow size class across forest stage followed by similar letter was not different].

3) Forest stage by river location interaction [Mean abundance by burrow size class within a river position across forest stage followed by similar symbols were not different]

All post-hoc comparison test were Tukey's HSD for unequal samples sizes.

Forest stage	Downstream	Mid Stream	Upstream	Total
New	32	24	24	80
Small	56.1 (5.2) ΦΩ	29.0 (3.3)	29.6 (3.0)	40.0 (2.8) ^{1}
Medium	42.5 (3.4)	25.5 (1.8)	15.3 (1.3)	29.2 (2.0) ^{1}
Large	6.3 (0.7) ăħ	8.7 (0.8) á	5.6 (0.7)	6.8 (0.4) ^{1}
Total	104.8 (7.1)	63.2 (4.8)	50.5 (3.2)	76.0 (4.3)
Recruiting	20	24	24	68
Small	61.8 (6.6) Φ	23.1 (3.6)	16.4 (2.1)	32.1 (3.4) ^{1}
Medium	43.5 (4.6)	26.3 (2.4)	7.0 (0.8)	24.5 (2.4) ^{1}
Large	4.6 (0.6) ăħ	4.2 (0.6) ũ	3.3 (0.9)	4.0 (0.4) ^{2}
Total	109.8 (5.5)	53.6 (5.2)	26.7 (2.8)	60.6 (4.9)
Growing	24	24	24	72
Small	37.3 (3.1) Ω	12.3 (1.6)	17.2 (1.7)	22.3 (1.8) ^{2}
Medium	40.7 (4.4)	17.9 (1.9)	10.9 (0.8)	23.1 (2.2) ^{1}
Large	8.5 (1.3) ă	9.2 (1.1) áē	2.8 (0.4)	6.8 (0.7) ^{1}
Total	86.5 (6.6)	39.3 (4.1)	30.8 (2.3)	52.2 (3.9)
Intact Forest	24	24	24	72
Small	59.5 (2.8) Φ	32.0 (5.4)	21.4 (3.0)	37.6 (2.9) ^{1}
Medium	39.9 (3.5)	19.7 (2.0)	11.3 (1.0)	23.6 (2.0) ^{1}
Large	4.4 (0.6) ħ	7.6 (0.6) áũ	3.9 (0.8)	5.3 (0.4) ^{1}
Total	103.8 (3.9)	59.3 (6.7)	36.5 (2.4)	66.5 (4.3)
Total	100	96	96	292
Small	53.6 (2.5) a	24.1 (2.0) b	21.2 (1.4) b	33.4 (1.5)
Medium	41.6 (1.9) a	22.3 (1.1) b	11.1 (0.6) c	25.5 (1.1)
Large	6.0 (0.4) a	7.4 (0.4) b	3.9 (0.4) c	5.9 (0.3)
Total	101.2 (3.2)	53.8 (2.8)	36.2 (1.6)	64.2 (2.2)

Table 10. Mean number of adult trees and saplings by species and river location. Gaps combined are the mean of new, recruiting (R) and growing (G) gaps. All values are standardized to 500 m^2.

		Adult Trees					Saplings				
		Intact Forest	Gaps combined	New	R	G	Intact Forest	Gaps combined	New	R	G
Down Stream	*A. germinans*	17	13	9	14	15	27	13	10	9	21
	L. racemosa	20	10	11	9	10	3	2	2	2	2
	R. mangle	33	34	30	24	53	36	247	61	437	194
	Total	70	57	49	47	78	67	262	73	448	217
Mid Stream	*A. germinans*	16	5	2	5	7	1	53	0	5	153
	L. racemosa	42	10	12	12	5	3	12	1	23	10
	R. mangle	72	33	29	32	38	32	318	32	227	694
	Total	130	47	43	49	50	36	382	33	255	858
Up Stream	*A. germinans*	8	3	3	1	3	2	22	13	41	12
	L. racemosa	28	5	7	7	0	2	1	4	0	0
	R. mangle	105	52	34	59	62	51	258	56	125	592
	Total	142	59	44	68	65	56	281	73	167	604
Entire Shark River	*A. germinans*	14	7	5	8	9	10	27	8	17	58
	L. racemosa	30	8	10	10	6	3	5	2	7	4
	R. mangle	70	39	31	36	51	40	270	51	295	464
	Total	114	55	46	53	66	53	302	61	319	525

Table 11. Mean biomass of adult trees and saplings by species and by river location. Gaps combined are comprised of new, recruiting (R) and growing (G) gaps together. Mean biomass of adults and saplings killed by lightning. All values are standardized to kg per 500 m^2.

		Biomass Adults and saplings					Biomass killed by lightning Adults and saplings
		Intact Forest	Gaps combined	New	R	G	New
Down Stream	*A. germinans*	2507	1122	202	1091	2082	672
	L. racemosa	1657	960	873	863	1169	1199
	R. mangle	2310	1622	1699	1295	1955	2141
	Total	6474	3705	2774	3248	5205	4012
Mid Stream	*A. germinans*	2199	221	274	143	247	176
	L. racemosa	3615	476	735	483	211	2811
	R. mangle	4557	1698	1145	1855	2094	2777
	Total	10370	2395	2154	2481	2551	5764
Up Stream	*A. germinans*	812	157	194	64	214	238
	L. racemosa	1909	213	396	243	0	823
	R. mangle	4405	2605	1729	2833	3253	3607
	Total	7125	2975	2319	3141	3467	4667
Entire Shark River	*A. germinans*	1839	581	221	552	971	393
	L. racemosa	2393	603	689	590	531	1569
	R. mangle	3757	1930	1542	1867	2386	2772
	Total	7990	3113	2452	3010	3887	4734

Table 12. Mean number of seedlings and propagules by species and river location. Gaps are the combined mean of new, recruiting (R) and growing (G) gaps.   All values are standardized to 500 m^2.

		Seedlings					Propagules				
		Intact Forest	Gaps	New	R	G	Intact Forest	Gaps	New	R	G
Down Stream	*A. germinans*	219	67	23	81	94	0	0	0	0	0
	L. racemosa	0	5	8	6	0	73	201	289	260	39
	R. mangle	1333	1609	1281	2040	1398	250	276	227	294	305
	Total	1552	1681	1313	2127	1492	323	478	516	554	344
Mid Stream	*A. germinans*	115	170	31	63	417	63	28	31	21	31
	L. racemosa	52	132	125	229	42	7177	2788	4010	292	4063
	R. mangle	885	3083	2021	4781	2448	510	545	500	490	646
	Total	1052	3385	2177	5073	2906	7750	3361	4542	802	4740
Up Stream	*A. germinans*	83	108	135	167	21	104	63	156	21	10
	L. racemosa	63	222	490	83	94	4865	4024	7354	2802	1917
	R. mangle	1396	4806	5583	6229	2604	760	1573	1365	2896	458
	Total	1542	5135	6208	6479	2719	5729	5660	8875	5719	2385
Entire Shark River	*A. germinans*	139	109	59	99	169	56	26	56	11	13
	L. racemosa	38	105	188	88	41	4038	2062	3525	962	1809
	R. mangle	1205	2965	2794	3930	2075	507	731	650	1057	453
	Total	1382	3179	3041	4117	2284	4601	2819	4231	2030	2275

Table 13. Summary table of ANOVA results showing the effects of forest stage (new gap, recruiting, growing and intact forest) and river location (downstream, mid stream, and upstream) on the population structure for all species and for the three species that comprises this mangrove forest. A= adults, Sap = saplings, Sed = seedlings, Pro = propagules NS= not significant, ***P ≤ 0.001, ** P ≤ 0.02, *P ≤ 0.05 All data $\sqrt{x+3/8}$ transformed unless noted with RK. RK indicates the data was rank transformed before parametric test was applied.

Source of		Summed for all spp.				*A. germinans*				*L. racemosa*				*R. mangle*			
Variation	Df	A	Sap	Sed	Pro	A	Sap	Sed	Pro	A	Sap	Sed	Pro	A	Sap	Sed	Pro
Forest stage (S)	3	***	***	**	NS	NS	NS	NS	NS	**	NS	NS	NS	*	***	**	NS
River Location (R)	2	NS	NS	**	***	*	NS	NS	NS	NS	NS	NS	***	*	NS	**	**
S x R	6	NS	***	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	**	NS	NS
Error	28						RK		RK		RK	RK					

Table 14. Summary table of ANOVA results showing the effects of forest stage (new gap, recruiting, growing and intact forest) and river location (downstream, mid stream, and upstream) on the biomass (kg per 500 m^2) for all species and for the three species that comprises this mangrove forest. ***P ≤ 0.001, ** P ≤ 0.02, *P ≤ 0.05 All data log (x+1) transformed.

Source of Variation		Adults and saplings combined				Saplings only	
	Df	Summed for all spp	*A. germinans*	*L. racemosa*	*R. mangle*	Summed for all spp	*R. mangle*
Forest stage (S)	3	***	**	**	**	***	***
River Location (R)	2	NS	NS	*	**	NS	NS
S x R	6	NS	NS	NS	NS	NS	NS
Error	28						

Table 15. Mean height of seedlings and initial saplings (height class 0.30 to 2.0 (m)) by forest stage and species. Followed by mean number of seedlings and initial saplings per 16 m^2 area sampled per gap. There was an interaction between species and forest stage for the mean height ($F_{3, 75} = 6.48$ $p < 0.001$). Mean values within a species followed by similar letters were not significantly different at a $\alpha = 0.05$. (Tukey's HSD for unequal samples sizes).

Species		New	Recruiting	Growing	Forest
A. germinans	Height	0.46 **a**	0.68 **a**	1.27 **b**	0.44 **a**
	n	1.7	2.9	2.9	2.7
L. racemosa	Height	0.33 **c**	0.63 **cd**	0.53**cd**	1.15 **d**
	n	6.0	2.6	1.5	1.1
R. mangle	Height	0.40	0.65	0.66	0.50
	n	88.9	124.5	72.2	38.9
All species	Height	0.39 **a**	0.65 **b**	0.70 **b**	0.54 **a**
	n	96.5	129.9	76.6	42.8

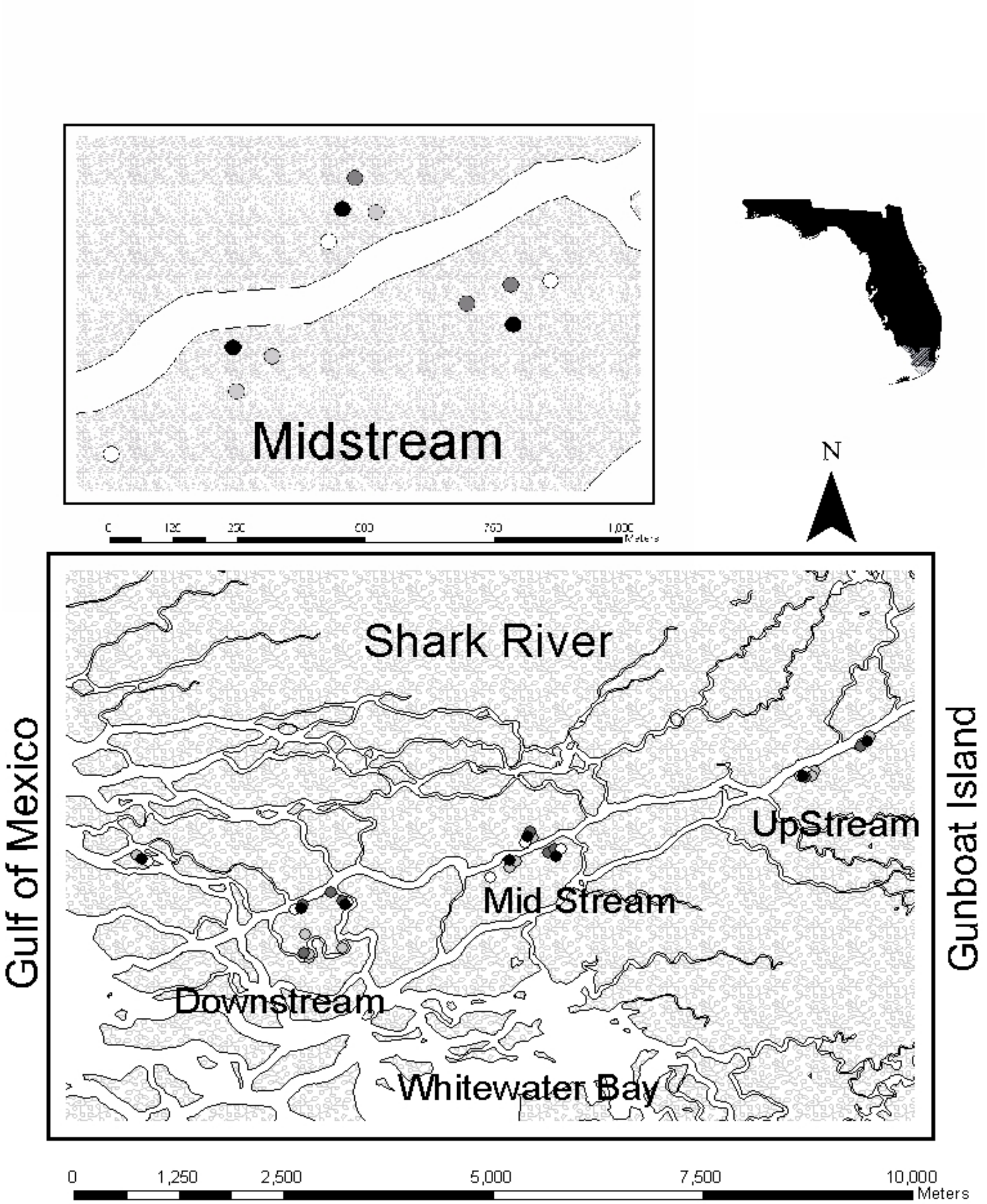

Figure 1. Locations for the 31 gaps and 9 forest sites surveyed for environmental and vegetative characteristics. Open circles represent new gaps, light gray circles recruiting gaps, dark gray circles growing gaps and dark circles intact forest sites. Insert of Midstream location.

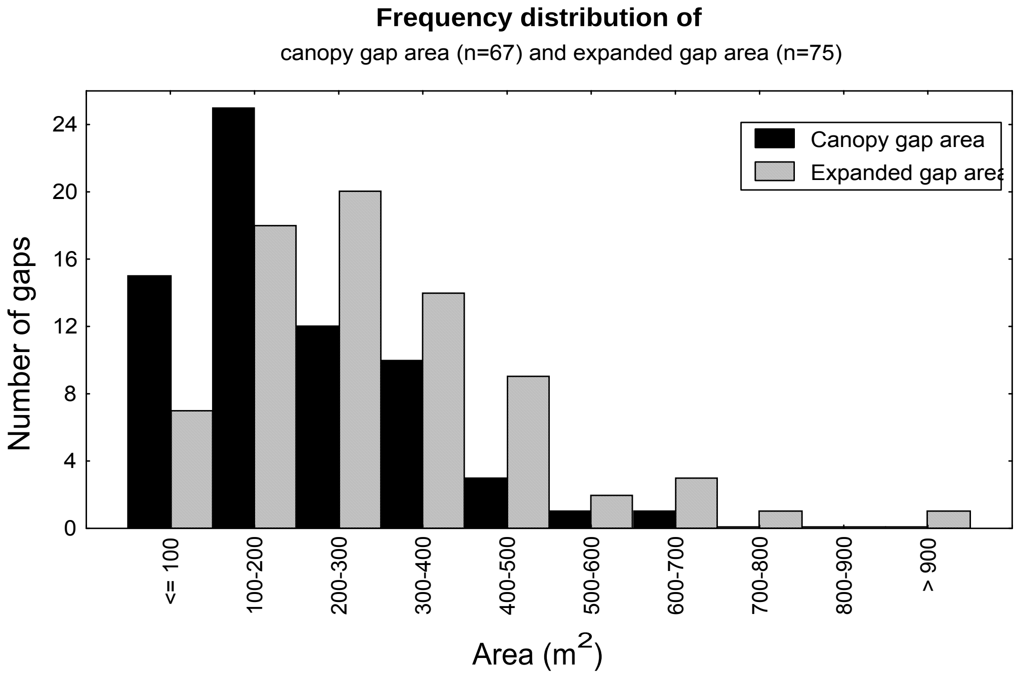

Figure 2. Frequency distribution of canopy gap area (*sensu* Runkle 1982) and expanded gap area (*sensu* Runkle) for lightning-formed gaps in the mangrove forest of Everglades National Park.

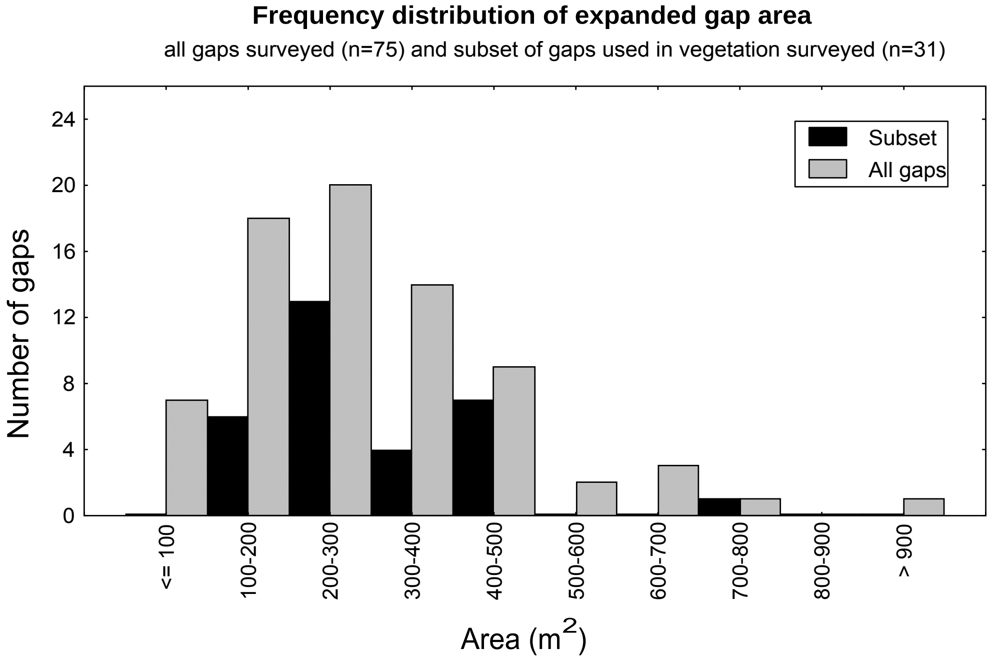

Figure 3. Frequency distribution of expanded gap area for all lightning-initiated canopy gaps surveyed (n=75) and the subset of gaps in which vegetation sampling occurred (n=31).

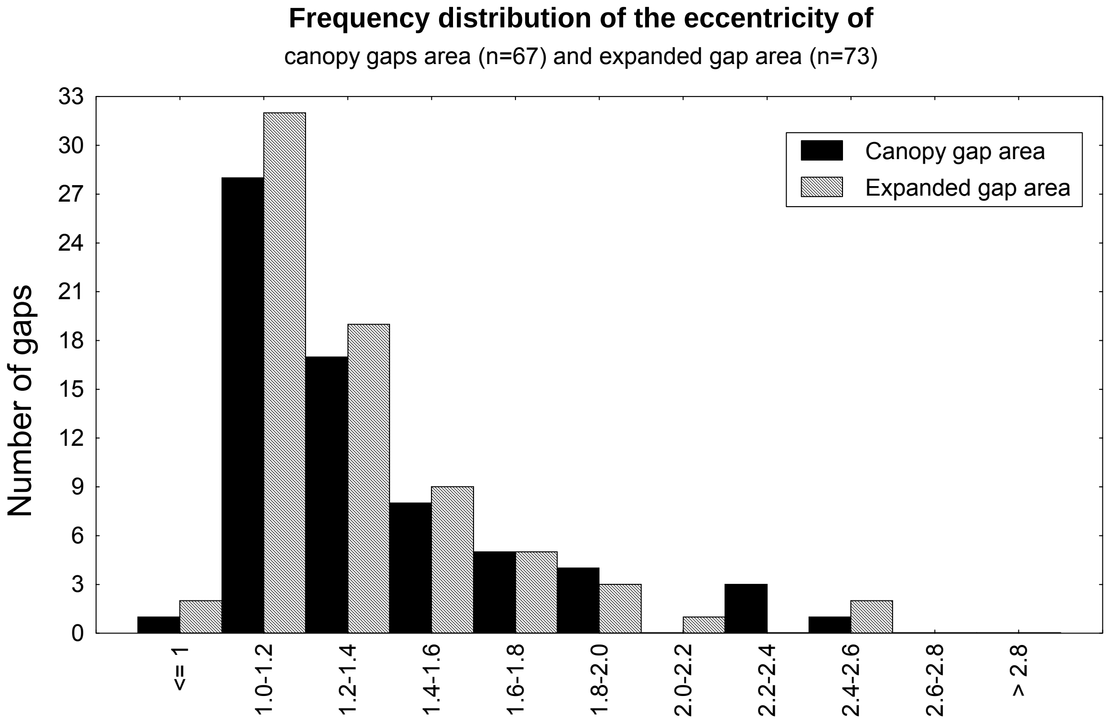

Figure 4. Frequency distribution of the eccentricity of canopy gap area and expanded gap area for lightning-initiated gaps. A value of 1.0 indicates a circular formation and values greater than 1.5 indicate elongated elliptical form.

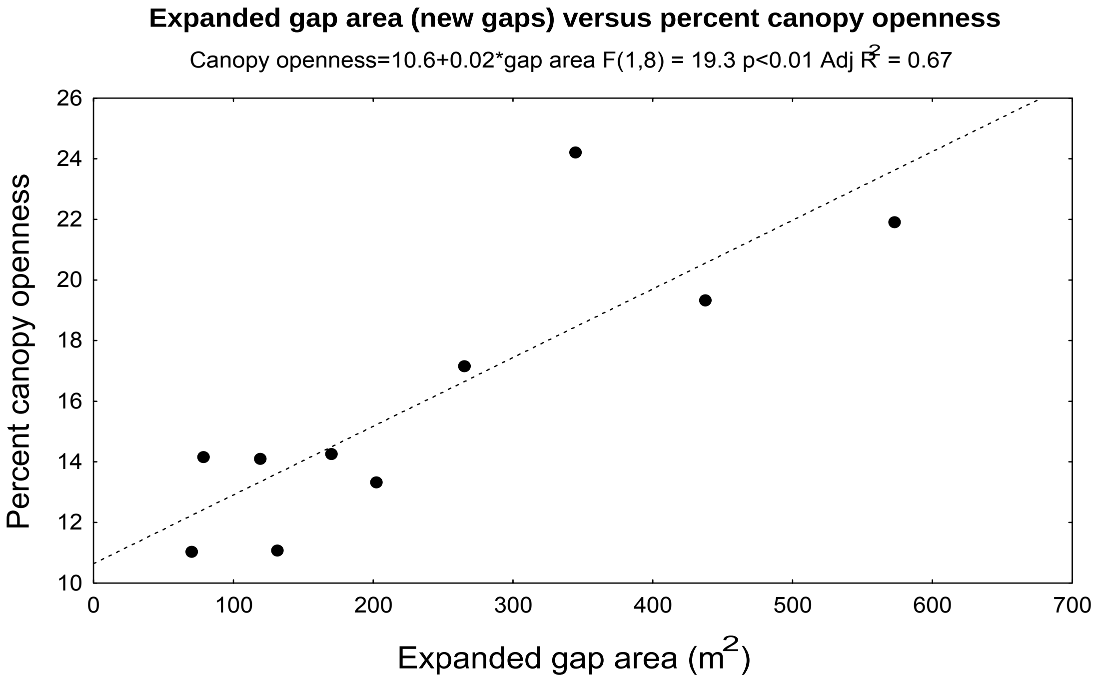

Figure 5. Expanded gap size (new gaps, n=10) versus canopy openness.

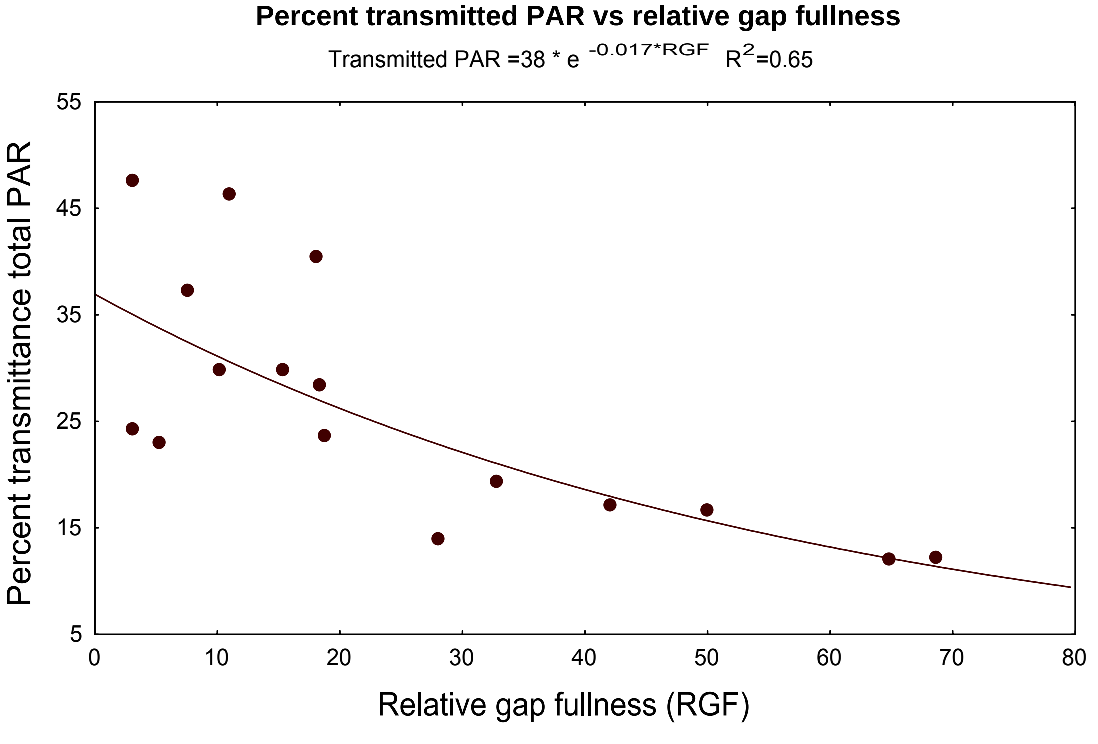

Figure 6. Percent transmittance of total photosynthically active radiation (PAR) as it relates to relative gap fullness (RGF) (n=16).

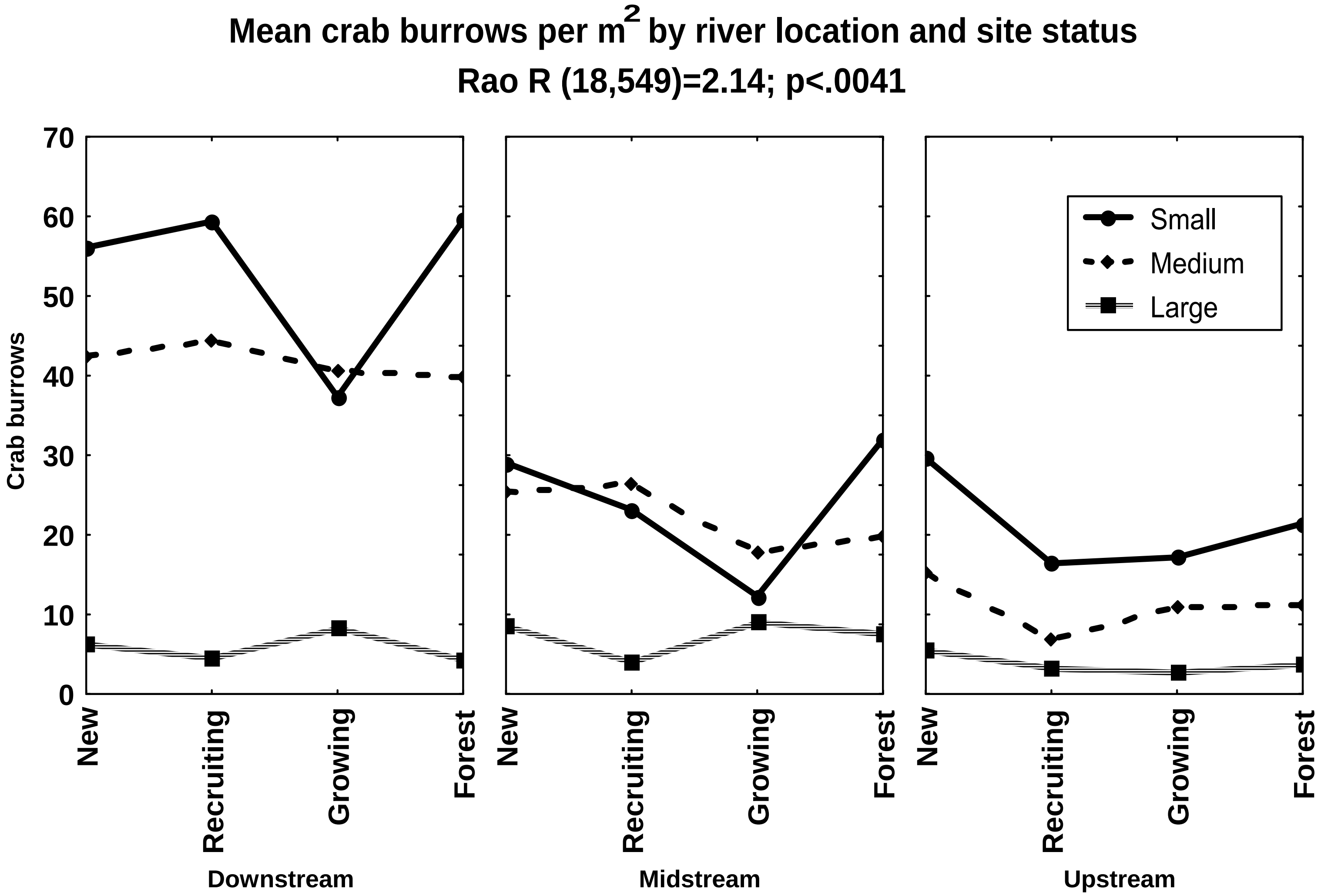

Figure 7. Mean crab burrows per m^2 by river location and forest stage.

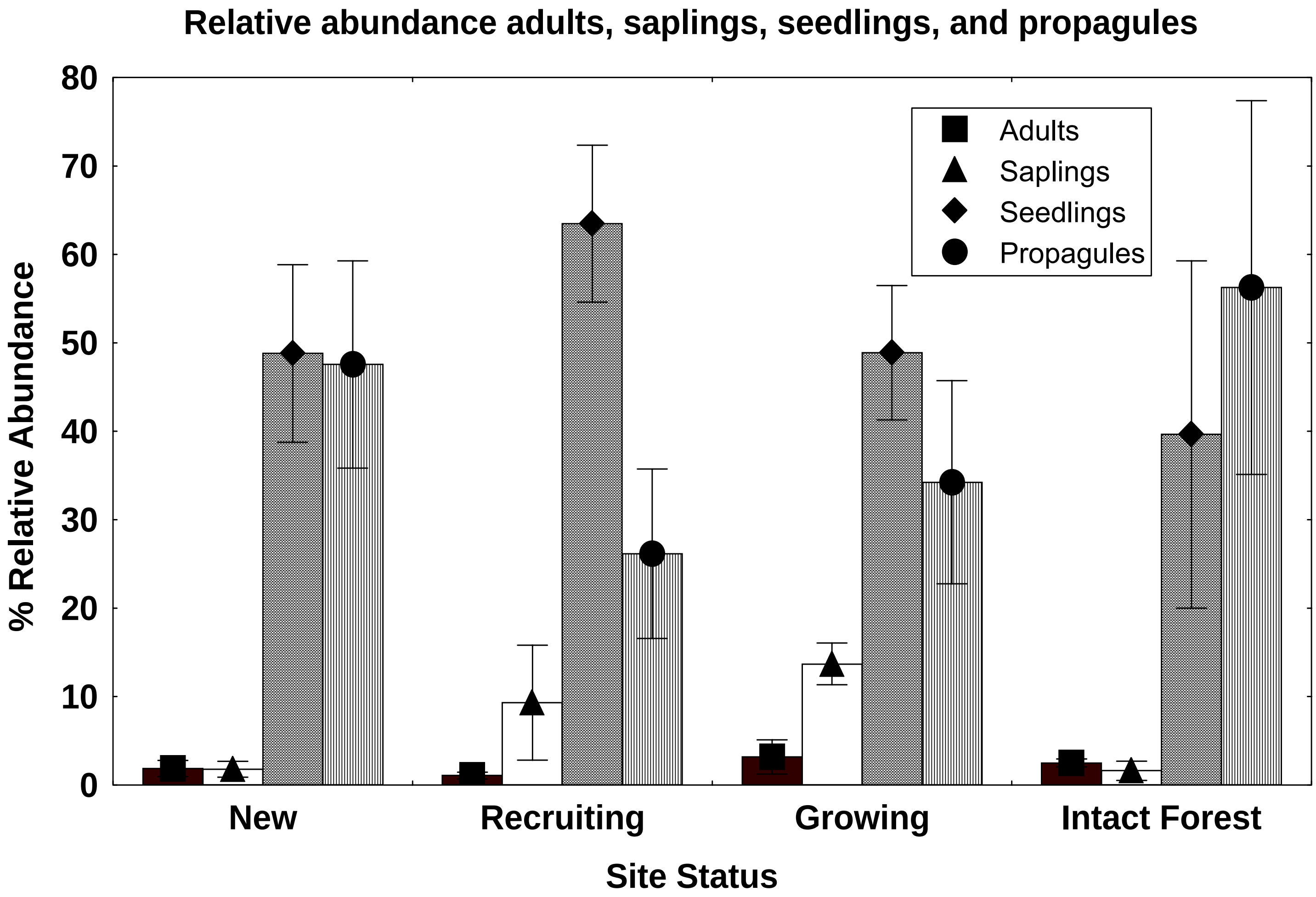

Figure 8. Percent relative abundance of adults, saplings, seedlings, and propagules for gaps of differing successional stages and surrounding intact forest. Relative abundance sum to 100 % within a forest stage.

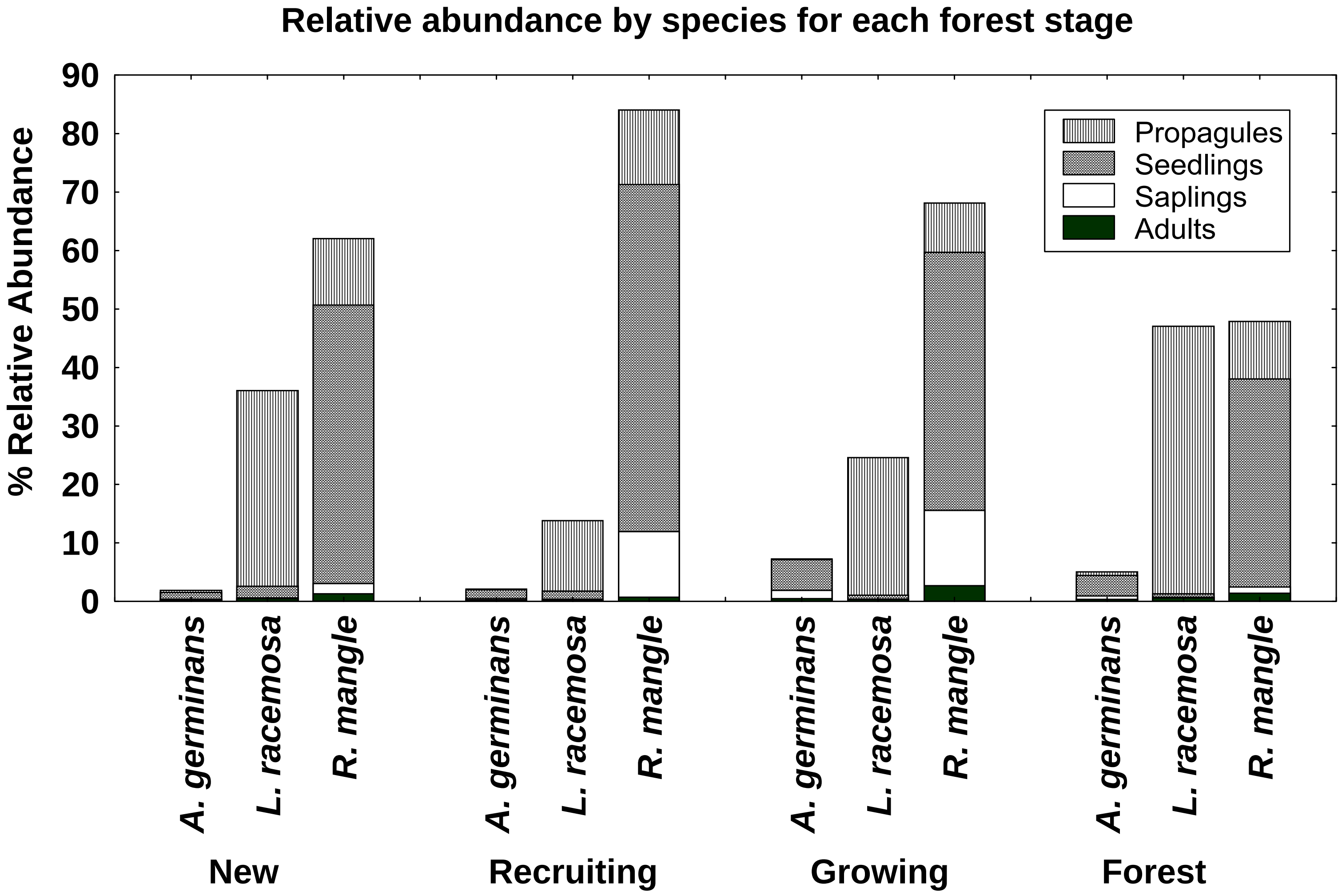

Figure 9. Percent relative abundance of the four life-history stages by species for each gap successional stage and the surrounding intact forest.

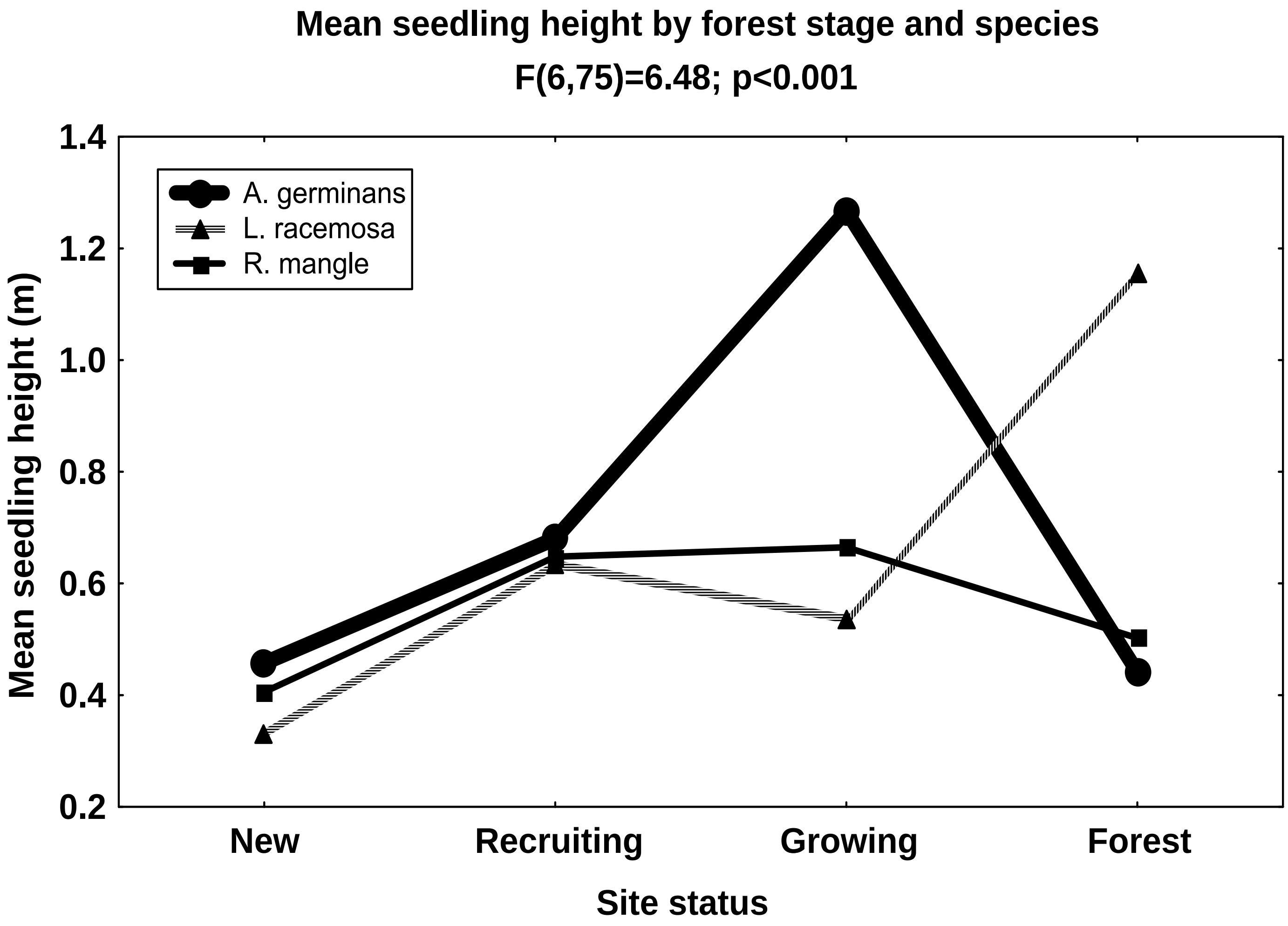

Figure 10. Mean seedling and initial sapling (0.3 to 2.0 m) height by forest stage and species. *A. germinans*, thick solid line; *L. racemosa,* dash line; and *R. mangle,* thin solid line.

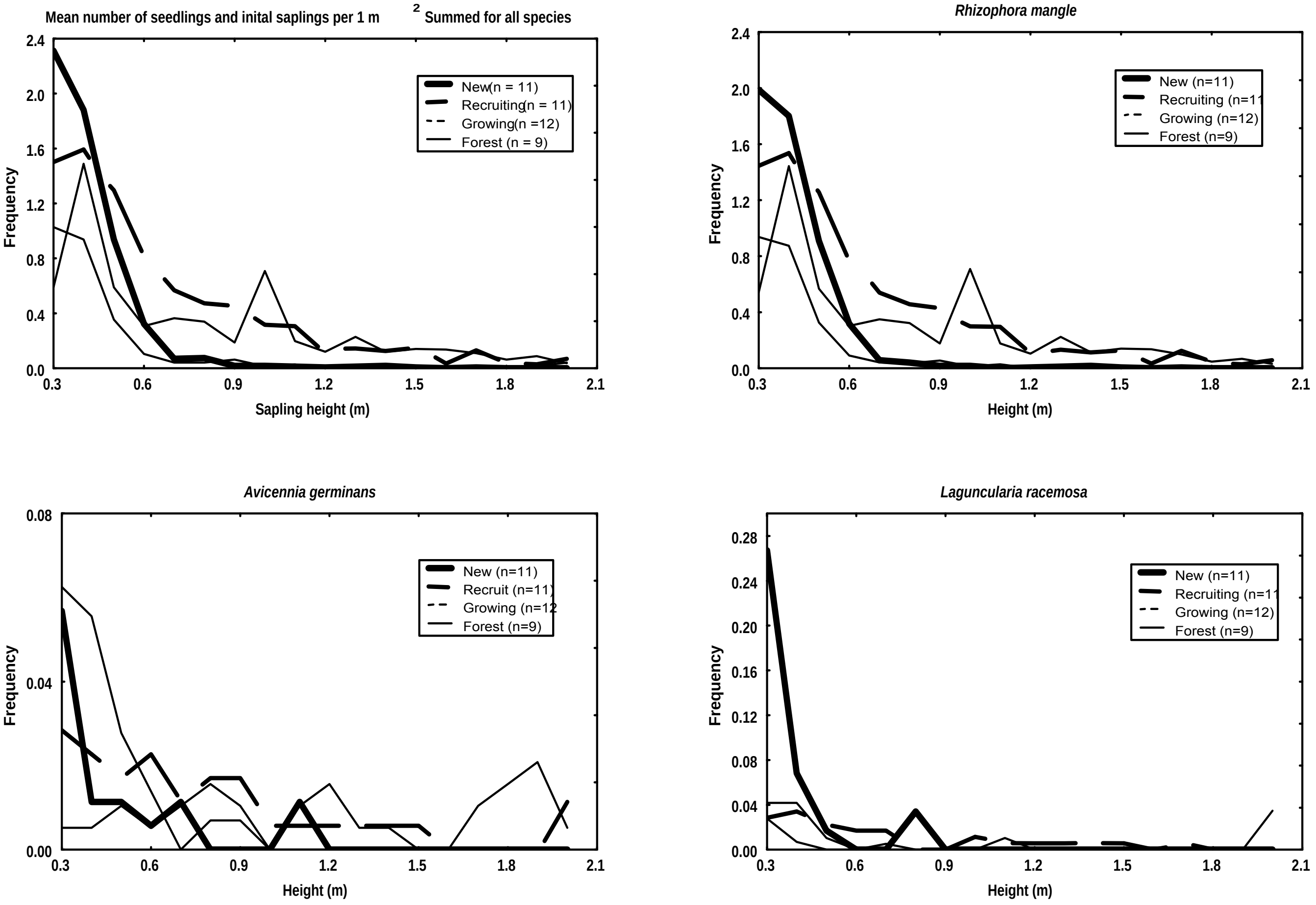

Figure 11. Frequency of seedlings and saplings per 1 m^2 by size class summed for all species and for *R. mangle*, *A. germinans*, and *L. racemosa* separately. New, recruiting, growing gaps and intact forest sites. Note the change in the frequency scale for *A. germinans*, and *L. racemosa.*

Chapter III

Mangrove survival, growth, and recruitment in lightning-initiated canopy gaps and closed forest sites in Everglades National Park, Florida USA.

Abstract

Lightning gaps, as well as other types of canopy gaps, have been reported as an important disturbance mechanism in mangrove forests around the world. This study is the first to report multiple species-specific recruitment/mortality rates across life stages within different forest stages. I studied the survival, recruitment, and growth across three successional stages of mangrove forest (newly initiated lightning gaps, growing gaps and intact forest) for four dominate life phases (propagules, seedlings, saplings, and adult) of the three dominant mangroves (*Avicennia germinans, Laguncularia racemosa, Rhizophora mangle)* in the Florida Everglades. In new lighting-initiated canopy gaps the seedling recruitment rate was twice as high as the other forest stages and the sapling population was increasing. At the growing gap stage, *R. mangle* seedling mortality was 10 times greater and sapling mortality was 13 times greater than recruitment. In growing gaps, there is reduced seedling stem elongation, and reduced sapling and adult growth, but a few individuals (*R. mangle* saplings) were able to recruit into the adult size class. Enumerating survival, recruitment, and growth across life stages by species is of critical importance in understanding and predicting changes in forest structure, composition and development especially in mangrove communities. This work provides the

critically needed field data for future modeling efforts to explore mangrove forest gap phase dynamics.

Introduction

How mangrove forests develop and establish has been the subject of numerous studies. Classical mangrove investigations reported species-specific zonation patterns in mangrove forest (Davis 1940, Lugo and Snedaker 1974, Chapman 1976). There have been numerous observations for and against mangrove forest zonation patterns in many parts of the world (Smith 1987, Smith 1992, Bunt 1996, Chen and Twilley 1998). Typically mangrove species specific sorting have been related to physical or biological gradients (Rabinowitz 1978a, Clarke and Allaway 1993, Smith 1992, Smith et al 1994, Chen and Twilley 1999, Clarke and Kerrigan 2000). More recently, interest has turned towards gap dynamics and applying concepts from upland terrestrial systems to mangrove forest dynamics in order to understand development within both mixed species and zonal patterned forest (Smith 1992, Feller and McKee 1999, Clarke and Kerrigan 2000, Sherman et al. 2000, Duke 2001, Ellison 2002).

Gaps generally are thought to provide an altered environment, which may facilitate conditions that can shift species-specific survivorship, recruitment, and growth of the flora both among and within a species across life stages (Brokaw 1985, Denslow 1987, Hubbell et al. 1999). Mangrove canopy gaps have been found to alter important physical factors and biogeochemical processes important for regeneration: humidity, evapotranspiration, light levels, and soil properties (salinity, temperatures, and nutrients) (Smith 1987a, Smith 1992). The two previous studies of naturally occurring small-scale mangrove canopy gaps found preferential facilitation of species-specific saplings (*R. mangle*, *Avicennia marina*) in the gaps as opposed to the surrounding forest (Sherman 2000, Smith 1987a). However, how gaps affect recruitment and mortality into other life stages were not addressed. Presumably recruitment, survivorship, and growth change for the different forest stages, which may allow a particular species to prevail at a particular life stage within the gap successional process. The objective of this paper was to determine how survival (mortality), growth, and recruitment (both as density and specific rates) varied across three successional stages of mangrove forest development (newly initiated lightning gaps, closing gaps and intact forest) for the four dominant life phases (propagules, seedlings, saplings, and adult) of the three mangrove species (*Avicennia germinans, Laguncularia racemosa, Rhizophora mangle)* in the Everglades mangrove forest of Florida. In this way I was able to follow change in density of stems but also change in population structure at these different successional stages as gaps progressed to closed canopy conditions.

Methods

Study area

This study examined the mangroves on the southwest coast of Florida, in Everglades National Park, (25ºN - 26ºN). This area encompasses approximately 60,000 ha of mangrove forest (Figure 1). These mangroves form a continuous band along the coast, varying in width from 0.1 to 15 km (Smith 1994). Tree height generally declines with distance from the coast (Chen & Twilley 1999). The climate is subtropical with an average maximum temperature above 27 °C. Rainfall has a distinct dry and wet season and varied from 86 to 224 cm over a 10-year period (Duever 1994). Tidal amplitude fluctuated from 10 to 60 cm. Three mangrove species [*Rhizophora mangle* L. (red mangrove), *Laguncularia racemosa* (L.) Gaertn. (white mangrove), and *Avicennia germinans* (L.) Stearn (black mangrove)] are found in this area varying from heterogeneous mixed stands to single species dominated forest. Hurricane disturbance to this region is common, with catastrophic hurricanes occurring approximately every thirty years (Doyle 1997). The 1935 “Labor Day” Hurricane, Hurricane Donna (1960) and Hurricane Andrew (1992) all strongly impacted the Everglades mangrove region. Additionally, lightning-initiated canopy gaps are common in this forest (Chapter I, Houston and Powell 2003, Smith et al. 1994).

I grouped gaps into two ages: (1) three new gaps that were known to have been initiated by lighting between July to September of 2002; and (2) growing gaps, approximately seven to 15 yrs old, generally with a very dense sapling layer. These categories correspond to the following stages within Duke’s (2000) small gap mangrove conceptual model: gap initiation combined with gap opening and gap filling, respectively. The growing gap category was assigned based on a subset of gaps of known approximate age (pers. obs. K. Whelan). To compare the community attributes of the lightning-initiated gaps to the surrounding intact forest, I established three intact forest sites. Each of the three groups were comprised of one new gap, one growing gap and one intact forest location (Table 1). At the group location, all gaps of the time series were within 300 m of each other. In this paper, “forest stage” includes new, growing gaps and intact forest sites whereas the phrase “gap phase” only refers to comparisons between new and growing gaps.

Additionally, at each gap site the gap size (expanded gap size *sensu* Runkle 1982), canopy openness (determined by hemispherical photography), distance to river and rivulet and canopy height (mean of six dominant stems) were determined (Table 1). A circular plot (radius eight-m) was established in the center of each gap (site). The plot size was chosen to confine sampling within the canopy gap area. I used the size class definition of Koch (1987) and Chen and Twilley (1998) to ensure comparability of this work with previous studies in this forest. Propagules were not established or rooted in the substrate (i.e. still in a dispersal phase). Seedlings were defined as all individuals attached to the substrate and < 1.4 m in height. Saplings were defined as all stems > 1.4 m and < 4 cm in diameter at breast height (dbh). Adults were defined as all stems greater than 1.4 m in height and ≥ 4 cm dbh. Seedlings and propagules were counted in four 4 m^2 plots; nested within the circular plot. All stems were permanently and uniquely tagged, identified to species, and had a condition status assigned. Vegetation plots were established from February to May 2003 (from five to nine months post-strike) and resurveyed in March to April 2004. During the 2004 resurvey, all new stems were permanently and uniquely tagged, identified to species, and had a condition status assigned. Recruitment in this work was defined as the number of individuals that were new to the life stage at the second survey. For example, five seedlings that had sufficient stem growth to be included in the sapling stages (> 1.4 m height) were considered recruiting saplings. The same was true for seedlings and adult stems.

Seedlings were tagged and total stem length (soil surface to the dominant meristem) was measured. For *R. mangle* seedling, the stem length was measured from the top of the propagule scar to the bottom of the leaf sheath of the main meristem. Seedling elongation rates (E-Rate, mm/d) were calculated as (*sensu* Koch 1997):

E-Rate (mm d^{-1}) = (Stem length $_{(t_1)}$ – Stem length $_{(t_0)}$) / ($_{(t_1) - (t_0)}$)

Seedling stem growth (cm yr^{-1}) was E-Rate * 365 days. Sapling and adult tree growth was determined by two successive measurements of dbh. I used the species-specific allometric formulas of Smith and Whelan (in review) to convert from dbh to living biomass. Growth was determined by converting dbh to biomass and determining the relative growth rate (*sensu* Evens 1977) as:

Relative Growth Rate (RGR) = Log (Biomass_2) – Log (Biomass_1)

expressed on an annual basis.

Specific per capita recruitment (R) and mortality (M) rates for the sample period were calculated using the following equations (*sensu* Padilla et al. 2004):

$R_{t+1} = \text{Ln}\{[(N_t + NR_{t+1})/N_t]/\Delta t\}$

$M_{t+1} = \text{Ln}\{[(N_t - D_{t+1})/N_t]/\Delta t\}$

where R_{t+1} is the specific recruitment rate annualized, and M_{t+1} is the specific mortality rate annualized, N_t is the total population at initial survey, NR_{t+1} is the number of new recruits at the second survey; D_{t+1} is the number of dead stems at the second survey; Δt is the number of days between first and second survey divided by 365.

Data analysis

Abundance within the propagule class (count data) was $\sqrt{x+3/8}$ transformed and followed with a parametric one-way way Analysis of Variance (ANOVA) (Quinn and Keough 2002, Zar 1999). Differences in initial seedling height, survival of seedling, and elongation rates were analyzed with a one-way and two-way ANOVA. Due to low sample size *L. racemosa* seedlings were removed from the elongation rate comparison. Logistic regression was used to determine the relationship between the probability of survival and species, initial seedling height, and forest stage.

For saplings and adult trees the initial dbh, change in dbh, annual change in biomass and relative growth rates were $\log_{10}$ (x+0.5) transformed to increase normality and meet homogeneity of variance requirements for the two-way ANOVA test of forest stage and species. *L. racemosa* saplings were removed from the analysis of change in dbh, annual change in biomass and relative growth rates due to low sample size. Half normality probability plots were used to assess normality for the linear regressions. Normality plots were used to assess normality for parametric tests. Unless otherwise noted, I used Tukey's Honestly Significantly Difference test for unequal sample sizes for post- hoc comparison. I used a Arcsin $\sqrt{x}$ transformation for proportional data. Analyses were performed using STATISTICA 5.0 (Statsoft, Inc., 1996), SPSS 11.0.1 (SPSS, Inc., 2001) and Statistix for Windows (96 Analytical Software, Inc).

Results

Propagules

At the initial survey of the new lightning-initiated gaps, I found no propagules with lightning damage within the study plots. Mean propagule abundance across forest stage per plot (4 m^2) varied between the two surveys for *R. mangle* and all species combined (*R. mangle,* 1.5 and 0.2, t = 3.2, d.f. = 36 p < 0.003; all species combined, 2.4 and 1.0, t = 2.5, d.f. = 36 p < 0.02 first survey and second survey, respectively, Table 2). The number of *L. racemosa* propagules in a plot did not vary between surveys (0.9 and 0.8, t = 0.4, d.f. = 36 n.s., Table 2). Propagule abundance varied by forest stage for *L. racemosa*, *R. mangle,* and both species combined for the first survey (Table 2, $F_{(2,24)} > 4.6$ $p < .02$ for all test). Propagules of *L. racemosa* were greatest in new gaps, with the highest amount in new gap 1 (Table 2). *R. mangle* propagules were most common in the intact forest sites (Table 2). The number of propagules was similar for new gaps and intact forest sites when I combined both species for the first survey (Table 2). For the second survey there was no relationship between forest stage and propagule abundance for the *L. racemosa*, *R. mangle* or the species combined (Table 2, $F_{(2,24)} < 1.3$ ns for all test, Table 2). No propagules of *A. germinans* were located during either survey.

Seedlings

At the initial survey of the new lightning-initiated gaps, I found no seedlings with lightning damage within the study plots. Initial mean seedling height was lowest in new gaps (25.6 ± 1.57) compared to growing gaps and intact forest (37.4 ± 4.8, 31.9 ± 1.40, respectively, $F_{(2,386)} = 10.5$, $p < 0.001$, Table 3). This difference was due to the presence of tall *A. germinans* seedling in the growing gaps and the forest sites. There was no difference in mean initial seedling height for *L. racemosa* or *R. mangle* by forest stage ($F_{(2,33)} = 1.31$, ns; $F_{(2,321)} = 1.88$, ns, Table 3).

The mean seedling survival did not vary by forest stage for all species combined or for *A. germinans* or *L. racemosa* analyzed separately (Table 4). The survival of *R. mangle* did vary by forest stage (Table 4). Growing gaps had the lowest survival of *R. mangle* (27 %), but there was no difference between new gaps and the intact forest sites (65 and 58 %, respectively).

Surviving seedlings were significantly taller (37.5 ± 1.64 cm) than dead seedlings (21.0 ± 1.27 cm, $F_{(1,386)} = 62.2$, $p < 0.001$, Fig. 2). Surviving *R. mangle* seedlings were taller than dead seedlings ($F_{(1,321)} = 16.3$, $p < 0.001$, Table 3). There was no difference in seedling height between live and dead *A. germinans* or *L. racemosa* ($F_{(1,27)} = 3.15$, ns, $F_{(1,34)} = 0.16$, ns, Table 3). Logistic regression analysis of the 392 individually tagged seedlings, revealed that the probability of seedling survival was significantly affected by initial seedling height across species and within *R. mangle* separately (Chi-square = 65.0 $p < 0.001$, Chi-square = 35.8 $p < 0.001$, respectively). However, the effect size was small (odds ratio 0.94-0.97, 0.93-0.96, respectively). Interestingly, forest stage did not add significantly into either model ($p = 0.49$, 0.08 respectively).

Stem elongation for all surviving seedlings across the three species ($n=213$) varied with forest stage with new gaps having greater stem elongation rates than growing and intact forest sites (Table 5). The difference was due to *R. mangle* seedlings, which had the highest elongation rates in new gaps, however, it was not significantly different from *R. mangle* seedling at the growing gaps (Fig. 3). *A. germinans* elongation rate did not differ by forest stage. Only two *L. racemosa* seedlings survived in one new gap (New gap 2, not included in growth comparisons). Across all forest types, *R. mangle* stem elongation (0.18 mm d^{-1}) was greater than *A. germinans* (0.03 mm d^{-1}, $F_{(1,206)} = 9.3$, $p < 0.003$).

Recruitment of total seedlings varied by forest stage ($F_{(2,24)} = 6.2$, $p < 0.01$, Table 3). The highest mean number of seedlings recruited in new gaps and the intact forest sites. The difference in total seedling recruitment was due to *L.racemosa* seedlings. *L. racemosa* seedling recruitment was highest in new gaps, and there was no difference between growing gaps and the intact forest sites ($F_{(2,24)} = 2.0$, $p < 0.01$, Table 3). The mean number of recruiting *A. germinans* and *R. mangle* seedlings did not vary by forest stage ($F_{(2,24)} = 0.9$, ns, Table 3). The average height of the recruiting seedlings did not differ by forest stage for *L. racemosa*, *R. mangle*, and all species combined ($F_{(2,7)} = 3.3$, ns; $F_{(2,33)} = 0.6$, ns; $F_{(2,49)} = 1.2$, ns). The average seedling height of new recruits was greater in the intact forest sites than in new gaps for *A. germinans* ($F_{(1,14)} = 9.3$, $p < 0.01$, Table 3).

Saplings

The percent of lightning killed saplings (biomass) for the three new gap sites did not by vary by species ($KW_{(2,6)}$ = 3.5, n.s., Table 6). The percent of lightning killed sapling biomass varied from 20 to 28 % for the three species (Table 7). When saplings with lightning damaged canopies were included, the total percent of saplings impacted by the lightning strike increased to 32 to 57 % of the biomass present at the site pre-strike (Table 7).

Survival of saplings varied from 82 to 100 % (Table 8). Growing gaps had the lowest survival (87 %) and there was no difference in survival between new gaps and the intact forest (99 and 96 %, respectively, $KW_{(2,9)}$ = 7.3, $p < 0.03$, Table 8). *R. mangle* saplings in the growing gaps had lower survival than in the forest ($KW_{(2,9)}$ = 6.2, $p < 0.04$).

L. racemosa saplings were extremely rare in the study, with only ten saplings out of a total of 777 saplings initially tagged, of which nine survived (Table 9). *L. racemosa* saplings were removed from the growth comparisons due to the low number, only comprising 1.3% of the 697 saplings that survived. Overall, *A. germinans* saplings were smaller than *R. mangle* in initial dbh size (1.5 and 1.8 cm, respectively, $F_{(1,682)}$ = 3.6 $p < 0.03$). Initial dbh in growing gaps was larger than that in intact forest, but there were no other differences between forest stages (Table 9). The interaction of species and forest stage was significant for initial dbh size ($F_{(2,682)}$ = 8.1 $p < 0.001$). The *A. germinans* saplings in new gaps were significantly larger than the *A. germinans* in growing gaps or the forest; otherwise there was no difference within species across the forest age class (Table 9).

The change in dbh was largest in new gaps; there was no difference between growing gaps and intact forest ($F_{(2,682)} = 14.9$ $p < 0.001$, Table 9). For saplings within the new gaps *R. mangle* change in dbh was greater than that of *A. germinans* (0.21 and 0.14 cm yr^{-1}, $F_{(1,100)} = 4.4$ $p < 0.04$). Across all forest types *R. mangle* change in dbh was greater than that of *A. germinans* saplings (0.12 and 0.08 cm yr^{-1}, $F_{(2,682)} = 6.8$ $p < 0.01$).

The mean annual change in sapling biomass was greatest in new gaps, there were no other differences ($F_{(2,682)} = 11.2$ $p < 0.001$, Table 9). Within the new and growing gaps, *R. mangle* change in biomass was greater than *A. germinans* ($F_{(1,100)} = 5.9$ $p < 0.02$, $F_{(1,508)} = 8.3$ $p < 0.004$, respectively). Across all forest types *R. mangle* mean change in dbh was greater than that of *A. germinans* (0.28 and 0.10 kg yr^{-1}, $F_{(1,682)} = 11.5$ $p < 0.001$). Mean relative growth rate (biomass kg yr^{-1}) of saplings in new gaps was twice as great as growing gaps and three times greater than intact forest ($F_{(2,682)} = 11.4$ $p < 0.001$, Table 9). The RGR in growing gaps did not differ significantly from intact forest. Within new gaps the RGR of *R. mangle* was greater than *A. germinans* ($F_{(1,100)} = 6.4$ $p < 0.01$, Table 9). Across all forest types *R. mangle* saplings RGR was greater than that of *A. germinans* (0.11 and 0.08 kg yr^{-1}, $F_{(1,682)} = 4.2$ $p < 0.04$).

Recruitment of seedlings to the sapling stage did not vary significantly by forest stage ($KW_{(2,9)} = 1.1$, ns, Table 8). Average recruitment in new gaps was 12.4 saplings per 500 m^2, average recruitment was 4.1 per 500 m^2 in the intact forest and 2.5 per 500 m^2 for growing gap locations. There was at least one site per gap stage that did not have any sapling recruitment. New saplings did not differ in size at recruitment by forest stage ($F_{(2,21)} = 0.9$, ns, Table 8).

Adults

Overall, lightning damage at the newly initiated sites varied from 50 to 94 % of the stem density, and 72 to 92 % of the adult biomass. The proportion of lightning killed biomass of the pre-strike adults for the three new gap sites did not vary significantly by species ($KW_{(2,7)} = 0.21$, n.s., Table 6). The highest proportion of biomass killed was recorded for *R. mangle* at new gap 1 (94 %, Table 6). The lowest proportion of biomass killed was recorded for *R. mangle* at new gap 3 (35 %, Table 6). Across the three species the biomass killed varied from 35 to 75 % (Table 7). When surviving adults with lightning-damaged canopies were included the total percent of adults impacted by the lightning strike at the first survey increase to 73 to 92 % of pre-strike biomass (Table 7).

The mortality of the lightning-damaged trees varied from 0 to 37 % by site. Overall 14 % of the lightning-damaged trees died during the study and the majority of this mortality (88 %) was from *L. racemosa*. Survival was low for *A. germinans* (50 %) and *L. racemosa* (45 %) whereas there was 100 % survival of *R. mangle* adults. *R. mangle* trees comprised 63 % of the lightning-damaged trees however, none of these trees died during the survey.

I recorded post-lightning strike mortality 12 months after the initial survey at new gap 1 and 2. There was a 21 % increase in the proportion of biomass killed by lightning at new gap 2, bringing the total proportion killed to 83 % of the initial pre-strike biomass. At new gap 1 I recorded a 9 % increase in the proportion of biomass killed by lightning. I did not find any post-lightning strike mortality at new gap 3 (Table 7). Survival of initial adults tagged varied from 71 to 100 % (Table 8). New gaps had the lowest survival (88 %) but it was not significantly different from growing gaps or intact forest (99 and 100 %, respectively, $KW_{(2,9)} = 0.32$, ns, Table 8).

L. racemosa adults comprised 14 % (33 individuals) of the 235 adults followed in the growth study and made up 19 % of the biomass. Therefore *L. racemosa* were included in all analysis except for species comparisons within the growing gaps, as there was only one adult stem tagged. Overall, *L. racemosa* mean adult initial dbh was larger than *A. germinans* followed by *R. mangle* (15.1, 12.5, and 9.2 cm, respectively, $F_{(2,226)} = 6.1$ $p < 0.002$). Intact forest sites had the largest mean adult dbh across the three species followed by new gaps and then growing gaps ($F_{(2,226)} = 12.9$ $p < 0.001$, Table 10). The interaction of species and forest stage was significant for mean initial dbh size ($F_{(2,226)} = 4.9$ $p < 0.001$). In the new gaps, the *A. germinans* adults were significantly smaller than the *A. germinans* adults of the intact forest (6.5 and 18.2 cm, respectively); otherwise there was no difference between the species across the forest age classes (Table 10). Within the new gaps *A. germinans* adults were smaller than *L. racemosa* and *R. mangle* ($F_{(2,63)} = 4.9$ $p < 0.001$, Table 10). There was no difference in the mean dbh of *A. germinans* adults and *R. mangle* in growing gaps ($F_{(2,82)} = 0.7$ ns). At the intact forest sites *A. germinans* and *L. racemosa* were larger than *R. mangle* adults ($F_{(2,81)} = 6.6$ $p < 0.002$).

The change in mean adult dbh was not different across forest stage ($F_{(2,226)} = 0.4$ ns, Table 10). Overall, *R. mangle* change in mean dbh was significantly larger than *A. germinans* and there was no difference from *L. racemosa* adults; no other differences existed (0.24, 0.10, and 0.16 cm yr^{-1}, respectively, $F_{(2,226)} = 4.5$ $p < 0.01$). The mean annual change in adult biomass was not different by forest stage ($F_{(2,226)} = 2.9$ ns, Table 10). Within the new gaps, *A. germinans* mean change in biomass was less than those of *R. mangle* and *L. racemosa* ($F_{(2,63)} = 5.0$ $p < 0.01$). Across all forest types the main effect species was significant for change in biomass, however, posthoc comparisons fail to distinguish a difference (1.15, 1.72, and 1.91 kg yr^{-1}, for *A. germinans, L. racemosa*, and *R. mangle*, respectively $F_{(2,226)} = 4.0$ $p < 0.02$). Mean relative growth rate of adults did not differ by forest stage ($F_{(2,226)} = 1.9$ ns, Table 10). Across all forest types *R. mangle* adults RGR was greater than those of *A. germinans* and *L. racemosa* (0.05, 0.02 and 0.02 kg yr^{-1}, $F_{(2,226)} = 5.1$ $p < 0.006$).

Adult recruitment was low within all forest stage (Table 8). In new gaps adult recruitment was 2.5 adults per 500 m^2, whereas it was 1.7 for growing gaps and no adults recruited in the forest locations. Recruitment of saplings to the adult stage did not vary significantly by forest stage ($KW_{(2,9)} = 4.0$, $p <0.13$, Table 8).

Discussion

Closed canopy forest stand structure and growth

The intact closed canopy forest structure and growth results were comparable with the other reported values for the mangrove forest along the lower Shark River drainage, Everglades. In the intact forest the three species (based on adult biomass) were co-dominants (39, 26, and 35%, *A. germinans*, *L. racemosa*, and *R. mangle*, respectively). If I combine the adult and sapling life stages (to make them comparable to Chen and Twilley 1999), the density (3,240 ha^{-1}) and aboveground biomass (156 Mg ha^{-1}) were in the same range as values reported by Chen and Twilley (site 1.8, 1999). I report approximately 100 Mg ha^{-1} less total aboveground biomass compared to Chen and Twilley (1999); however, this is most likely due to the difference in the allometric relationships used to calculate biomass. It appears that mangroves allometric relationships are area specific (see Smith and Whelan, in review). The allometric equations used in this study were determined in this forest (Smith and Whelan, in review) and Chen and Twilley (1999) used relationships generated for mangroves found in Puerto Rico and Mexico. Additionally, the intact forest sites in this study had a greater proportion of *A. germinans,* both as stem density and biomass than was found by Chen and Twilley (1999, 33 and 39 compared to 8 and 21 %, respectively).

Rates of mangrove seedling survival in closed canopy forest have rarely been reported (Rabinowitz 1978b [*Rhizophora mangle, Avicennia germinans, Laguncularia racemosa*], Clarke 1995 [*Avicennia marina*], Ha et al 2003 [*Kandelia candel*], Padilla et al 2004 [*Rhizophora sp.*]). Generally, seedling survivorship is reported in reference to disturbance or in experimental manipulations (e.g. Smith 1987, Osborne and Smith 1990, Clarke and Allaway 1993, Sousa et al. 2003). I found that seedling survival differed by species in the closed forest. *A. germinans* had the greatest seedling survival (91 %), *R. mangle* survival was moderate (59 %) and no *L. racemosa* seedlings survived. In Panama, Rabinowitz (1978b) reported 70 % survival for *R. mangle* and 10 % survival of *A. germinans* after one year and no survival of *L. racemosa* after 100 days. In the Rabinowitz study, the three species were located in closed canopy forest, but at different locations within the forest. For example *R. mangle* seedlings were at the water's edge and the *A. germinans* seedlings were 0.5 km from the waters edge. In my study all seedlings were co-located in the same plots. Sousa et al (2003) recorded low *R. mangle* seedling survivorship (< 38 %) in closed forest in Panama, but a stem boring scolytid beetle, *Coccotrypes rhizophorae*, reduced survivorship. Even though *Coccotrypes rhizophorae* has been reported in Florida (Atkinson and Peck 1994), I found no evidence (rust-colored frass emitted from entrance holes, Sousa et al 2003) of seedlings being attacked.

To the best of my knowledge, recruitment rates of seedlings in intact canopy mangrove forest have only been reported three times prior to this study (Clarke 1995 *[Avicennia marina]*, Ha et al 2003 [*Kandelia candel*], Padilla et al 2004 [*Rhizophora sp.*]). Clearly, more work needs to be done in this area of mangrove research. Seedling recruitment rate in the forest was 0.11 yr^{-1} (per capita) and dominated by *A. germinans* and *L. racemosa* (0.87 and 0.26 yr^{-1}, respectively, Table 11). My values are similar to the values reported for *Rhizophora sp*. in a mangrove forest in the Philippines (0.07 compared to 0.05 yr^{-1}, for a site with relatively low recruitment). Recruitment was three times greater than mortality for *A. germinans* seedlings. For the other species, the seedling recruitment rate was less than half the mortality rate (Table 11), even though *R. mangle* seedlings were very abundant in both the initial survey and at the second survey. These results suggest that *A. germinans* seedling population was increasing whereas *R. mangle* seedling population was decreasing. Additionally, the lack of *L. racemosa* survivorship (1.0 yr^{-1} mortality rate) supports the observation that *L. racemosa* needs higher light conditions than closed canopy forest to survive (Ball 1980, Mckee 1995).

The seedling stem elongation rate of *R. mangle* (0.12 mm yr^{-1}) was lower but similar to that reported by Koch (1997, 0.2 mm yr^{-1}) for closed canopy sites on the nearby Little Shark River (approximately 3 km from my study sites, size class 25-40 cm stems). *R. mangle* stem elongation rate (0.36 cm mo^{-1}) from this study was lower than the average monthly reported value (0.8 cm mo^{-1}) from a study of seedlings growing in a closed canopy forest in Columbia (Elster et al. 1999). The annual growth of seedlings in this study is also lower than that in a year-long study of *Rhizophora sp.* seedling in the Philippines (4.28 cm yr^{-1} compared to 5.6 to 10.6 cm yr^{-1}). The seedling stem elongation rate of *A. germinans* in the closed canopy forest decreased during my study period (-0.08 mm d^{-1}) mainly due to a single individual, in which the stem length deceased from 87 to 61.5 cm from unknown causes. However, the total leaves on the seedling increased from 39 to 45 during this same period of time. Removing this one individual, I found that *A. germinans* essentially had no stem elongation during this period of time (-0.01 mm d^{-1}). *A. germinans* ability to translocate energies to other meristems (having a shrub like appearance) has been noted by others, but in reference to hurricane damage of adult trees (Baldwin et al. 2001). Elster et al (1999) also reported negative stem elongation growth of *A. germinans* but it was attributed to attacks by *Junonia evarte* caterpillars.

Sapling survival was high (97 %) overall but lower for *L. racemosa* (83 %). Sapling recruitment was 0.3 and 1.3 saplings per 500 m^2, (a per capita recruitment rate of 0.04 and 0.10) for *A. germinans* and *R. mangle*, respectively, compared to estimates by Chen and Twilley (5 and 30 saplings per 500 m^2, *A. germinans* and *R. mangle*, respectively, 1998). *A. germinans* recruitment rate was four times greater than mortality, whereas, *R. mangle* recruitment was 2.5 times the morality rate (Table 11). This would suggest that at the sapling stage *A. germinans* is slowly increasing in population size in the intact forest whereas *R. mangle* sapling population while expanding is at a slower per capita rate once corrected for mortality within the sapling size class.

The change in sapling biomass and relative growth rate was not different among the three species within the forest sites. Average change in adult biomass (1.94 ± 0.34 SE kg $tree^{-1}$ yr^{-1}) for the forest is comparable but lower than values reported by Chen and Twilley (1999). Unlike the high values reported by Chen and Twilley, for *L. racemosa* (9.17 kg $tree^{-1}$ yr^{-1}), in my study, all three species had similar value for change in biomass for the forest sites (Table 10).

Additionally, there was no difference in the relative growth rate between the species. Survival of adults was high (100 % during our study period) and there was no recruitment to the adult stage. These results suggest that future changes in forest structure are due to replacement of adult trees by non-conspecifics (ie. seedling and sapling recruitment and mortality dynamics).

New gaps versus intact forest

Post-disturbance mortality has been found from corals to trees (Knowlton et al. 1981, Platt et al 2000, Sherman et al. 2001), so it is not surprising that I documented post-lightning strike mortality at two of the three new gap sites. The plots were established six months post strike so I may have missed some of the delayed mortality that may have occurred and this may be included in my initial mortality estimates. Knowlton et al. (1981) cautioned against delayed disturbance monitoring indicating that mortality could be underestimated due to decomposition or loss of dead members. However, I feel that due to extremely slow mangrove decomposition (Romero et al. 2005) this was not an issue at my site. I also did not find any evidence of lightning killed seedlings or propagules in my smaller study plots within each gap. Overall, I only found 3 to 5 lightning killed seedlings within the new lightning initiated gaps. These were always located at the center of the gap associated with the tree assumed to be the initial strike tree. Within the new gaps the majority of the lightning damaged but surviving trees were located on the edge of the gap. The dead trees and saplings were concentrated in the center of the gap opening.

The propagules were assumed to be transitory in nature since they were not attached to the substrate when censused (i.e. dispersal phase). Tomlinson (1986a) reported that in Florida, *L. racemosa* and *A. germinans* fruit drop occurs during the late summer and fall (July to November and September to October, respectively). *R. mangle* fruit drop can occur through the year (Tomlinson 1986a). The objective of my January to March vegetation sampling was to mainly capture the newly recruiting seedlings and I feel that the three-month period allowed adequate time for the propagules to attach to the substrate. I found significantly more *L. racemosa* propagules in the new gaps compared to the intact forest for the first survey, however this trend was not significant at the second survey (Table 11). For both surveys *L. racemosa* comprised the majority of the all the propagules censused in the new gaps. For both surveys there were at least half as many *R. mangle* propagules in the new gaps compared to the forest (Table 11). The low number of *R. mangle* propagules within the new gaps may be due to the reduction in nearby propagule source trees. The gaps are small in size and my assumption was that the surrounding *R. mangle* trees would be a source of propagules to disperse into the new gaps. Even though *R. mangle* propagules are believe to be a good long distant dispersal structure, it has been reported that *R. mangle* trees within a forest (i.e. not adjacent to a waterway) have limited dispersal of the propagules ("maximum of 8 m, and on average less than 3 m from the point of release", Sousa et al. 2003), suggesting that *R. mangle* propagules may be dispersal limited within the forest. I am unaware of dispersal distance data for *L. racemosa* propagules, however, the dispersal by a small propagule through the tangle of mangrove prop roots should be greater than the larger *R. mangle* propagule.

Even though there were twice as many *R. mangle* propagules in the intact forest compared to the new gaps, I did not find a corresponding increase in *R. mangle* seedling recruitment (Table 3 and 11). Overall, the greatest number of recruiting seedlings was *R. mangle* (26 of 52) and there was no difference between the forest and the new gaps based on seedling density; however, the seedling recruitment rate was twice as high in the new gaps compared to the forest (Table 11). New gaps and the forest had similar numbers of *A. germinans* seedling recruits, however; the per capita recruitment rate was twice as great in the new gaps compared to the forest (Table 11).

I found significantly higher seedling recruitment for *L. racemosa* within the new gaps compared to the forest (Table 11). My data suggest that there maybe-additional dispersal of *L. racemosa* propagules into these new opened sites, since I recorded *L. racemosa* propagules at a new gap (new gap 3) where no canopy trees of *L. racemosa* were present. Additionally, five of the ten recruiting *L. racemosa* seedlings that occurred in the study were found at new gap 3. These results would support suggestions by Ball (1980) that canopy openings (i.e. lightning strikes) within a monospecific stand of *R. mangle* would allow *L. racemosa* seedlings to recruit.

Contrary to the results of Ellison and Farnsworth (1993), in which there was increased survivorship of *R. mangle* and *A. germinans* seedling in an experimentally removed canopy, in my study the survival of seedlings were similar to the intact forest sites (Table 11). Additionally, I did not find a difference in sapling survivorship between new gaps and the intact forest (Table 11). Typically seedlings and saplings predisposed to low light conditions will suffer harmful effects to being exposed to high light ("irreversible photo-oxidation", Luttge 1997). In my study there was no greater amount of mortality associated with the high light new gaps compared to low light intact forest (16 and 8 % mean canopy openness, respectively). The greatest seedling survival was for *A. germinans* followed by *R. mangle. L. racemosa* survival was low in both forest types (mortality rate of –2.76 and –1.00 yr^{-1}, respectively Table 11). This finding is contrary to the suggestion in the literature that *L. racemosa* should have increased survivorship in high light environments (i.e. new gaps) due to its higher light needs for establishment (Ball 1980). However, some species do not have the ability to survive dramatic changes in light conditions as well as others. Increased mortality of *L. racemosa* seedlings in high light new gaps may be more of an indication that once *L. racemosa* develops under certain light condition, transition to others could be difficult. Transplant experiments of the seedlings of the three species from closed canopy forest to highlight open marsh found (10, 40, 80 % survivorship, *A. germinans, L. racemosa*, and *R. mangle*, respectively, K. Whelan and T. Smith, unpublished data). Mckee (1995) also reported 20 % *A. germinans* and 40 % *R. mangle* seedling survivorship when transplanted from closed canopy forest to open canopy site within forest dominated by nonconspecifics.

Summed across all species seedlings had greater stem elongation in the high light new gap sites compared to the forest. The few *L. racemosa* seedlings (n = 2, all in new gaps) had a high growth rate (11.5 cm yr^{-1}) and the few *A. germinans* seedlings in the forest had negative growth. The seedling stem elongation rate of *R. mangle* (0.26 mm d^{-1}) was greater in new gaps than the forest (Table 11). This is approximately half the elongation rate reported by Koch (1997, 0.6 mm d^{-1}) for gap sites on the Little Shark River. Seeing that no mortality was reported for any of the tagged seedlings in the Koch study, some selection may have occurred for more vigorously growing seedlings. Additionally, the high rate of seedling growth occurred over the dry season whereas in this study sampling occurred over the majority of the year (11 to 13 month time period between sampling). Similar to my results, Ellison and Fransworth (1993) found greater stem elongation rates of *R. mangle* seedlings in canopy removal sites. In summary, the seedling stem elongation in the new gaps appears to have been greater than that in the lower light forest sites.

Sapling relative growth rate was three times higher in the new gaps compared to the forest, suggesting a release of resource limitations (presumably light) for surviving stems. Within the new gaps, *R. mangle* saplings had higher relative growth rate than *A. germinans* (*L. racemosa* could not be compared due to low sample size). These results are contrary to those of the Sherman et al. (2000) study in which *A. germinans* had the highest relative growth rate within lightning-initiated gaps. Additionally, sapling survival in this study was high for all three species within the new gaps. This is contrary to the results of Sherman et al. (2000), who reported < 60 % survivorship of *A. germinans* saplings within a two-year period. Direct comparison of sapling growth and survivorship is difficult because in the Sherman et al. (2000) study, sites ranging from new gaps to 10-year-old gaps were lumped together, with no reporting of the proportions of the sample sizes for the different gap stages.

I found no difference in adult recruitment, survival, or relative growth between the new gaps and the forest. The results of this study suggest that if adult stems survive the lightning strike disturbance event (New gap adults), in the short term, then there is little difference in the forest dynamic compared to close canopy settings. Not surprisingly the influence of lightning-initiated gaps is greatest at the other life stages.

Growing gaps versus intact forest

I found significantly less propagules in the growing gaps compared to the intact forest, specifically, fewer *R. mangle* propagules (Table11). These sites were full of sapling size stems (Table 1), which previously have been reported as capable of seed production (Tomlinson 1986b). However, no observation of reproduction was ever found in the growing gap sites. Presumably these areas are under stress (low light and high density of saplings) and the plants do not have the resources to flower and fruit. Seedling recruitment was lower in growing gaps than the forest sites, specifically; I found no *A. germinans* recruitment and low (but not significant) *R. mangle* recruitment compared to the forest (Table 11). The *R. mangle* seedling population was decreasing in both forest types. Mortality was 10 times greater than recruitment in the growing gaps and 7 times greater in the forest. The survival of *R. mangle* seedlings and saplings was lower in the growing gaps compared to the forest based on density and the specific mortality rate, and was at least two times greater in the growing gaps. There was no other difference between the forest and the growing gaps based on density. Additionally, *A. germinans* sapling mortality rate was greater in the growing gaps compared to the forest.

As far as I am aware, this is the first study of gaps in which advanced stages of regeneration have been monitored separately for survival, growth and recruitment in the mangroves. Albeit, the study only covers one field year, I still found distinct differences in recruitment, survivorship and growth by species and life stages, suggesting that this type of approach is appropriate and insightful when trying to determine how these populations parameters change during gap phase succession.

A study of long-term recovery from hurricane disturbance, in terrestrial forest, reports similar findings of minimal sapling growth and increased mortality six years post-hurricane disturbance at the “building phase of forest development” (Vandermeer and Cerda 2004). The results from my study have allowed confirmation of the presumed reduction in seedling recruitment, and increase mortality of saplings as the gaps fill (Brokaw 1985, Duke 2001). Eventually the sites will begin to thin and return to intact forest densities and biomass (Brokaw 1985, Duke 2001).

Conclusion

In the intact forest, *A. germinans* seedling and sapling recruitment was three times greater the mortality rate. Additionally, *L. racemosa* and *R. mangle* seedling mortality rate was two times greater the recruitment, and sapling mortality was 28 times greater than recruitment rate. In general, growth was low across all life stages within the intact forest compared to the new gaps. These results give insight into how *A. germinans* becomes a co-dominant to dominant in closed canopy mature (climax) mangrove forest of South Florida (Craighead 1971), and the observation that *L. racemosa* needs light gaps for sapling to survive to the adult stage (Ball 1980).

The seedling and sapling recruitment rates of *A. germinans* were > 1.5 times greater than mortality in new lighting-initiated canopy gaps, indicating an increasing population. New gaps also had 2.6 to 10.6 times greater rate of seedling mortality for *R. mangle* and *L. racemosa* compared to recruitment, indicating decreases in these populations. Seedling stem elongation was greatest in the new gaps. Taken together, the seedling recruitment rate in new gaps was twice as high as that in the other forest stages. Presumably this recruitment rate will continue to increase as the conditions within the gaps favor propagule establishment (**Chapter II**). Additionally, new light gaps likely favor *A. germinans* seedling recruitment in this initial stage of gap succession.

At the growing gap stage of development, seedling mortality rate of *R. mangle* was 10 times greater and sapling mortality was 13 times greater than recruitment. The recruitment of *R. mangle* adults was 4 times greater than mortality. The gaps have developed to a phase in which there was reduced stem elongation, sapling and adult growth, and few individuals able to recruit into the adult life stage. Sapling populations are high (~ 1 sapling m^2), and seedling populations are low (0.6 seedling m^2). *R. mangle* dominates seedling and sapling stages of the growing gaps and eventually are making the transition to the adult life stage. The end results indicate that at the growing gap stage of succession of the lightning gaps *R. mangle* stems were being favored as adult trees.

Lightning gaps have been reported as an important disturbance mechanism in many mangrove forests around the world. I found differences in survival, recruitment, and growth by species within and across life stages and these differences changed depending on the forest stage. In summary, these results provide population parameters needed to understand and predict recruitment and survivorship for each of the three dominant species (*A. germinans*, *L. racemosa*, and *R. mangle*) during the gap-phase dynamics of the mangrove forest. Additionally, these growth estimates enable better understanding of intact forest and development within the stages of gap-phase dynamics. The results of this study are of considerable importance in these lightning disturbed systems and for other mangroves systems experiencing gap dynamics mechanisms.

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Table 1. Site description. Size of gap, percent canopy openness, distance to main river, distance to rivulet, density of adults (≥4 cm dbh), density of saplings (< 4 m dbh), density of seedlings, biomass of trees and saplings combined (kg). All densities and biomass values are from 2004 survey year and are live stems standardized to per 500 m^2.

Site	Stage	Gap Size (m^2)	Percent canopy openness	River (m)	Rivulet (m)	Canopy height (m)	Adult	Sapling	Seedling	Biomass (kg)
1	New Gap	265	17.16	22	NA	2.87	47	219	1687	1362
	Growing	491	7.63	40	NA	14.11	87	259	406	3376
	Forest	NA	7.67	27	NA	17.19	45	109	969	4899
2	New Gap	437	19.34	14	20	NA	60	32	1187	4129
	Growing	486	7.59	37		13.34	97	271	312	3212
	Forest	NA	7.66	20	25	18.30	109	40	1625	7634
3	New Gap	132	11.08	30	10	NA	85	15	844	5384
	Growing	393	7.6	32	5	5.83	30	933	156	3122
	Forest	NA	8.47	40	20	21.01	57	52	1125	6888

Table 2. The mean (±1 SE) number of propagules per plot (4 m^2) by forest stage and species. A Student paired t-test was used to determine difference between the first and second survey. A one-way ANOVA was used to determine forest stage differences within a survey and by species. Values followed by similar letters were not different.

	Site	*L. racemosa* 1st survey		*L. racemosa* 2nd survey		*R. mangle* 1st survey		*R. mangle* 2nd survey		Total 1st survey		Total 2st survey	
New	1	4.8	±2.3	1.0	±0.7	1.3	±0.9	0.0	±0.0	6.0	±2.1	1.0	±0.7
	2	0.8	±0.5	1.8	±0.3	0.8	±0.5	0.3	±0.3	1.5	±0.9	2.0	±0.4
	3	1.0	±0.4	0.5	±0.3	0.8	±0.5	0.0	±0.0	1.8	±0.8	0.5	±0.3
	AVG	2.2 **a**	±0.9	1.1	±0.3	0.9 **ab**	±0.4	0.1	±0.1	3.1 **a**	±1.0	1.2	±0.3
Growing	1	0.0	±0.0	0.0	±0.0	0.8	±0.5	0.0	±0.0	0.8	±0.5	0.0	±0.0
	2	0.0	±0.0	1.5	±1.2	0.0	±0.0	0.0	±0.0	0.0	±0.0	1.5	±1.2
	3	0.0	±0.0	0.0	±0.0	1.0	±0.4	0.8	±0.8	1.0	±0.4	0.8	±0.8
	AVG	0.0 **b**	±0.0	0.5	±0.4	0.6 **a**	±0.2	0.3	±0.3	0.6 **b**	±0.2	0.8	±0.5
Forest	1	0.3	±0.3	0.0	±0.0	1.5	±1.0	0.3	±0.3	1.8	±0.9	0.3	±0.3
	2	1.5	±1.0	2.3	±0.9	4.5	±2.6	0.0	±0.0	6.0	±2.8	2.3	±0.9
	3	0.0	±0.0	0.0	±0.0	3.3	±1.9	0.8	±0.5	3.3	±1.9	0.8	±0.5
	AVG	0.6 **b**	±0.4	0.8	±0.4	3.1 **b**	±1.1	0.3	±0.2	3.7 **a**	±1.2	1.1	±0.4

Table 3. Seedlings stem height (mean, ± 1 SE, n) at initial survey. Initial population tagged in 4 plots (4 m^2 each) for 3 new, 3 growing and 3 forest locations. Live represents initial seedlings that were alive at the one-year census. Dead represents initial seedlings that were dead at the one-year census. Recruits represent the newly established seedling in the plots that were alive at the one-year survey (Stem height at the one-year census). Values followed by the same letter within a species are not different.

		Initial				Live				Dead				Recruits			
Height		Ag	Lr	Rm	Tot	Ag	Lr	Rm	Tot	Ag	Lr	Rm	Tot	Ag	Lr	Rm	Tot
New	Mean	40.4 **a**	13.5	28.0	25.6 **a**	58.8	12.5	32.6	33.3	16.0	13.6	18.7	16.5	24.9 **a**	14.0	13.6	17.1
	S.E.	15.3	0.5	1.8	1.6	23.4	1.5	2.4	2.5	5.0	0.5	1.9	1.1	1.6	0.5	1.8	1.3
	N	7	33	124	164	4	2	83	89	3	31	41	75	9	8 **a**	13	30 **a**
Growing	Mean	94.3 **b**	12.5	24.5	37.4 **b**	89.4		27.5	52.9	138	12.5	23.1	26.4		12.0	15.9	15.3
	S.E.	9.1		3.1	4.8	8.7		6.4	8.3			3.5	5.0			2.3	2.0
	N	10	1	42	53	9		13	22	1	1	29	31		1 **b**	5	6 **b**
Forest	Mean	53.9 **a**	10.3	30.6	31.9 **b**	58.0		35.7	37.9	33.8	10.3	23.5	23.4	31.8 **b**	17.0	11.6	20.8
	S.E.	5.8	0.8	1.4	1.4	6.2		1.8	1.9	1.8	0.8	2.0	1.9	1.5		3.0	3.0
	N	12	2	161	175	10		93	103	2	2	68	72	7	1 **b**	8	16 **a**
All	Mean	64.6	13.3	28.8	30.0	70.4	12.5	33.8	37.5	42.3	13.3	22.0	21.0	27.9	14.1	13.4	18.0
	S.E.	6.7	0.5	1.1	1.1	6.4	1.5	1.4	1.6	19.6	0.5	1.3	1.3	1.4	0.5	1.4	1.2
	N	29	36	327	392	23	2	189	214	6	34	138	178	16	10	26	52

Table 4. Survival proportion of tagged seedling at one-year census by species and forest stage.

Stage	Site	*A. germinans*	*L. racemosa*	*R. mangle*	Total
New	1	100.00	0.00	78.57	58.97
	2	40.00	33.33	62.50	55.81
	3		0.00	52.78	44.19
	AVG	**70.00**	**11.11**	**64.62 a**	**52.99**
Growing	1			35.71	35.71
	2	100.00	0.00	25.00	71.43
	3	0.00		20.00	18.18
	AVG	**50.00**	**0.00**	**26.90 b**	**41.77**
Forest	1	100.00	0.00	59.57	59.18
	2	81.82	0.00	66.67	68.25
	3			49.21	49.21
	AVG	**90.91**	**0.00**	**58.48 a**	**58.88**
		$F_{(2,3)} = 0.6$, ns	**$F_{(2,3)} = 0.6$, ns**	**$F_{(2,6)} = 11.3$, $p<0.01$**	**$F_{(2,6)} = 0.8$, ns**

Table 5. Elongation of surviving seedlings at one-year census by forest stage. Mean (1 SE, n) height (cm), elongation rate (E-Rate, mm d^{-1}), and annual stem growth (cm yr^{-1}) by species and summed across species. Values followed by the same letter are not different.

Stage		*A. germinans*			*L. racemosa*			*R. mangle*			Total		
		Ht	E - Rate	Growth yr^{-1}	Ht	E - Rate	Growth yr^{-1}	Ht	E - Rate	Growth yr^{-1}	Ht	E - Rate	Growth yr^{-1}
New	Mean	58.8	0.26	9.39	12.5	0.32	11.50	32.6	0.26 **a**	9.69 **a**	33.3	0.27 **a**	9.72 **a**
	SE	23.4	0.11	3.94	1.5	0.23	8.37	2.4	0.02	0.91	2.47	0.02	0.87
	n	4			2			83			89		
Growing	Mean	89.4	-0.09	-3.24				27.5	0.15 **ab**	5.56 **ab**	52.9	0.05 **b**	1.96 **b**
	SE	8.6	0.10	4.00				6.4	0.04	1.44	8.3	0.05	2.02
	n	9						13			22		
Forest	Mean	58.0	-0.08	-3.07				35.8	0.12 **b**	4.28 **b**	37.9	0.10 **b**	3.57 **b**
	SE	6.2	0.08	2.95				1.8	0.02	0.56	1.87	0.02	0.61
	n	10						93			103		
			$F_{(2,20)}$ = 2.47, ns			NA	NA		**$F_{(2,186)}$ = 14.0, $p<0.001$**			**$F_{(2,206)}$ = 8.9, $p<0.001$**	

Table 6. Live and dead (lightning mortality) adult trees and saplings by species at the three new gap sites. Mean dbh (cm), abundance (N), biomass (Bio, kg) and percent of total biomass by species. Abundance and biomass were standardized to 500 m^2.

		Adults						Saplings					
		A. germinans		*L. racemosa*		*R. mangle*		*A. germinans*		*L. racemosa*		*R. mangle*	
		Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead
New 1	dbh	6.53	9.76	11.43	19.17	5.10	19.63	2.17	2.09	2.24	3.90	1.37	1.39
	N	32	25	7	7	5	7	40	12	10	2	172	32
	Bio	562	964	374	999	65	1036	88	30	19	12	255	51
	%	**36.8**	**63.2**	**27.2**	**72.8**	**5.9**	**94.1**	**74.7**	**25.3**	**60.2**	**39.8**	**83.3**	**16.7**
New 2	dbh	13.70	14.18	16.34	13.54	8.19	10.48	1.25			1.27	2.52	3.10
	N	2	20	35	45	22	32	2			2	30	7
	Bio	158	1695	3101	2919	747	1836	2			1	122	42
	%	**8.5**	**91.5**	**51.5**	**48.5**	**28.9**	**71.1**	**100.0**			**100.0**	**74.4**	**25.6**
New 3	dbh					10.78	12.53					3.48	3.00
	N					82	32					15	7
	Bio					4490	2448					101	40
	%					**64.7**	**35.3**					**71.8**	**28.2**

Table 7. Live and dead (lightning mortality) adult trees and saplings combining all species at the three new gap sites. Mean dbh (cm), abundance (N), biomass (Bio, kg) and percent of total biomass of all species combined. Abundance and biomass were standardized to 500 m^2. Percent of total biomass of lightning damaged and post lightning mortality was added to initial lightning mortality.

New Gap		Adults Live	Adults Dead	Saplings Live	Saplings Dead	Lightning damaged Adults	Lightning damaged Saplings	Post lightning mortality Adults
New 1	dbh	7.19	13.38	1.55	1.70	6.95	1.99	14.70
	N	45	40	221	47	20	52	5
	Bio	1000	2999	362	93	392	124	348
	%	**25.0**	**75.0**	**79.5**	**20.5**	**84.8**	**47.8**	**83.7**
New 2	dbh	13.2	12.7	2.4	2.6	11.49	2.80	20.0
	N	60	97	32	10	25	2	17
	Bio	4006	6449	123	43	1167	11	2237
	%	**38.3**	**61.7**	**74.0**	**26.0**	**72.8**	**32.9**	**83.1**
New 3	dbh	10.78	12.53	3.48	3.00	12.64	3.85	
	N	82	32	15	7	57	5	
	Bio	4490	2448	101	40	3955	40	
	%	**64.7**	**35.3**	**71.8**	**28.2**	**92.3**	**56.4**	

Table 8. Number of stems and percent survival of the adult and sapling in the initial tagged population. Additionally, recruitment of new stems into the adult and sapling size class at the second survey. Mean sapling dbh of the new recruits in also included. All abundances have been standardized to 500 m^2.

		Adults		Saplings		Recruitment		
Stage	Site	Initial n	% Survival	Initial n	% Survival	Adults	Saplings	Dbh
New	1	45	88.9	221	97.8	2	20	0.7
	2	60	70.8	32	100.0	2	5	0.6
	3	82	100.0	15	100.0	2	0	
Growing	1	87	100.0	259	91.3	0	0	
	2	97	97.4	271	81.7	0	5	0.3
	3	30	100.0	933	87.7	5	7	0.6
Forest	1	45	100.0	107	97.7	0	2	0.6
	2	107	100.0	40	93.8	0	10	0.6
	3	57	100.0	52	95.2	0	2	0.7

Table 9. Sapling mean (1SE) initial dbh, annualized change in dbh (ΔDBH), summation of biomass, annualized change in biomass (ΔBiomass), and relative growth rate in biomass (RGR). Values followed by similar letters are not different (comparison of means test). The letters **abc** indicate differences of species within a forest stage, letters **ijk** indicate differences between forest stagees and letters **xyz** indicate differences for interaction in 2-way Anova.

	Sp. n	DBH (cm)	ΔDBH (cm yr^{-1})	Biomass (kg)	ΔBiomass (kg yr^{-1})	RGR (kg yr^{-1})
New	A.g.	2.1 **x**	0.14 **a**	36	0.24 **a**	0.14 **a**
	17	0.3	0.04		0.07	0.044
	L.r.	2.2	0.12	8	0.16	0.12
	4	0.4	0.06		0.09	0.057
	R.m.	1.7	0.21 **b**	190	0.41 **b**	0.24 **b**
	85	0.1	0.01		0.04	0.020
	Total	**1.8 ij**	**0.19 i**	**234**	**0.38 i**	**0.22 i**
	106	**0.1**	**0.01**		**0.03**	**0.018**
Growing	A.g.	1.2 **y**	0.05	16	0.06 **a**	0.07
	23	0.1	0.02		0.03	0.029
	L.r.	2.9	0.24	6	0.52	0.14
	2	0.4	0.15		0.36	0.071
	R.m.	1.9	0.11	1262	0.28 **b**	0.09
	488	0.0	0.01		0.02	0.006
	Total	**1.9 i**	**0.11 j**	**1284**	**0.27 j**	**0.09 j**
	513	**0.0**	**0.01**		**0.02**	**0.006**
Forest	A.g.	1.4 **xy**	0.08	35	0.05	0.05
	33	0.2	0.04		0.01	0.018
	L.r.	1.9	0.07	4	0.10	0.07
	3	0.1	0.03		0.04	0.029
	R.m.	1.8	0.05	102	0.09	0.06
	42	0.2	0.01		0.02	0.010

Table 10. Adult mean (1SE) initial dbh, annualized change in dbh (∆DBH), summation of biomass, annualized change in biomass (∆Biomass), and relative growth rate in biomass (RGR). Values followed by similar letters are not different (comparison of means test). The letters **abc** indicate differences of species within a forest stage, letters **ijk** indicate differences between forest stages and letters **xyz** indicate differences for interaction in 2-way Anova.

	Sp. n	DBH (cm)	∆DBH (cm yr^{-1})	Biomass (kg)	∆Biomass (kg yr^{-1})	RGR (kg yr^{-1})
New	A.g.	6.5 **a x**	0.06	226	0.26 **a**	0.02
	13	0.8	0.02		0.12	0.009
	L.r.	11.9 **b**	0.13	418	1.07 **b**	0.02
	9	1.2	0.06		0.50	0.009
	R.m.	10.0 **b**	0.19	2132	1.56 **b**	0.03
	44	0.8	0.03		0.30	0.006
	Total	**9.6 i**	**0.16**	**2776**	**1.24**	**0.03**
	66	**0.6**	**0.02**		**0.22**	**0.004**
Growing	A.g.	8.0 **xy**	0.19	223	1.40	0.04
	9	0.9	0.10		0.79	0.019
	L.r.	21.3	0.10	133	1.16	0.01
	1					
	R.m.	7.4	0.30	2162	2.03	0.07
	75	0.4	0.03		0.28	0.006
	Total	**7.7 j**	**0.29**	**2517**	**1.95**	**0.06**
	85	**0.4**	**0.03**		**0.26**	**0.006**
Forest	A.g.	18.2 **a y**	0.09	2989	1.61	0.01
	21	2.3	0.03		0.57	0.003
	L.r.	16.1 **a**	0.18	1970	2.01	0.02
	23	1.2	0.07		0.77	0.009
	R.m.	11.8 **b**	0.18	2684	2.07	0.02
	40	1.1	0.04		0.47	0.004
	Total	**14.6 k**	**0.16**	**7643**	**1.94**	**0.02**
	84	**0.9**	**0.03**		**0.34**	**0.003**

Table 11. Summarized findings comparing new gaps to intact forest sites and growing gaps to intact forest sites by density and proportions. Below: specific rates of recruitment and mortality (yr^{-1}) three sites combined

	Sp.	Prop	Seedlings			Saplings			Adults		
			Rec.	Sur.	Grow	Rec.	Sur.	Grow	Rec.	Sur.	Grow
New	A.g.	**NA**	=	=	=	=	=	=	=	=	=
	L.r.	>	>	=	=	=	=	**NA**	=	=	=
	R.m.	<	=	=	>	=	=	>	=	=	=
	Total	=	=	=	>	=	=	>	=	=	=
Growing	A.g.	**NA**	**NA**	=	=	=	=	=	=	=	=
	L.r.	=	=	=	=	=	=	**NA**	=	=	=
	R.m.	<	=	<	=	=	<	=	=	=	=
	Total	<	<	=	=	=	<	=	=	=	=

		Seedlings Rates		Saplings Rates		Adults Rates	
		Rec	Mort	Rec	Mort	Rec	Mort
New	A.g.	0.87	-0.52	0.12	-0.04	0.03	-0.11
	L.r.	0.26	-2.76	0.77	-0.04	-0.04	-0.68
	R.m.	0.14	-0.36	0.04	-0.06	0.01	-0.04
	Total	0.21	-0.57	0.09	-0.06	0.00	-0.04
Growing	A.g.	0.00	-0.11	0.08	-0.11	0.01	-0.11
	L.r.	0.69	-1.00	0.01	0.01	0.01	0.01
	R.m.	0.11	-1.17	0.01	-0.13	0.04	0.01
	Total	0.11	-0.88	0.02	-0.13	0.03	0.01
Forest	A.g.	0.48	-0.16	0.04	0.01	0.01	0.01
	L.r.	0.43	-1.00	0.01	-0.28	0.01	0.01
	R.m.	0.07	-0.53	0.10	-0.04	0.01	0.01
	Total	0.11	-0.51	0.07	-0.03	0.01	0.01

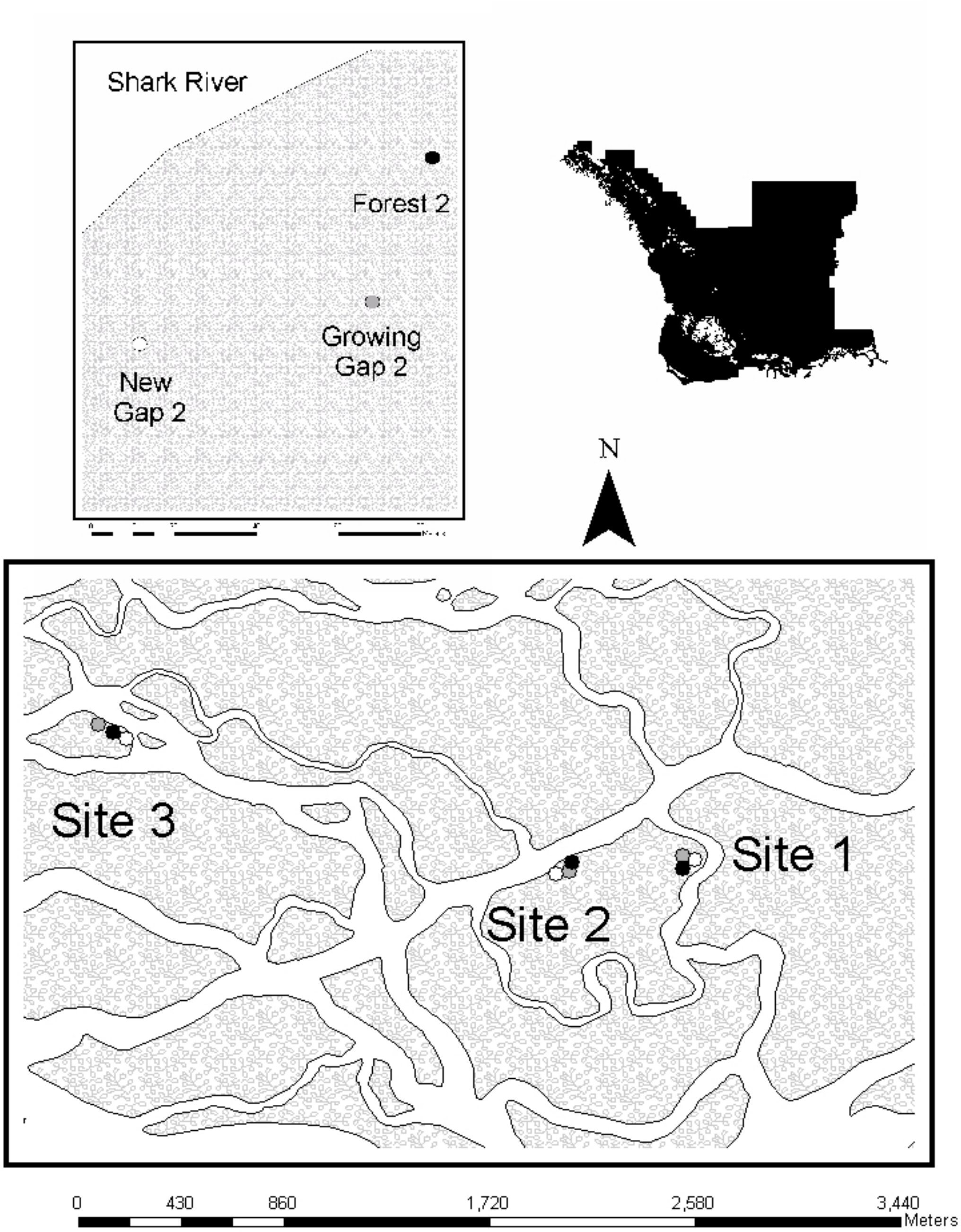

Figure 1 Location of three sites on the lower Shark River, Everglades National Park, Florida, USA. Open circles represent new gaps, gray circles growing gaps and dark circles are intact forest locations. More detailed view is shown in insert of Site 2.

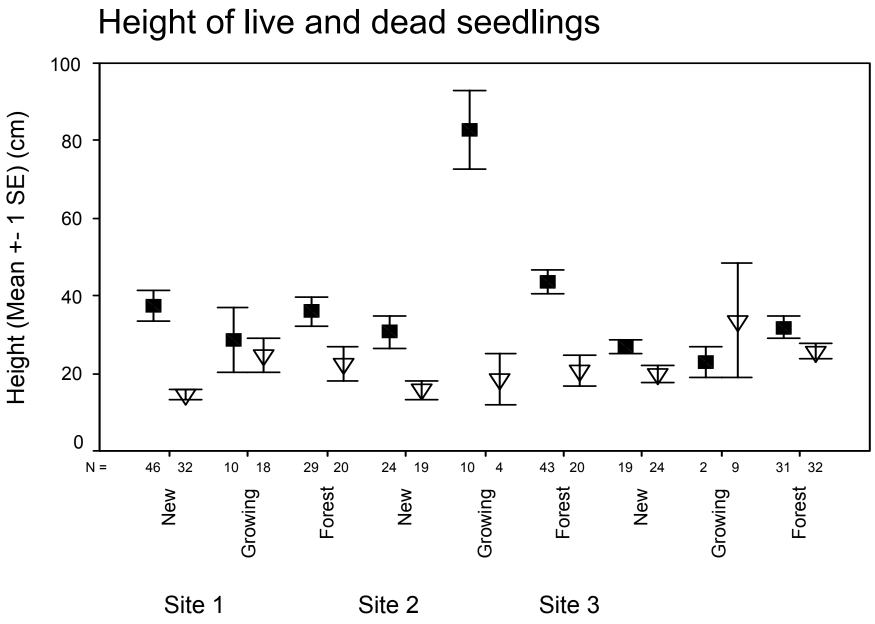

Figure 2 Height of live and dead seedlings in new gaps, growing gaps and forest sites.

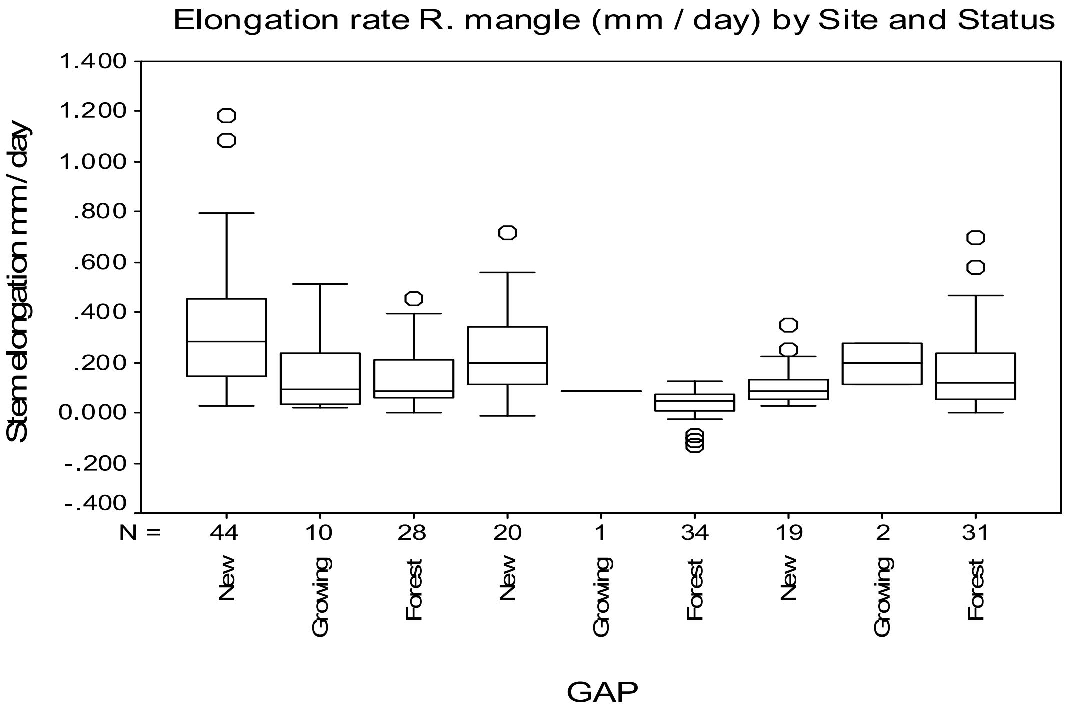

Figure 3 Elongation rate for *R. mangle* seedlings in new gaps, growing gaps and forest sites

Chapter IV

Recent lightning-initiated Neotropical mangrove forest canopy gaps decline in soil surface elevation.

Abstract

Lightning-initiated canopy gaps are an important but relatively understudied disturbance in mangrove forests around the world. To test the hypothesis that root death caused by lightning strikes leads to a decline in mangrove peat surface elevation, I investigated soil surface properties subsequent to lightning-initiated canopy gap formation in a Neotropical mangrove forest, Florida, USA. Specifically, I sampled the amount of live and dead roots, soil bulk density, compaction, and maximal torsional shear strength along with soil surface elevation in new gaps, recovering gaps, and the intact forest. Newly formed lightning gaps had greater dead root biomass, but in general had similar surface soil physical metrics compared to the intact forest. Soil surface elevation declined between 8.5 mm to 60.9 mm in newly formed lightning gaps; this loss was due to superficial erosion (8.5 mm) and subsidence (60.9mm). Recovering gaps had a smaller live root biomass, no difference in soil physical metrics, and a similar soil surface elevation pattern as the intact forest. Lightning apparently kills many of the shallow surface roots and leads to a decline in the soil surface elevation in new gaps. Subsidence occurring below the shallow soil zone generated the greatest overall soil elevation loss. Soil surface elevation loss in newly initiated lightning gaps can lead to a increased hydroperiod, and because

many mangrove seedlings have species-specific responses to surface flooding, soil surface elevation loss can affect long-term recruitment patterns.

Introduction

Canopy gaps are an important form of disturbance in forest environments. Gaps affect aboveground biotic processes by increasing light levels, temperature, and wind velocity, changing light quality, and by decreasing humidity (Denslow 1987). Canopy gaps also strongly influence the belowground environment. Gap formation in tropical forests increases soil temperature (Fetcher et al. 1985), soil water (Denslow et al. 1987, Becker et al. 1988), and decreases root formation (Denslow et al. 1987). In turn, these abiotic effects decrease site quality, promoting emigration of soil fauna (e.g., ants, Ferner and Schupp 1988). Despite the importance of soil processes during succession, most investigations of canopy gap in mangrove forest have concentrated on only aboveground effects, focusing on the existence of gap specialist species, differential species recruitment, and fauna versus faunal interactions (Smith 1992, Ewel et al. 1998, Sherman et al. 2000, Clarke and Kerrigan 2000, Duke 2001). In a few cases, soil chemical properties have been measured to determine differences between gaps and the surrounding forest (e.g. sulfides, redox, and salinity; Smith 1987 ab, 1992, Clarke and Kerrigan 2000).

Canopy gaps from lightning strikes are a common disturbance in mangrove forests around the world, including Australia (Smith 1992), Papua New Guinea (Paijmans and Rollet 1977), Panama (Smith 1992), Dominican Republic

(Sherman et al. 2000), and United States of America (Craighead 1971, Smith 1994). However, few studies have addressed the effects of lightning strike mortality on mangrove succession (Sherman et al. 2000). In the Dominican Republic, Sherman et al. 2000 observed that approximately 2 years post lightning gap formation the soil elevation decreased. I propose that this loss in soil surface elevation in a peat-dominated substrate might be a result of root death of lightning killed trees. Root mortality may lead to a decrease in the cohesiveness of the soil allowing the soil surface to erode, resulting in a decline in surface elevation. Additionally root mortality may lead to a collapse or subsidence of the peat layer, which would also result in a decline of the soil surface elevation. Soil elevation and surface flooding are important factors in mangrove species recruitment and survival (McKee 1993, 1995, Ellison and Farnsworth 1993, Rabinowitz 1978a, b, McMillan 1971). For example, under more flooded conditions survival of *R. mangle* is greater than that of *Avicennia germinans* and *Laguncularia racemosa* (McKee 1995).

In this study, I measured the amount of live and dead root biomass in the shallow surface soil (0-10 cm), collected metrics of soil cohesion (soil bulk density, maximal torsional shear strength, and compaction) and monitored the soil elevation in newly created lightning gaps, recovering lightning gaps, and the surrounding intact forest. I hypothesized that lightning mortality of trees also results in root mortality. Consequently, I predicted that the amount of dead roots will be greater in newly initiated gaps and that the reduced volume of live roots will increase the bulk density and decrease shear strength and compaction strength (ie. the force required to penetrate the soil will be lower). The reduction in soil strength should allow for increased superficial erosion, which will reduce the soil surface elevation. Additionally, root mortality should lead to a collapse of the peat substrate and that would additionally reduce the soil surface elevation. Recovering gaps (7 to 10 yrs post lightning strike) should have soil characteristics (soil bulk density, shear strength, compaction and change in surface elevation) similar to the surrounding forest because of the strong substrate stabilizing effects of the recolonizing roots of regenerating mangroves. These recolonizing roots will increase the soil shear strength and soil compaction and the bulk density will decrease due to added volume of live roots.

Materials and methods

Site description

Three study sites (Sites 1, 2, and 3) were located at the downstream end of the Shark River in the Florida Everglades (Fig 1). At each site I identified three successional stages (gap type): a new lightning strike (approximately 1 to 3 months old = new gap), a recovering gap (approximately 7 to 10 yrs post lightning strike = recovering gap), and an intact forest site (= forest). Specific identifiers are a combination of successional stage and site. For example, the new lightning initiated gap at site one is New 1. All gap types within a site were less than 120 m from each other. The three sites were approximately 2 km apart (Fig 1). New gaps were located in September of 2002. New gaps were readily identified based on condition of leaves and small branches; leaves are retained approximately 3 months following mangrove death by lightning (K. Whelan, personal observation). Specific physical metrics of each gap type and site are given in Table 1.

Shark River stage data were obtained from the "Shark River" hydrological monitoring station of Everglades National Park located within 1 km of all of the sites. This station records tidal influences as well as seasonal changes in river discharge for the area. Shark River stage data was collected at 15-minute intervals. The Shark River stage data used a relative benchmark but was correct to a North American Vertical Datum (NAVD) 88 datum. For my analysis, I used daily averages of the Shark River stage in order to remove the diurnal tidal signal. The daily averaged signal of the above hydrological parameters reports the monthly lunar influences on the tide (Provost 1973), annual change in sea level (Provost 1973), and the seasonal changes in water level due to regional wet season. The hourly tidal signal was assumed to have minimal impact upon my SET measurements because elevation data were always collected at low tide.

Root sampling

Three soil cores were collected from each gap type at each site on May 8, 2003 (total n = 27 cores (3X3X3)). Cores were collected haphazardly from within a six-meter radius of the center of the gap or forest location. Cores were cylindrical, 7.5 cm in diameter and 10 cm deep. Root cores were confined to upper soil layer in order to determine the relationships to surface measurements of soil cohesion. After collection, the cores were return to the lab and frozen at –

20 °C until sectioning. Cores were sectioned into 0-5 and 5-10 cm depths, washed, and sieved (1.0 mm). Roots were classified as live and dead using a two-part serial sorting with 11% and 6% Ludox solution (Robertson and Dixon 1993). After sorting roots as dead or live, roots were further partitioned into three diameter-based size classes: < 2 mm (very fine roots), 2 mm to 5 mm (fine roots), and > 5 mm (coarse roots). Roots were oven dried at 80C° for 48 h.

Soil bulk density, torsion and compaction

At 9, 14, 18, and 21 months post lightning strike, I sampled soil bulk density, soil torsion, and soil compaction at all locations. Cores were taken to determine bulk density. Core locations were haphazardly located within a six-meter radius of the center of the gap or forest location. At each location, for each sampling event I took three soil bulk density cores for a total of 108 cores. Bulk density cores were extracted with a 140 cc syringe (3.7 cm diameter) with the end removed and sharpened. Due to compaction of peat soils, the hole depth (resulting from core removal) was measured three times and averaged (values ranged from 7 to 13 cm). Soil samples were oven dried at 50C° for 7 days. Percent water content was determined from the difference in wet weight and dry weight divided by original samples wet weight. At each micro-core collection location I took three paired samples of soil torsion and compaction for a total of 324 samples. Maximum soil surface shear strength was sampled under field-saturated conditions with the Torsional Vane Shear Tester with the 2.5 kg cm^{-2} vane adapter (Forestry Suppliers, Inc, Jackson MS). I used the pocket penetrometer with the 2.5 cm adapter foot (Forestry Suppliers, Inc, Jackson MS) to sample soil compaction in these peat soils.

Soil Surface Elevation Table theory

The Surface Elevation Table (SET), based on the design of Boumans and Day (1993), allows for precise measurements of soil surface elevation (± 1.4 mm total error, Cahoon et al. 2002a). The SET consists of a mechanical arm that is attached to a benchmark and leveled, establishing a fixed measuring point. Each SET has four fixed measurement directions, where nine pins are lowered to the soil surface to obtain a relative soil elevation. The shallow-rod surface elevation table (Shallow-RSET) uses a plate to support the mechanical arm. This plate has four legs (10.2 diameter aluminum pipe), which are driven to a depth of 0.35 m. The Shallow-RSET records elevation change in the upper soil zone which generally includes the majority of the active root zone. The deep-rod surface elevation table (Deep-RSET) is installed on benchmarks (3 to 7 m) that encompass the entire soil profile above the bedrock (Fig 2). By using a combination of SET designs at a single study site it is possible to partition changes in soil elevation among processes occurring in specific parts of the soil profile, such as the shallow and deep soil zones (Cahoon et al. 2002b, Fig 2). Accretion rates were determined by using marker horizons (Cahoon and Turner 1989). By using the combination of SET measurements and marker horizons, it is possible to follow the surface elevation and determine how soil surface elevation changes and why (Cahoon et al 1995)). In this study I was able to monitor the entire soil profile and determine the fate of the original soil surface (the soil surface originally measured at the first sampling corrected for accretion and subsidence). Surface Elevation Tables-marker horizon combinations have been successfully used to monitor changes in elevation and accretion in a number of wetland environments. They have been used to monitor mangrove vertical accretion and subsidence (Cahoon and Lynch 1997) and to follow the response of wetland soil elevation to season (Childers et al. 1993), water management (Hensel et al. 1999), bioturbation from vertebrate herbivores (Ford and Grace 1998) and hurricane disturbance (Cahoon et al. 2003). This study is the first to use SET-marker horizon combination to monitor soil elevation change resulting from canopy gap formation.

SET installation

At each new gap and forest location I installed a Shallow-RSET, a Deep-RSET, and 3 marker horizons. At each recovering gap I only installed a Deep-RSET and 3 marker horizons since the purpose was to compare overall soil surface elevation with that of the forest sites. SETs were installed during October and November 2002, with baseline SET readings and feldspar marker placement occurring in December 2002. This was a minimum of 4 months post lightning strike. I monitored a total of nine Deep-RSET, six Shallow-RSET, and 27 marker horizons. Soil elevation and feldspar marker horizons readings were made at 4 (December 5-12, 2002), 9.5 (May 20-23, 2003), 14.5 (October 15-18, 2003), 18.5 (February 11-13, 2003), and 21 (May 5-7, 2003) months post strike.

Measurements were taken during low tide exposure. At a given site, all three-gap types (five SETs and 9 feldspar marker horizons) were sampled on the same day. The three sites were sampled over a 3 to 7 day period of daytime low tidal exposure.

Marker horizons were comprised of a 3-mm thick layer of white feldspar sprinkled on to the soil surface. Feldspar marker horizons were sampled by extraction of sediment cores. The cores were extracted with a 140 cc syringe (3.7 cm diameter) with the end removed and sharpened. After the syringe was removed from the ground, the soil plug was pushed through using the syringe plunger from below to minimize compaction. The soil plug was cut in two and three measurements of the accreted soil layer were taken. These values were averaged. Soil plugs were reformed and returned to the ground. At each location the three marker layers were averaged to determine the average amount of material accreted for the location. If the marker layer was not found I would resample, up to three cores. The marker layer would again be resampled during the next sampling event to confirm loss of the feldspar layer.

Data analysis

Root data were analyzed using a two-way analysis of variance (ANOVA) with gap type and site as main effects. Root size-class data were analyzed with a three-way ANOVA with root size class, gap type, and site as main effects. All root analyses were run on values standardized to g m^{-2}, following Cahoon et al. (2003). Soil bulk density, torsion, and compaction data were analyzed using one-way repeated measures ANOVA with gap type and time as the main effects. The repeated measure ANOVA model used mean values with no replication and the three-way interaction (site*age*time) was the error term (Hicks and Turner 1999). Normality was assessed by inspection of the half normality probability plots.

An assumption of this SET analysis was that the measurement at each level (direction and benchmark) was independent. For each SET in each gap type per sampling event the n was four. This design has been used by a number of researchers who used SETs (Day et al. 1999, Cornu and Sadro 2002, Ford and Grace 1998). I used one way and two-way repeated measures ANOVA for analysis of elevation and accretion data. Due to a site-specific confounding effect all SET were analyzed by site. Normality was assessed by inspection of the half normality probability plots for each time period. I used simple linear regression analysis to determine the relationship between the change in soil elevation (mm month^{-1}) and the change in river stage (mm month^{-1}). Normality of linear regression was determined by inspection of the residuals.

I tested the differences in the slopes of regression relationships using a modified t-test (Zar 1999). Tests were considered significant at $\alpha = 0.05$ except for those regarding live and dead roots, which were considered significant at $\alpha = 0.10$. I felt that this higher alpha level was necessary to mitigate the large variability commonly encountered with root sampling generally caused by decreased sample sizes. All models were analyzed using STATISTICA 5.0 (Statsoft, Inc., 1996) and SPSS 11.0.1 (SPSS, Inc., 2001).

Results

Live and dead roots

Overall, new gaps had more total (live and dead) root biomass than recovering gaps ($F_{(2,18)}$ = 8.32 $p<0.01$, Table 2 and 3), but total root biomass in new gaps and forest did not differ significantly. The interaction of site and gap type explained a significant amount of the variation in the amount of total roots ($F_{(4,18)}$ = 5.55 $p<0.01$). New gaps had twice as much dead root biomass as recovering gaps and the forest ($F_{(2,18)}$ = 13.50 $p<0.001$, Table 2). The interaction of site and gap type explained a significant amount of the variation in the amount of dead roots ($F_{(4,18)}$ = 2.62 $p<0.07$). For new gaps, I measured the difference between the three sites, with New Gap 3 (554 g m^{-2}) had a greater amount of dead roots than New Gap 1 (403 g m^{-2}) which was equivalent to New Gap 2 (279 g m^{-2}).

Recovering gaps had fewer live roots compared to new gaps and the forest ($F_{(2,18)}$ = 3.00 $p< 0.08$, Table 3). However, there was a strong interaction between site and gap type ($F_{(4,18)}$ = 3.49 $p<0.03$), apparently as a result of the large amount of live roots at Forest 2 (798 g m^{-2}) compared to the other forest locations (452 and 218 g m^{-2}, Forest 1 and 3, respectively). Even when the analysis was rerun with Forest 2 removed (leaving in New Gap 2 and Recovering Gap 2), there still was a significant gap type main effect ($F_{(2,16)}$ = 2.69 $p<.10$). Recovering gaps (277 g m^{-2}) had less live root biomass than new gaps (444 g m^{-2}) and were not different from forest (335 g m^{-2}). The difference between new gaps and recovering gaps was significant even when I removed all forest sites from the analysis ($F_{(1,12)} = 7.23$ $p<.02$). The differences in the main effect of gap type for total roots were a consequence of the amount of dead roots present. The site and gap type interaction for total roots was caused by the large amount of live roots at Forest 2 (mentioned above).

Very fine roots (<2 mm) combined across all gap types comprised the greatest proportion of live, dead, and total roots (overall mean 169.5, 170.7, and 340.2 g m^{-2}, respectively, Tables 1 and 2). There was a three-way interaction of total dead roots among gap type, size class of roots, and site ($F_{(8,54)} = 4.49$ $p<0.01$). This was a consequence of New Gap 3 having a large amount of very fine dead roots (519.9 g m^{-2}). Even when New Gap 3 was removed from the analysis, very fine roots still comprised the greatest amount of dead roots (133.8 g m^{-2}), but the interaction between root size class and gap type was no longer significant ($F_{(4,69)} = 1.67$ n.s.). Therefore, I believe root mortality in new lightning gaps does not select against a particular root size class, but rather reflects the size class distribution present at the location before the strike (Table 2).

Soil bulk density, torsion and compaction

Bulk density did not change over the study period ($F_{(3,12)} = 0.99$ n.s.), and in general, new gaps, recovering gaps, and the surrounding forest within each site did not differ. Site 2 had greater bulk density than the other sites ($F_{(2,12)} = 138.2$ $p<0.001$, Table 3). There was a site by gap type interaction with New Gap 2 having greater bulk density than Recovering Gap 2 and Forest 2 ($F_{(2,12)} = 28.9$ $p<0.001$).

Maximal torsional shear strength and compaction values were quite variable (Table 3, maximum and minimum values). The effect of gap type on the soil torsion was not significant ($F_{(2,12)} = 0.01$ n.s.). However, the main effect of site was significant ($F_{(2,12)} = 4.83$ $p<0.03$). The soil torsion at site 1 was lower than at site 2 but not different from site 3 (4.01, 4.87, 4.70 X 10^{-3} kg cm^{-2} respectively, Table 3). Soil compaction was also not different among gap types ($F_{(2,12)} = 1.81$ n.s.), but varied by site ($F_{(2,12)} = 4.08$ $p<0.05$). Soil compaction at Site 1 was not different from Site 2 but was different from Site 3 (7.55, 8.83, and 9.95 X 10^{-2} kg cm^{-2}, respectively, Table 3).

Maximal torsional shear strength and soil compaction varied seasonally ($F_{(3,12)} = 20.1$ $p<0.001$, $F_{(3,12)} = 34.4$ $p<0.001$, respectively, Fig 3a,b). The pattern did not have a simple relationship to river stage or percent soil water content. Torsion values were additionally affected by the interaction between time and site ($F_{(6,12)} = 5.51$ $p<0.006$), with site 1 and 3 following the seasonal pattern and site 2 having a slightly different pattern (Fig 3a). Compaction also showed a similar seasonal pattern with a time by site interaction ($F_{(6,12)} = 5.39$ $p<0.006$, Fig 3b).

Soil surface elevation

Seasonal patterns

I present the accretion, the elevation of the entire profile soil surface, the original soil surface, and shallow soil zone for each of the nine study locations (Fig 4). Site had a confounding effect on the interpretation of the soil surface elevation. The main effect of site interacted strongly with gap type and time

($F_{(4,27)} = 90.6$ $p<0.001$, $F_{(6,81)} = 6.98$ $p<0.001$, respectively). Therefore, I analyzed the effect of gap type within each site separately.

Two consistent patterns were evident in the elevation and accretion data. The first pattern was that deposition (when marker horizons were recovered) was similar for all the gap types within a site, and time had significant effect (ANCOVA covariate = site, $F_{(2,14)} = 1.14$ n.s, $F_{(3,45)} = 3.54$ $p <0.02$). As the study progressed, sediment accreted at similar rates within the sites (Fig 4). The annual deposition rate was 8.5, 5.4, and 6.0 mm yr^{-1} at sites 1,2, and 3, respectively.

The second pattern was an increase in the soil surface elevation of the Deep-RSET at 9.5 (May 2003) and 14.5 (October 2003) months post strike followed by a reduction back to near original elevation at 18.5 and 21 months (all but New gap 1 and 2, Fig 4). To investigate this pattern I analyzed the three forest locations together. I investigated only the forest locations because there should be no confounding effect from gap processes. Absolute soil surface elevation of the Deep-RSET for the three forest locations were similar ($F_{(2,9)} = 1.4$ n.s., Fig 4, Forest 1,2,3). Time had a significant effect on the soil elevation ($F_{(3,27)} = 39.0$, $p<0.01$). Months 9.5 and 14.5 had positive elevation (overall mean 5.25 and 6.28 mm, respectively). Months 18.5 and 21 had elevations near zero (-0.38 and –0.47 mm, respectively). These changes in soil elevation were a result of changes in the river stage. I found that the rate of change of the soil surface elevation of the forest had a positive linear relationship with the rate of change in Shark River stage [Soil elevation (mm $month^{-1}$) = 0.03 * Shark River Stage (mm month^{-1}) + 0.20, $F_{(1,46)}$ = 38.9, p <0.001, R^2 = 0.46]. I used the daily average river stage data to remove the daily tidal signal. As river stage increased the soil surface elevation increased. This water signal appears multiple times in the elevation data; at the three forest locations, the three recovering gaps and at New Gap 3 (Fig 4). A relationship between site hydrology and soil elevation is considered in detail for this mangrove forest (**Chapter 4**).

New gaps versus the forest

At New Gap 1, both the entire soil surface and original soil surface recorded an extremely large drop in elevation (-60.9 and -66.2 mm, respectively) during the first measurement period, 4 to 9.5 mo post strike. Forest 1 recorded a 1.5 mm gain for the entire profile and the original soil surface –4.4 mm during this same period. At site 1, for the entire monitoring period, the new gap lost 59.3 mm in absolute elevation whereas the forest gained 0.9 mm in absolute elevation ($F_{(1,6)}$ = 192.7 p<0.001). The loss in surface elevation gained at New Gap 1 was mainly a result of subsidence below the shallow soil zone. There was slight loss in shallow soil zone surface elevation (-2.5 mm) in the new gap, where as the shallow zone in the forest gained in elevation (7.4 mm, $F_{(1,6)}$ = 27.6 p<0.002). The gain in the shallow zone soil elevation at the Forest 1 was caused by deposition of material. The slopes of the accretion and shallow zone elevation relationships did not differ (t = 0.42 n.s., Fig 4 Forest 1). At New Gap 1 the three marker horizons were unrecoverable after the 14.5 month sampling, possibly a result of erosion or perturbation by crabs.

The entire profile elevation at New Gap 2 initially increased but then decreased for the remaining sampling periods (Fig 4 New Gap 2). Marker horizons were lost after the 14.5 month sampling at New Gap 2. The original soil surface, the entire profile and the shallow soil zone all recorded a similar elevation 21 months post strike (-8.5, -8.5, and -9.3 mm, respectively). Surface erosion appears to be the reason for the loss in soil surface elevation at this new gap. The entire profile elevation of New Gap 2 (-8.5 mm) was significantly lower than that at Forest 2 (0.3 mm, $F_{(1,6)} = 25.8$ $p<0.003$). The marker horizons at Forest 2 recorded slight erosion during the 14.5 to 18.5 month sampling period (-4.5 mm), however, surface erosion did not appear to greatly affect Forest 2. At Forest 2 the shallow zone soil elevation was not driven by accretion. The linear relationships for accretion and the shallow zone elevation over time had different slopes ($t = 5.13$ $p < 0.001$).

The entire profile surface elevation of the New Gap 3 and the Forest 3 had a similar pattern ($F_{(1,6)} = 0.28$ n.s., Fig 4). Subsidence occurred at New Gap 3 affecting both the shallow soil zone as well as the soil below. The elevation gain from accretion balanced with the elevation loss from subsidence so that the entire profile elevation remained stable near zero (-0.3 mm). Subsidence occurred at Forest 3 as well, however, this occurred mainly below the shallow soil zone. The gain in shallow zone elevation at Forest 3 was due to deposition of material. The slopes of the accretion and shallow zone elevation did not differ ($t = 1.88$ n.s., Fig 4 Forest 3). Overall, there was no difference for the original soil surface elevation between New Gap 3 and Forest 3 ($F_{(1,6)} = 0.02$ n.s., Fig 4).

Recovering gaps versus the forest

At site 1, the soil surface elevation for the entire soil profile of the recovering gap and the forest had similar patterns ($F_{(1,6)}$ = 4.27 n.s., Fig 4). In addition, both locations had similar subsidence patterns ($F_{(1,6)}$ = 2.13 n.s., Fig 4). Overall, absolute soil surface elevation remained near zero after 21 months (–5.4 mm Recovering Gap 1 and 0.9 mm Forest 1). There was a similar pattern at site 2. Change in entire profile elevation and the original soil surface elevation was the same for Recovering Gap 2 and Forest 2 ($F_{(1,6)}$ = 2.13 n.s., $F_{(1,6)}$ = 4.03 n.s., respectively, Fig 4). Additionally, time interacted with the elevation for both the entire profile and the original surface ($F_{(3,18)}$ = 4.3 $p<0.02$, $F_{(3,18)}$ = 3.5 $p<0.04$, respectively). The forest subsidence was consistent for the four sample events. At Recovering Gap 2, subsidence was least during the first sample period then similar for the next three samples. At Recovering Gap 3, the soil surface elevation of the entire profile and the original soil surface was lower than Forest 3 ($F_{(1,6)}$ = 13.9 $p<0.01$, $F_{(1,6)}$ = 8.3 $p<0.03$, respectively). At the end of sampling, the entire profile elevation was 3.4 mm for the Forest 3 and –4.0 mm for the Recovering Gap 3. Time had a significant effect and there was an interaction of time and gap type ($F_{(3,18)}$ = 59.6 $p<0.001$, $F_{(3,18)}$ = 3.3 $p<0.05$, respectively).

Discussion

In this study I was able to determine the effects of lightning disturbance on the soil surface elevation by sampling superficial roots, superficial soil strength, and monitoring the processes of accretion, erosion and subsidence. Because I was interested in the relationship of live and dead roots to the superficial values of bulk density, soil torsion and compaction, I limited the depth of the root cores to 0-10 cm. Additionally, processing these peat dominated root cores is very time consuming and as a compromise to have some replication within a study location, I opted for multiple short cores rather than a few longer cores. By using the combination of the Shallow-RSET, the Deep-RSET, and the feldspar marker layers I was able to determine if erosion or subsidence, which in this study is essentially root mortality and compaction, occurred. Furthermore, if subsidence occurred I could determine if it occurred in the shallow upper soil layer (0-35 cm) or below this layer. I was able to report erosion using the feldspar marker horizon technique because I recorded some superficial accretion over the layer and then a reduction in the material above the marker horizon or loss of the marker layer at a later sampling event. I have taken a conservative approach in the data analysis of this study in order to not overstate the findings in light of the limitations of root core depth and the averaging of soil parameters for the repeated measures sampling used.

I found that lightning strikes do indeed lead to a greater amount of dead roots (Table 2). New gaps had twice as many dead roots as the recovering gaps or the forest. Mangrove roots are highly refractory (Middleton and Mckee, 2001) and I feel that my sampling has adequately captured the pulse of dead roots from the lightning strike. Mortality was in general not size-class specific, but reflected a general mortality of roots present at the site pre-strike. The total amount of live roots was the same for the new gaps and the forest. Considering that the sample cores were collected within the center parts of the new gaps to minimize edge effects, I speculate that there was a rapid root exploitation of the new gaps by surviving saplings and surrounding forest trees. The lightning strikes appear to have killed a majority of the living roots present at the site pre-strike followed by rapid recolonization within the 9 months to post-strike sampling. This rapid root regrowth was unexpected since insufficient time had passed for invasion by newly recruiting seedlings. Some of these live roots in new gaps must belong to the saplings and seedlings that survived the lightning strike. This observation is supported by the finding that coarse roots (> 5 mm) comprised 44% of the live biomass in new gaps (Table 3). I believe that there was probably insufficient time for these large roots to develop since the strike occurred. At a hurricane impacted forest in Honduras only 35 % (mean) of new root production was > 2 mm after a one year ingrowth core study (Cahoon et al 2003), suggesting that my interpretation is correct.

In the recovering gaps, live root biomass was roughly half the amount found in either the new gaps or the intact forest. At this stage of recovery, recolonizing mangroves are under tremendous competitive pressure to allocate resources to aboveground stem elongation due to the high number of saplings (mean 0.98 m^{-2}) competing for light (compared to 0.13 m^{-2} for the intact forest Table 1). Smith and Lee (1999) found that under lower light conditions (reduced photon flux density) *R. mangle* seedlings had reduced root biomass because they allocated more energy to aboveground biomass. Additionally, I hypothesize that the rapidly growing saplings in the recovering gaps probably need only limited structural root support as they are aided by neighboring saplings for additional reinforcement. Recovering gaps have similar elevation patterns to the intact forest, however the recovering gaps have greater subsidence. These findings suggest that the effects of the lightning strike disturbance can impact surface elevation patterns for a long time especially in peat-dominated systems dependent on root production for maintaining soil surface elevation (i.e. recovering gaps have lower total superficial roots, Cahoon and Lynch 1997, Smith and Cahoon 2003, Cahoon et al 2003).

I hypothesized that as roots died in new gaps, the soil surface matrix cohesiveness would decrease, resulting in lower compaction (i.e. strength to penetrate the soil) and torsion and higher bulk density due to a reduction in root volume. I found neither an indication of a systematic reduction in torsion or compaction nor an increase in soil bulk density. Bulk density was generally an indication of site-specific conditions and not related to gap status. Maximal torsional shear strength and compaction both indicated no difference for the three types of forest status. There was no indication of the soil matrix becoming weaker (i.e. lower compact or lower shear strength), especially at the new gap sites. These results agree with the finding of rapid root exploitation of the new gaps indicating no loss of surface root stability at least at 9 mo post strike. It should be noted that the first measurements of soil bulk density, shear strength and compaction were not collected until 9.5 months post strike. There is the possibility of a reduction in the soil cohesion measurements before this sampling event. However, I believe this did not occur since there was no difference between in the status (new gap, recovering gap, intact forest) within a site. The repeat measures sampling design of this study does limit my ability to strongly test for gap status effects, however, I was interested in the time effect as it related to a progression to a soil collapse condition two years post strike (observation from Sherman et al. 2000).

This study is the first to provide direct evidence that lightning strike tree mortality can lead to loss of soil surface elevation within the gap area. In two of the new gaps, the soil surface elevation decreased while the forest elevation remained nearly unchanged. At New Gap 1, the majority of the loss in elevation was caused by sediment compaction (subsidence) below the shallow 35 cm soil zone. Even though the marker horizons were unrecoverable after the 14.5 mo sampling, I do not believe that the soil elevation loss was due to superficial erosion. I know this because the Shallow-RSET at New Gap 1 had a minor loss in elevation (-2.5 mm), whereas, the entire profile (Deep-RSET) had a loss of 59.3 mm in soil surface elevation. During this period the forest gained 0.9 mm in absolute elevation of the entire profile. I believe that compaction of the soil below the 35 cm depth at this site is probably a result of root mortality.

Since my dead and live root sampling was confined to the top 10 cm of the soil profile I cannot confirm this. Preliminary root sampling within this mangrove forest indicated a large variation in the vertical distribution of live roots with 37.3 % (± 9.3 se) of all live roots occurring in the top ten centimeters. In contrast, only 13.7 % (± 3.7 se) of total dead roots were accounted for in the top 10 centimeters of the core (6 cores, length varied from 30 to 65 cm in depth, unpublished data, Whelan and Smith). Other mangrove researchers have found that the majority of the fine live roots are produced in the top 50 cm of the soil profile in this mangrove forest using ingrowth core methodology; additionally they predict that there is a significant amount of large coarse roots biomass below this 50 cm depth (V. H. Rivera-Monroy, personal comm.). Furthermore, at an Indo-Pacific site, root sampling to 1 m depth found that fine roots comprise between 47 to 65 % of the total live root biomass (Komiyama et al. 1987). Assuming a significant amount of coarse root distribution is occurring below the shallower depth, I feel that root mortality, as a reason for soil compaction below the 35 cm soil zone, is possible.

Elevation loss at New Gap 2 was caused by surface erosion or root collapse in the top 35 cm of the soil profile. This was clearly evident at the 18.5 and 21 months post strike sampling when both the Shallow-RSET and the Deep-RSET had similar elevations (final elevations of -8.5 and -9.3 mm, respectively). In addition, the marker horizons were unrecoverable at this site after 14.5 months, possibly from erosion or bioturbation. Loss of marker horizons due to biological activities (grazing) has been attributed to vertebrate herbivores in a brackish marsh study in Louisiana (Ford and Grace 1998). However, I feel that the marker horizons at New Gap 2 were not lost due to bioturbation. Neither the Forest 2 nor Recovering Gap 2 lost marker horizons. Additionally, fiddler crab (*Uca thayeri*) burrows were surveyed at the 3 sites, in eight 1 m^2 plots. New Gap 2 and Recovering Gap 2 had similar densities (61.9 m^2 and 49.6 m^2) and both were significantly lower that the mean density of burrows of Forest 2 (115.6 m^2, $F_{(2,21)} = 51.7$ $p < 0.001$, **Chapter 2**). If I found increased burrow density I might suspect bioturbation of the marker horizon. Additionally, New Gap 2 is the closest of all the sites to the river (Table 1). Since elevation loss was recorded with the SETs and the marker horizons disappeared, I believe this elevation loss was partially due to superficial erosion.

During the first two sampling periods, the entire profile elevation increased at New Gaps 2 and 3. I believe this was caused by increased river water expansion of the peat substrate. Soil surface elevation at New Gap 3 tracked the forest pattern. The lack of decline in surface elevation at New Gap 3 could be caused by its small size compared (132 m^2) to the other new gaps (265 m^2 and 437 m^2). Additionally, the New Gap 3 had greater soil compaction (12.1×10^{-2} kg cm^{-2}) compared to the other two new gap sites (6.22×10^{-2} kg cm^{-2} and 7.82×10^{-2} kg cm^{-2}). Additionally, New Gap 3 had the third highest amount of live tree and sapling biomass (allometric estimates based on diameter at breast height measurements) of all the sites studied (Table 1). These factors taken together along with the short time period of this study (21 months) may have mitigated the effects of the lightning strike disturbance.

My study did not fully support the hypothesis that massive root mortality would lead to a reduction in the cohesiveness of the soil substrate, promoting erosion of the upper soil layer, which would result in a loss in soil elevation. In general, the soil surface elevation for the entire profile, as measured with the Deep-RSET, decreased post strike. I attributed the loss of surface elevation to erosion at one site and to subsidence at the other new gap site. This loss may be affected by increased root mortality; however, new roots (within the 10 cm of soil surface) appear to have rapidly recolonized the area. The soil matrix did not lose soil cohesiveness at least in the short time period of this study (approximately 21 months) and given the measurement techniques used. It will be important to follow how these results may change in a longer term study, especially as the new gaps are affected by the rain of tree trunk debris and tip-ups as the dead trees decompose and as seedlings invade this open space. Sherman et al. (2000) observed elevation loss two years post strike. I found evidence of elevation loss in the new gaps as early as 9.5 months post strike. In all likelihood, these losses in soil elevation will be apparent for many years since the overall deposition rate (across the all sites and gap types) for the entire sampling period was 6.57 mm yr^{-1} and correcting for shallow subsidence the absolute soil elevation expansion is near zero after 21 months for the three forest locations (0.9 mm, 0.3 mm and 3.4 mm, respectively). I found that recovering gaps, 7 to 10 yrs post strike, have similar soil elevation patterns as the forest at two of the three sites. Although the elevation pattern of Recovering Gap 3 indicated a loss, this may be caused by the combined effects of its “younger age” (shorter saplings and higher density of saplings) and proximity to a mangrove rivulet (Table 1). This loss in absolute elevation of the entire profile is from subsidence and not erosion (marker horizons were retained for the study period) suggesting that the subsidence is more likely related to age of the site rather than its proximity to the rivulet.

Lugo (1997) speculated in Florida that when aboveground mangrove forest has been removed by human activities the peat substrate oxidized and can be washed away by tidal actions. Although his study lacked quantitative data so direct comparison is difficult, the implication is that mangrove roots stabilize the peat substrate. A difference between a lightning strike disturbance and forest clearing could be the lack of any live roots able to recolonize the impacted area.

Lightning gap disturbances are smaller than hurricane disturbances but appear to have similar effects on belowground processes in the mangrove ecosystem. Rapid root decomposition and sediment compaction were the reasons for the massive mangrove peat collapse (–37 mm yr^{-1} for the first 2 years post impact) following Hurricane Mitch (Cahoon et al 2003). Soil torsion decreased and there was no root growth in the high impact sites (~ 100 % tree mortality). Peat collapse was predicted to continue for up to 8 years post hurricane impact. These results are similar to the findings of my study. I found soil subsidence (caused by consolidation or compaction) below the shallow root zone produced the largest elevation loss (-59.3 mm). Elevation patterns appear to return to the intact forest level 7 to 10 yrs post strike. The differences between the lightning and hurricane disturbances were that I found rapid root recolonization and I did not find a reduction in soil torsion. The small sizes of the lightning gaps (average 300 m^2) probably allow roots of the surrounding forest trees to colonize the unoccupied space.

The contrary findings relating to the soil torsion are probably caused by different sampling techniques used and different statistical analysis. The soil torsion sampling for Hurricane Mitch disturbance entailed sediment core removal and bisection for sampling with a Torvane sampler. Additionally, in this study I used a repeated measures design to detect change in torsion at a site over time and this reduced my ability to detect gap-type treatment differences.

As with hurricane disturbance, lightning strikes cause tree mortality, which can cause peat collapse that may facilitate specific species recruitment, and eventually influence the community forest structure trajectory. This is the second work to provide direct evidence that peat collapse maybe an outcome from discrete disturbance events in the mangrove ecosystem. These works taken together indicate the importance of including monitoring of soil elevation when trying to determine the mangrove community response to discrete disturbance events and when trying to predict species recruitment success. The mangrove species that comprise this forest are known to have seedling specific responses to surface flooding which may dictate survival. At a minimum, this study suggests that if *Rhizophora mangle* can exploit the increased flooding from soil surface elevation loss in new lightning strike gaps, then it would have to occur in the first 7 to 10 years. After this period of time the soil surface elevation patterns (recovering gap) reflect the intact forest eventually removing this opportunity.

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Table 1. Site description. Size of gap, depth of Deep-RSET benchmark (m), distance to main river, distance to rivulet, density of trees (≥4 cm dbh), density of saplings (< 4 m dbh), biomass of trees and saplings combined (kg), Density of seedlings (> 30 cm in height). All densities are standardized to per 500 m^2.

	Size (m^2)	Depth (m)	River (m)	Rivulet (m)	Tree	Sapling	Biomass (kg)	Seedling
New Gap 1	265	7.06	22		47	219	1362	1281
Recovering Gap 1	491	6.18	40		87	259	3376	719
Forest 1		8.61	27		45	109	4899	1219
New Gap 2	437	5.59	14	20	60	32	4129	781
Recovering Gap 2	486	4.06	37		97	271	3212	375
Forest 2		6.89	20	25	109	40	7634	1750
New Gap 3	132	7.01	30	10	85	15	5384	938
Recovering Gap 3	393	4.21	32	5	30	933	3122	219
Forest 3		4.08	40	20	57	52	6888	1688

Table 2. Mean mass (g m^{-2} ± 1 SE) of dead roots by size class for new gaps, recovering gaps, and forest. Cores are 10 cm in depth. Percentage calculated as of mean mass from mean total of dead roots in sample by forest stage. Values with similar letters are not different Tukey's post hoc test.

Forest Stage	<2 very fine	2-5 fine	>5 coarse	Total Dead
New	298 ± 185	62 ± 36	52 ± 76	412 ± 75 a
	72.3%	15.1%	12.6%	
Recovering	99 ± 45	36 ± 21	68 ± 98	204 ± 98 b
	48.7%	17.9%	33.4%	
Forest	114 ± 66	26 ± 29	43 ± 55	183 ± 55 b
	62.6%	14.1%	23.3%	

Table 3. Mean mass (g m^{-2} ± 1 SE) of live roots by size class for new gaps, recovering gaps, and forest. Cores are 10 cm in depth. Percentage calculated as of mean mass from mean total of dead roots in sample by forest stage. Values with similar letters are not different Tukey's post hoc test.

Forest Stage	<2 very fine	2-5 fine	>5 coarse	Total Live
New	152 ± 69	97 ± 37	194 ± 199	444 ± 151 a
	34.4%	21.9%	43.6%	
Recovering	169 ± 96	38 ± 27	69 ± 65	277 ± 133 b
	61.2%	13.8%	25.0%	
Forest	186 ± 85	108 ± 73	195 ± 299	490 ± 350 a
	38.0%	22.1%	39.9%	

Table 4. The overall mean (± 1 StDev), maximum, minimum value for bulk density, maximal torsional shear strength, and soil compaction per forest stage by site combination. The repeated measure ANOVA was run on mean values per sampling period with no replication and the three-way interaction was used as the error term. Values with similar letters are not different Tukey's post hoc test.

Forest Stage	**Bulk density G cm^{-3}**	**Maximal torsional shear strength kg cm^{-2} X 10 $^{-3}$**	**Soil compaction kg cm^{-2} X 10 $^{-2}$**
New Gap 1	0.159 ± .010	3.73 ± 1.58	6.22 ± 2.46
	0.169	5.67	7.92
	0.145	1.84	2.67
Recovering Gap 1	0.161 ± .011	4.40 ± 1.81	8.97 ± 3.63
	0.172	6.53	13.5
	0.146	2.28	4.65
Forest 1	0.145 ± .007	3.91 ± 1.80	7.46 ± 3.42
	0.154	5.76	11.9
	0.137	2.04	3.65
Overall Site 1	**0.155 ± .011 a**	**4.01 ± 1.59 a**	**7.55 ± 3.14 a**
New Gap 2	0.341 ± .045 **	5.18 ± 1.56	7.82 ± 2.29
	0.382	7.11	10.4
	0.300	3.42	5.56
Recovering Gap 2	0.229 ± .034	4.21 ± 0.54	6.75 ± 1.10
	0.254	4.93	7.88
	0.200	3.75	5.35
Forest 2	0.267 ± .050	5.23 ± 0.72	11.9 ± 3.92
	0.308	5.69	17.5
	0.240	4.16	8.82
Overall Site 2	**0.279 ± .055 b**	**4.87 ± 1.06 b**	**8.83 ± 3.37 ab**
New Gap 3	0.172 ± 016	4.76 ± 1.02	12.1 ± 3.47
	0.187	5.62	17.2
	0.150	3.29	9.30
Recovering Gap 3	0.167 ± 011	4.92 ± 1.40	9.09 ± 3.90
	0.180	6.78	14.4
	0.160	3.58	6.04
Forest 3	0.157 ± 013	4.43 ± 2.12	8.67 ± 5.87
	0.163	7.11	17.3
	0.148	2.22	4.13
Overall Site 3	**0.165 ± .012 a**	**4.70 ± 1.45 ab**	**9.95 ± 4.39 b**

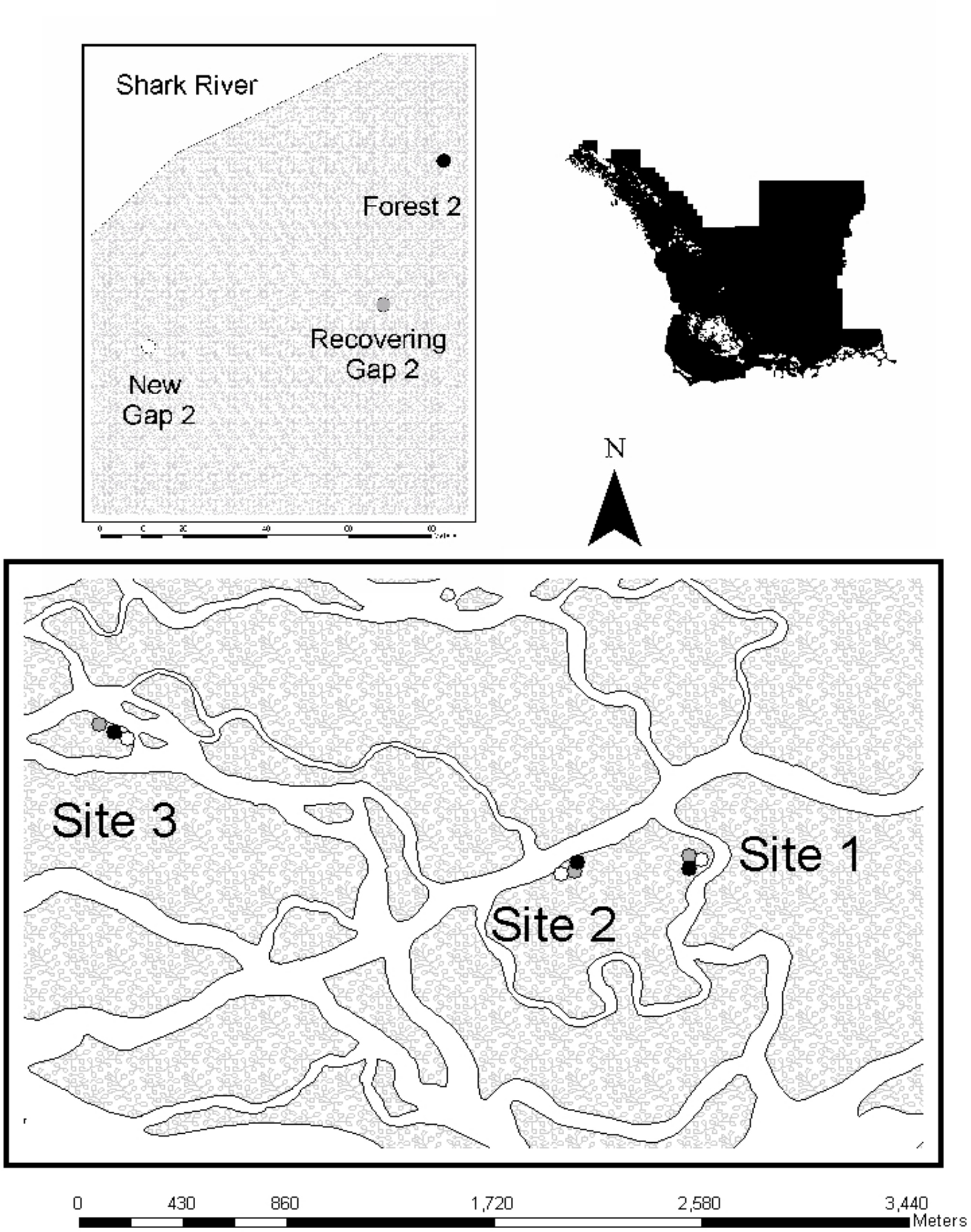


Figure 1 Location of three sites on the lower Shark River, Everglades National Park, Florida, USA. Open circles represent new gaps, gray circles growing gaps and dark circles are intact forest locations. More detailed view shown in insert of Site 2.

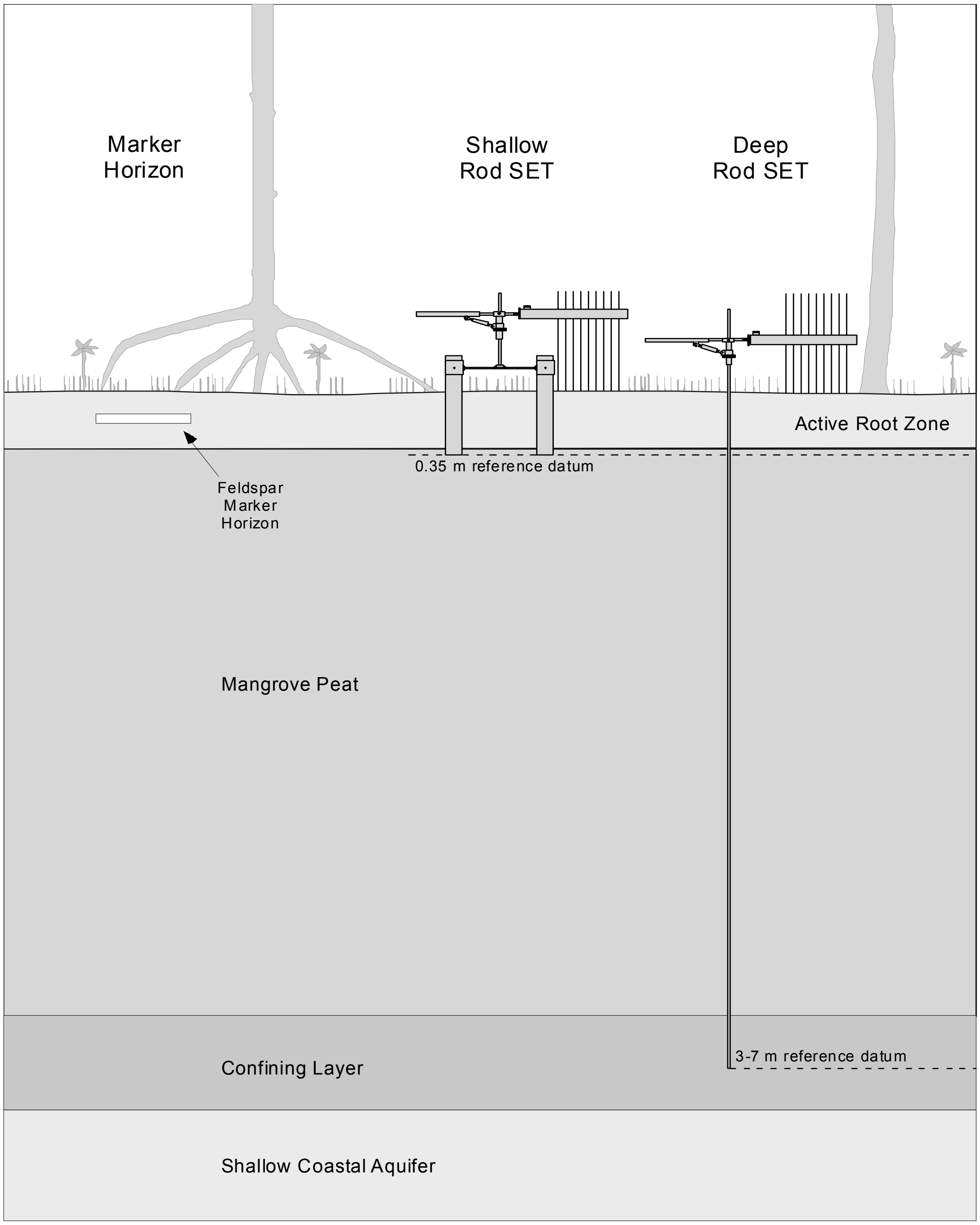
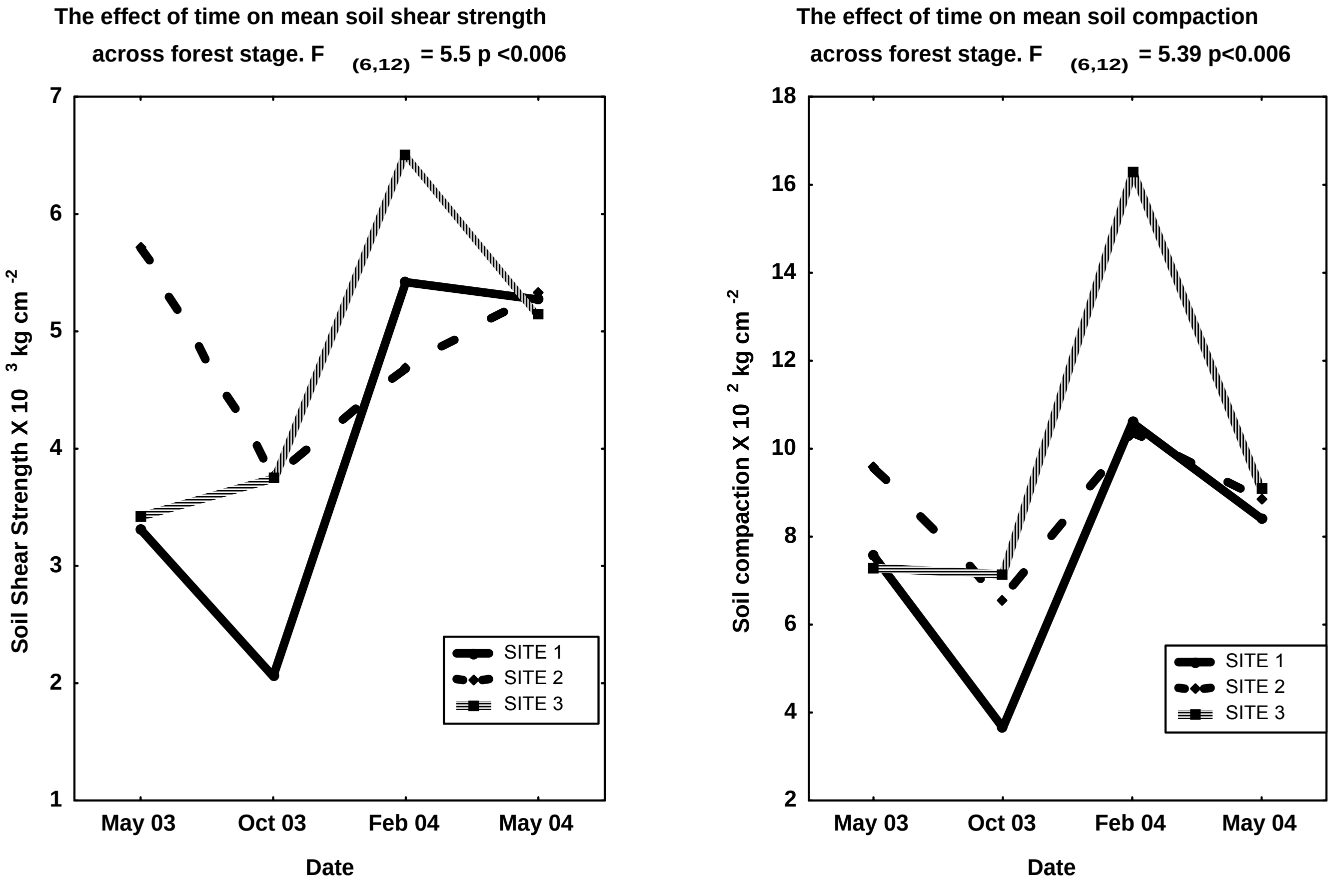


Figure 2. Profile of the substrate showing Deep and Shallow-RSETs and the relative depths of each benchmark. (Adapted from Cahoon et al. 2002b with permission of the author). Drawing at 1:24 scale.



The effect of time on mean soil shear strength across forest stage. F $_{(6,12)}$ = 5.5 p <0.006

The effect of time on mean soil compaction across forest stage. F $_{(6,12)}$ = 5.39 p<0.006

Figure 3. The interaction effects of time by site on mean soil shear strength and soil compaction across forest stage.

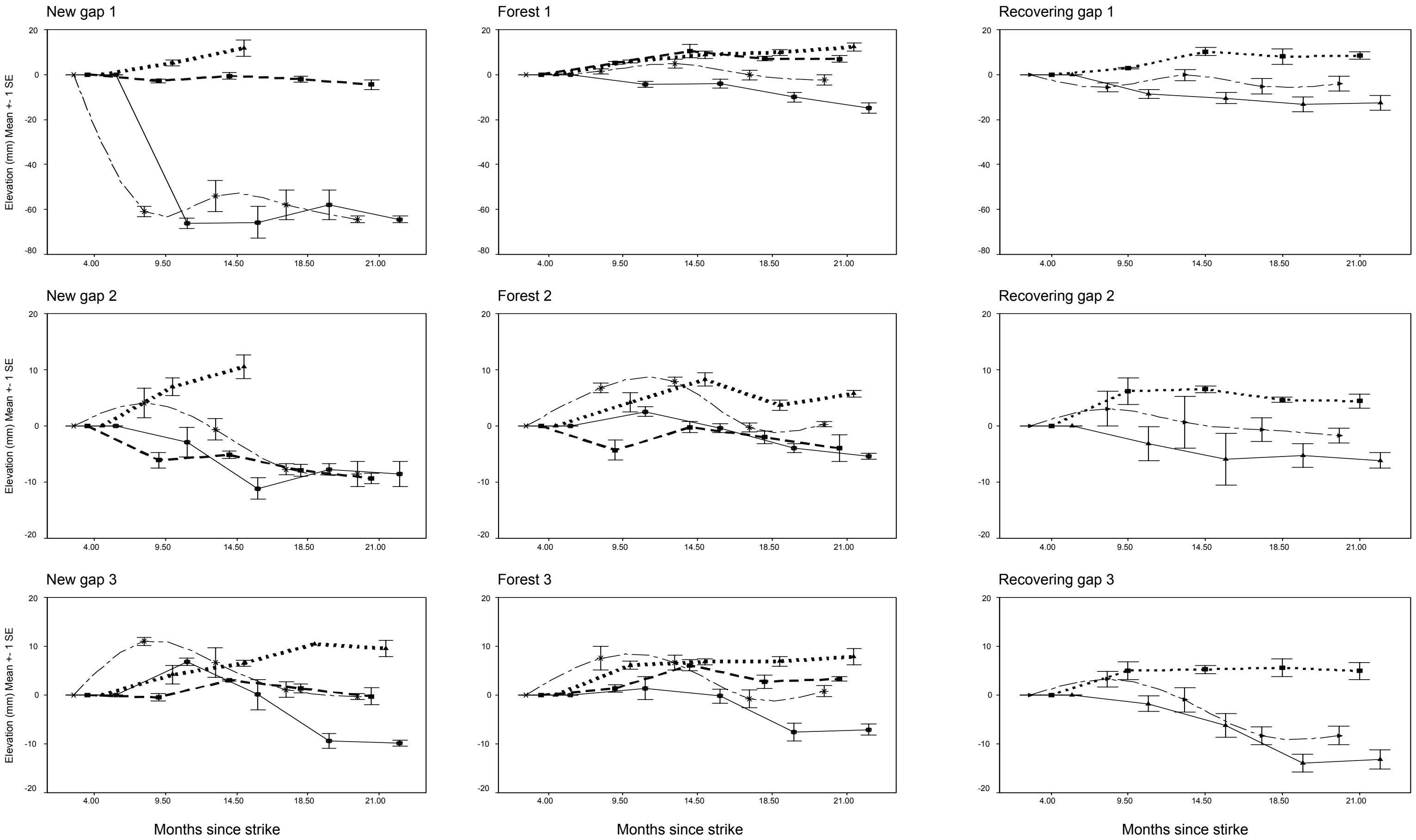


Figure 4. The absolute soil surface elevation (mean ± 1 SE) for the three forest stages (New, recovering, forest) at three sites (1,2,3). Accretion dotted line, Original soil surface solid line, surface elevation of Shallow-RSET dashed line, surface elevation of entire soil profile dot dash line (Deep-RSET).

Chapter V

Groundwater control of mangrove surface elevation: shrink-swell varies with soil depth.

Abstract

I measured monthly soil surface elevation change and determined its relationship to groundwater changes at a mangrove forest site along the Shark River, Everglades National Park, Florida. I combined the use of an original-design surface elevation table with new rod-surface elevation tables to separately track changes in the mid zone (0-400 cm), the shallow root zone (0-35 cm), and the full sediment profile (0-600 cm), respectively, in response to site hydrology (daily river stage, and daily groundwater piezometric pressure). In addition, we calculated expansion/contraction for each of the four constituent soil zones (surface [accretion/erosion; above 0 m], shallow zone [0-0.35 m], middle zone [0.35-4 m], and bottom zone [4-6 m]) that comprise the entire soil column. Changes in groundwater pressure correlated strongly with changes in soil elevation for the entire profile (Adj. $R^2 = 0.90$); however, this relationship was not proportional to the depth of the soil profile sampled. The change in thickness of the bottom soil zone accounted for the majority ($R^2 = 0.63$) of the entire soil profile expansion and contraction. The influence of hydrology on specific soil zones and absolute elevation change must be considered when evaluating the impact of disturbances, sea level rise, and water management decisions on coastal wetland systems.

Introduction

Soil surface elevation is an important response variable in wetland environments (Childers et al. 1993). Soil elevation affects hydroperiod, inundation frequency, and soil oxidation-reduction state. In turn, the hydrological conditions of a site are also known to substantially affect soil processes including sedimentation, erosion, and the shrink and swell of soil materials. Additionally, soil elevation and surface flooding have been identified as important factors in wetland species colonization, recruitment and survival (McMillan 1971, Rabinowitz 1978ab, McKee 1993, 1995, Ellison and Fransworth 1993, Cornu and Sadro 2002). Changes in soil surface elevation can be an important indicator of soil processes that are linked to hydrology, as well as those attributed to bioturbation (Ford and Grace 1998), decomposition (Cahoon et al. 2003), and subsidence (Cahoon et al. 1995). Soil surface elevation change is an integration of several processes occurring within the soil profile; yet most methods used to measure surface elevation changes do not distinguish among processes within the profile (Kaye and Barghoorn 1964; Childers et al. 1993; Cahoon et al. 1995). For example, the elevation loss from subsidence and the elevation gain from accretion are incorporated into the absolute change in soil elevation. However, it is possible to partition the change in soil elevation into its component processes of surface accretion, and subsurface expansion or compaction using the surface elevation table – marker horizon approach (Cahoon et al. 1995).

In a 3-year study of a coastal mangrove forest along the Shark River, Florida Everglades, soil surface elevation was found to vary linearly (R^2=0.38) with surface water stage 15 to 30 days prior to sampling (Smith and Cahoon 2003). The investigation was limited in that the benchmarks used to measure soil elevation extended just 4 m into the soil and stopped approximately 2 m above the limestone bedrock. Consequently, processes occurring below the 4 m deep benchmark were not included in the elevation readings. Additionally, the influence of processes within the active root zone (e.g., root growth/decomposition or shrink/swell) on soil elevation could not be determined because the benchmarks integrated processes over the entire 4 m soil column. Because of these limitations we added sampling devices, which allowed us to measure the shallow active root zone (0-0.35 m) and the deeper soil zone (4-6 m).

I present here a study of soil elevation dynamics in the lower Shark River drainage that extends over the entire soil profile and distinguishes between three depths within the soil profile; the 0-0.35 m, 0-4 m, and 0-6 m. My main objective was to investigate the relationship among changes in soil surface elevation and changes in the hydrological parameters of river stage and groundwater piezometric head pressure at the site over the three depths. Additionally, we wanted to determine the relative contribution to soil elevation by each of the four components of the soil profile: surface (i.e., accretion), shallow zone (active root zone; 0 – 0.35 m), middle zone (0.35 – 4 m), and bottom zone (4 – 6 m).

A comprehensive understanding of the influences of hydrology on the soil profile at this site is of considerable importance. The site is located in the Shark River estuary, downstream of the Shark River Slough, and receives freshwater inputs from the greater Everglades drainage and thus is under the influence of upstream water management practices of the Greater Everglades. The Everglades drainage is currently undergoing an ecosystem restoration concentrating on modifying water deliveries to mimic pre-drainage flows. In addition to the changing freshwater flows linked to restoration, this mangrove forest is impacted by sea level rise. Determining how hydrology influences the specific soil zones and surface elevation will allow managers to make more informed decisions regarding these two opposing hydrological processes.

Materials and Methods

SET theory

The Surface Elevation Table (SET), based on the design of Boumans and Day (1993), allows for precise measurements of soil surface elevation (± 1.4 mm total error; Cahoon et al. 2002a). The SET consists of a mechanical arm that is attached to a benchmark and leveled, establishing a fixed measuring point. Typically each SET has four fixed measurement locations (directions), where nine measuring pins are lowered to the soil surface to obtain a relative soil elevation. The elevation is the mean of 36 measuring pin readings per benchmark. SETs have been successfully used to monitor changes in elevation in a number of wetland environments (Cahoon et al.1999). They have been used to monitor mangrove vertical accretion and subsidence (Cahoon and Lynch 1997) and to follow the response of soil elevation to season (Childers et al. 1993), water management (Boumans and Day 1994, Hensel et al. 1999), vertebrate herbivores (Ford and Grace 1998) and hurricane disturbance (Cahoon et al. 2003).

New SET designs have recently been described that measure the change in soil elevation of specific parts of the soil profile (e.g. root zone, below the root zone; Cahoon et al. 2002b). At the Shark River, the shallow-rod surface elevation table (Shallow-RSET) benchmarks were installed to a depth that measures elevation change in the majority of the active root zone (top 0.35 m of the soil profile). The deep-rod surface elevation table (Deep-RSET) benchmarks were driven to bedrock and thus measure the full soil profile. The original design SET (Original-SET) benchmarks used by Smith and Cahoon (2003) were driven to ~ 4 m (Fig. 1). Further information on the design and accuracy of the original SET and RSET can be found in Cahoon et al. (2002a; b). By using a combination of SET designs at a single study site it is possible to partition changes in soil elevation among specific parts of the soil profile, such as the shallow root zone and deeper soil zones (Fig. 1). By determining the absolute change for each depth zone we can calculate expansion and contraction for each zone (surface [accretion/erosion; above 0 cm], shallow [active root; 0-0.35 m], middle [0.35-4 m], and bottom [4-6 m]) of the profile.

Site description

Vegetation

The study site, SH3 of Smith and Cahoon (2003), is located near the mouth of the Shark River (Zone 17 N 2805254 mE. 0492112 mN., UTMs WGS 1984) in a mature mixed mangrove riverine forest comprised of *Rhizophora* *mangle* L. (red mangrove), *Laguncularia racemosa* (L.) Gaertn. (white mangrove), and *Avicennia germinans* (L.) Stearn (black mangrove). The site has a sparse understory. The canopy ranges in height from 13 to 17 m. The site has mixed tides. During the study period the Shark River had a daily average conductivity of 40 mS cm $^{-1}$ and varied between a low of 25 mS cm $^{-1}$ to a high of 51 mS cm $^{-1}$. Shark River discharge was greatest at the end of the wet season, from September to November for 2002.

Soil profile

The soil profile of this site was determined from the well drilling log (G. Anderson, unpublished, Fig 1). The mangrove peat was 5.5 m in depth. The peat matrix lay directly on top of limestone, into which the well was drilled 1.8 m. The transition between the peat matrix and limestone was rapid. The limestone-peat interface was difficult to drill but had softer material below it. Otherwise, the entire peat layer was of similar constituency. No clay deposits were encountered during the drilling.

Cohen (1968) described the stratigraphy of the mangrove soil column at the mouth of the Little Shark River, a location approximately 2.5 kilometers away from SH3. He found that the mangrove peat was 3.81 m in depth and the total depth to bedrock at the site was 3.86 m. The peat types did not have recognizable petorgraphic constituents. All of the peat types were marine or brackish and dominated by *R. mangle*. There was a general increase of fine granular debris at the top and bottom of the profile. Fine granular debris comprised approximately 35 % of the sample at the top and the bottom of the core. At the top of the core it was suggested that an increase in fine-grained marine carbonates were responsible for this high number. The increase in fine granular debris at the bottom of the core may be due to greater amount of degradation of the organic constituents of the peat. Pyrite content was relatively high (2 % to 18%) throughout the core suggesting reducing conditions. Fusinite only occurred at the bottom of the core and comprised a small percentage of the constituents. There were no clays reported from this core.

Additionally, preliminary sampling of the mangrove peat hydraulic conductivity (at a site 4 km away) yielded relatively low values (hydraulic conductivity field saturation method (Guelph permeameter) = k_{fs} = 1.87 m day $^{-1}$, see Hughes et al. 1998), which suggest slow water transmittance through the surface layer of the peat (Anderson et al. 2001).

SET installation

I installed three groups of SETs within 18 m of each other and 45 m of the Shark River. All groups were within 15 m of a United States Geological Survey (USGS) hydrological monitoring station (USGS station # 252149081044301, described below). Each group included one Shallow-RSET, one Original-SET, and one Deep-RSET along with four feldspar marker horizons (Cahoon and Turner 1989). The three Original-SETs, used in the Smith and Cahoon study (2003), were installed on July 16, 1998. Three Shallow-RSETs and three Deep-RSETs were installed on February 28, 2002 (Table 1). On March 18, 2002, four separate layers of feldspar (0.5 - 3 mm deep) were laid as marker horizons with each group for a total of twelve new marker horizons. Shallow-RSETs benchmarks were installed to a depth of 0.35 m. The original-SET benchmarks (76 mm (3”) diameter aluminum pipe (1 mm thick wall) were driven approximately 4 m deep. The Deep-RSET benchmarks (1.43 cm (9/16”) diameter stainless steel rods) were driven to approximately 6 m deep (Table 1). All SETs and feldspar markers were measured monthly from March 18, 2002 to March 21, 2003. Measurements were taken during low tide exposure on the same day. Two sampling events occurred with minimal water (a few puddles) present on the soil surface. On November 9, 2002 and on February 10, 2005 we surveyed the elevation of only the group number 3 Shallow-RSET, Original-SET, and Deep-RSET with standard survey methods (± 3 mm). There was no movement of the SET devices, over this period of 2 yrs 4 mos, in relation to an established benchmark, suggesting that the assumption of a stable datum (Childers et al. 1993, Cahoon et al. 1995, Cahoon and Lynch 1997, Cahoon et al. 2002b) was valid during the study (Table 1).

Hydrological data

The hydrological conditions investigated were (1) daily rate of change in groundwater piezometric pressure and (2) river stage. Groundwater head pressure was collected from a USGS station installed at the site in 1996 (Anderson and Smith 2005, Fig. 1). A piezometer recorded groundwater head pressure of the shallow coastal aquifer in a layer of limestone (hereafter referred to as groundwater). The 7.33 m piezometer consisted of threaded 7.62 cm diameter PVC pipe that was screened (0.20 slot PVC) from 5.7 m to 7.2 m depth. The slotted part of the well was entirely within the limestone. The well was sealed with "formation packer" at 5.5 m depth, the interface of the limestone and the peat layer to prevent vertical flow. Piezometric head pressure measurements were collected at hourly intervals. The pressure transducer was located at the depth of the well screen (further details see Anderson and Smith 2005).

Shark River stage data were obtained from the "Shark River" hydrological monitoring station of Everglades National Park located 2.37 km downstream from SH3. This station records tidal influences as well as seasonal changes in river discharge for the area. Tidal flooding occurred at the site when the Shark River stage was above 0.07 m (Fig 2b). Shark River stage data were collected hourly. The groundwater piezometric head pressure and the Shark River stage were reported in North American Vertical Datum (NAVD) 88 datum (Geiod 99) (Fig 2). Hourly Shark River stage and groundwater head pressure for the interval from December 13, 2002 to January 9, 2003 is included in Fig. 2b and 2d. I used daily averages of the above parameters in order to remove the diurnal tidal signal. The daily averaged signal of these parameters shows the monthly lunar influences on the tide (Provost 1973), annual change in sea level (Provost 1973), and the seasonal changes in water level due to regional wet season (Fig 2a and c). The hourly tidal signal was assumed to have minimal impact upon my SET measurements because elevation data were always collected at low tide. Sensor malfunction resulted in the loss of daily groundwater piezometric head pressure data from October 7, 2002, to November 8, 2002, an interval that included the October 10 SET sample measurement.

Data Analysis

Soil elevation at each SET benchmark was averaged across all measuring pins at four directions (n=36) for each sampling event. To determine the average daily rate of change (DRC) in the soil elevation between sampling events we used the following formula:

Daily rate of change = average soil elevation ($X_{t+1} - X_t$) / (# days in interval)
(1)

Where X_t is average elevation at time t and X_{t+1} is the average elevation at time t+1. The daily rates of change for all hydrological metrics were determined in a similar fashion. For example, river stage averaged for day X_{t+1} was subtracted from river stage averaged for day X_t and divided by the number of days in the interval. The daily average hydrological metrics were used in the analysis to remove hourly tidal effects (Fig. 2).

Within the three SET types, we used forward stepwise multiple regression to investigate the relationship between daily rate of change in soil elevation for each of the three benchmarks and the rates of change in the hydrological parameters and accretion. Stepwise multiple linear regression was used to discern the most important hydrologic variables associated with incremental elevation change. Stepwise regression not only allows for the identification of the most parsimonious model, but accounts for correlation among two or more variables (Zar 1999). All parameters included in the models were tested for collinearity and normality of the residuals (Quinn and Keough 2002). All models were analyzed using STATISTICA 5.0 (Statsoft, Inc., 1996) and SPSS 11.0 (SPSS, Inc., 2001). The final models included the two hydrological parameters: (1) daily rate of change in groundwater piezometric pressure, and (2) daily rate of change in river stage. Within each SET type, we used a data set reduced from 36 data intervals (12 monthly intervals X 3 benchmarks) to 30 data intervals as a result of the hydrological data gap for groundwater piezometric pressure. Because there was only one well at the site, the hydrologic data was used three times, once for each SET type analysis. This may call into question the independence of the hydrology well data. I felt justified in presenting the hydrologic data with individual SET data for two reasons: 1) to emphasis small scale spatial variation in soil surface elevation; 2) we had no reason to expect hydrological variation over this small distance mainly due to consistency in the soil matrix.

I felt that regression using interval rate of change (as opposed to a regression of cumulative change) was justified because the focus of the study was to discover the relationship between elevation change and hydrologic variable from one sampling interval to the next. Furthermore, interval data should reduce the influence of any serial correlation. Due to the length of time between samples (monthly intervals), we felt that there was little influence of prior values on the relationships within a given interval. Regressions between the interval rate of change of soil elevation and the interval rate of change of hydrologic variables have been used previously (Childers et al. 1993).

By using the absolute change for each benchmark depth sampled by the three types of SET (Shallow-RSET, Original-SET, and Deep-RSET) we could calculate expansion and contraction for each component of the soil profile using the following formula.

Entire profile expansion/contraction = Accretion + (Shallow-RSET – Accretion) + (Original-SET – Shallow-RSET) + (Deep-RSET – Original-SET).

(2)

Thickness of the entire soil profile is equal to the sum of surface accretion (above 0 m), and changes in thickness of the active root zone (0-0.35 cm), the middle zone (0.35 - 4 m), and the bottom zone (4-6 m).

Results

Site hydrology

Both seasonal and monthly lunar influences were important for the hydrological conditions at the site (Fig. 2). The highest monthly mean stages at the Shark River were in September and October (-0.23 and –0.19 m respectively), typical for this drainage. The high river stage was a result of the maximum discharge of accumulated water from the wet season (June to

September, Fig. 2). Groundwater piezometric head pressure was also high during September and October (0.06 and 0.12 m respectively) due to hydrological recharge from the wet season. Daily river stage was a reflection of monthly lunar tidal flooding, wet season river discharge and annual sea level variability (thermal expansion, Provost 1973).

There was moderate correlation between the two hydrological metrics used in the multiple regression with an r = 0.72 for Shark River stage to groundwater piezometric head pressure. Tolerance values were above 0.547 and Variance Inflation Factors were less than 1.829, suggesting that despite some correlation between predictor variables, collinearity was not a serious issue for these data (Quinn and Keough 2002; Neter et al. 1996).

Accretion

The feldspar marker horizons did not become completely covered until 172 days after installation (September 10, 2002). The marker horizons were covered with mineral, organic and root matter. The annual accretion rate was 6.64 ± 0.56 mm yr^{-1} (± 1 SE). Sediment deposition values were intermittent in nature with high rates in October 2002 and March 2003 (Fig. 3a). Slight erosion was evident during the November to December 2002 period (-1.8 mm) and the December 2002 to January 2003 (-0.8 mm) sampling.

Soil elevation

Changes in absolute soil surface elevation for both the Deep-rod and Original- SETs followed a similar pattern (Fig. 3c and d). Both devices recorded the highest mean soil elevations at the end of the wet season (8.89 mm on October 10, 2002 for the Original-SET and 15.14 mm on November 9, 2002 for the Deep-RSET) and the lowest mean elevations during the dry season (January 09, 2003; -2.24 mm and -0.06 mm respectively). The Shallow-RSETs had a distinctly different pattern of soil surface elevation, with the highest elevation at the end of the wet season (6.83 mm on November 9, 2002) and the lowest early in the wet season (-0.66 mm on June 03, 2002, Fig. 3b).

Relationships between soil elevation and hydrology

The daily rate of soil elevation change of the Shallow-RSET was partially explained (Adjusted $R^2 = 0.16$) by a negative relationship with the daily rate of change of the river stage at the site (Table 2). That is, as river stage increased, the soil elevation that was influenced by the shallow soil zone decreased (Fig. 4a). The rate of soil elevation change of the Original SET was positively related with the daily rate of change of the groundwater head pressure (Adjusted $R^2 = 0.61$; Fig. 4b; Table 2). This model was run with a reduced data set (n=28) due to a one time sampling error of Original SET 2. The daily rate of change of soil elevation for the Deep-RSET had a strong positive relationship to the daily rate of change of the groundwater head pressure (Adjusted $R^2 = 0.90$; Fig. 4c; Table 2).

When groundwater head pressure increased the soil elevation increased for both the Original SET and the Deep-RSET.

Contribution of each zone to expansion/contraction of the entire profile

I calculated the variation in thickness of each of the four constituent soil zones (Eq. 2) and for the entire soil profile. I determined how much each of these soil zones contributed to absolute change of the entire profile by using a stepwise multiple regression model in which absolute change in the thickness of the entire profile was the dependent variable and the absolute change in thickness for each soil zone were independent variables.

The contribution of each soil zone was not equivalent to the relative proportion of soil profile it comprised (Fig. 5). The bottom zone (4-6 m) accounted for 63% of the variation in the absolute change in thickness of the complete profile whereas the middle zone (0.35 – 4 m) accounted for only 22% (Table 3, Fig. 5). However, the bottom zone comprises only 31% of the entire profile whereas the middle zone comprises 63%. Accretion and the shallow zone were not significant contributors to the overall absolute change in thickness of the entire profile (Table 3).

Discussion

The soil surface elevation changed substantially during the year; the Deep-RSETs recorded the greatest average elevation (15.14 mm) at the end of the wet season (November 09, 2002). The patterns of cumulative change in soil surface elevation were very similar for both the Deep-RSET and Original-SET, but the pattern of the Shallow-RSET was distinctly different (Fig. 3). The overall annual accretion rate of 6.6 mm yr^{-1} was similar to the 4.4 to 7.8 mm yr^{-1} reported in another mangrove study in SW Florida (Cahoon and Lynch 1997). The influence of accretion and/or erosion on the change in soil elevation was minimal over the duration of this study, as it was not a significant factor in any of the regression models. Furthermore, elevation for all three SETs had changed substantially before accretion at the site was even measurable, indicating the importance of subsurface processes. In addition to accretion and soil swelling, shallow and deep subsidence have been reported to be significant factors for the interpretation of soil elevation change (Cahoon et al 1995). Here we were able to account for the opposing influences of subsidence and soil swelling by sampling the entire soil profile while including deposition/erosion in multiple regression models.

Subsurface hydrological processes and soil elevation change

The entire mangrove peat-dominated soil profile was strongly influenced by groundwater. The rate of change in groundwater head pressure had a strong positive linear relationship to the rate of change in soil surface elevation for the Deep-RSET (Adj. R^2=0.90), suggesting that the entire soil profile is swelling in response to hydrological recharge. In this area, change in the daily groundwater piezometric pressure reflects freshwater recharging of the estuary and monthly tidal influences. Other mangrove SET researchers (e.g., Cahoon and Lynch

1997; Smith and Cahoon 2003) have reported seasonal response to soil elevation. However, a direct relation to forcing by a hydrological parameter has not been previously shown. Because this particular peat has relatively low superficial hydrological conductivity and is typically continuously saturated, peat swelling may not be the only mechanism explaining this relationship. Nevertheless the tight coupling suggests this is the most likely mechanism driving changes in soil elevation.

Soil shrink-swell has been reported numerous times but almost exclusively in regards to soils with high clay compositions (Hillel 1971). As far as the author's are aware there are few reported shrink-swell observations in regards to wetland soils composed almost exclusively of peats driven by changes in groundwater head pressure. Those studies reported are confined to *Sphagnum* peatlands (Price and Schlotzhauer 1999) along with one reference to surface elevation changes in a saltmarsh, but this was linked to semidiurnal surface tidal flooding (Nuttle et al. 1990). My study indicates that changing groundwater head pressure was driving the monthly shrink-swell of the soil surface elevation in this peat matrix. Another study (Cahoon and Lynch 1997) suggested the importance of mangrove peat shrink and swell, in addition to growth/decomposition and shallow subsidence as possible mechanisms for explaining annual elevation patterns. In my study, we were able to show that the peat matrix undergoes shrink and swell and that the majority of the expansion/contraction occurs in the bottom zone.

The shallow soil zone

Soil elevation over the depth of the root zone had a moderate relationship with the daily rate of change in Shark River daily stage (adjusted $R^2 = 0.16$). The first five sampling events recorded no deposition since marker horizons were not completely covered; yet we recorded substantial change in surface elevation influenced by the shallow soil zone suggesting belowground influences. It should be noted that the marker horizons showed progression towards complete coverage by having less of the marker horizon visible each of the five successive sampling events. I were able to remove the influence of deposition and erosion by determining the relationship between thickness of the shallow zone (0-35cm) and river stage. As daily rate of change for the river stage increased, the thickness of the shallow active root zone decreased ($R^2 = 0.24$, $F_{(1,34)} = 10.57$ p <0.004). This analysis indicates that changing river stage has a stronger influence than previously noted for elevation change; however, it is still only a moderate relationship. The lack of a strong hydrological link to the shallow soil profile is not wholly unexpected. Biological (root growth, crab burrow dynamics) processes rather than strictly hydrological influences dominate this shallow soil zone. Other possible explanations for the lack of a strong hydrological coupling are a shift in redox to more reducing conditions, or a decline in root growth.

Erosion and deposition were not a great influence in explaining the change in surface elevation of the Shallow-RSET over the short period of this study for the following reasons: 1) The rate of deposition/erosion was not a significant parameter in the Shallow-RSET model; 2) the first five sampling events indicate substantial change in surface elevation influenced by the shallow soil zone when no deposition / erosion was measured; 3) the model was rerun for only those periods with marker horizons measurements and no difference was found in the final model.

Cumulative proportion of profile sampled and the role of the bottom zone.

The response of the soil elevation change does not appear to be directly proportional to the depth of the soil profile encompassed by the SET device. The Original-SET (0-4m) followed the groundwater influence (R^2 = 0.61), but not as strongly as the Deep-RSET (0-6 m; R^2 = 0.90). Compared to the Deep-RSET, the Original-SETs encompassed 2 m less of the soil profile, which reduced the coupling between change in soil elevation and change in groundwater piezometric pressure (slope of the regression equation $ß_1$ = 0.040 for the Original-SET vs. $ß_1$ = 0.074 for the Deep-RSET, Table 2).

I used the proportion of the soil profile sampled by the Original-SET as compared to the Deep-RSET to predict the average elevation of the Original-SET based on the corresponding Deep-RSET readings. For example, Original-SET number one benchmark depth was 4.04 m and the Deep-RSET number one benchmark depth was 5.47 m, resulting in a proportion of the entire soil profile sampled by Original-SET number one of 0.74 (i.e., 4.04 / 5.47 m). If the relationship was linear with proportion of soil profile sampled then the actual values should fall near the calculated values along the one to one line (Fig. 6). The values predicted for Original-SET based on this ratio were higher than the actual elevation values recorded (Fig. 6), suggesting that the deepest 2 m of peat not encompassed by the Original-SET have a disproportionately larger influence on the absolute soil elevation.

To further corroborate the importance of the influence of the bottom zone on overall soil profile expansion and contraction; we determined the percent of variation explained by each component zone to overall soil column expansion and contraction. I determined that the largest constituent zones, the middle and bottom zones drive the expansion and contraction of the entire profile. These two parts account for 94.2 % of the soil profile and explain 85 % of the variance in overall soil profile expansion and contraction. However, the bottom zone accounted for 63% of the variation in the absolute change in thickness but comprised only 31% of the profile. The middle zone accounted for only 22% of the variation but comprised 63% of the profile (Table 3; Fig. 5). These data suggest that the bottom zone has a greater influence on overall change in soil surface elevation than would be expected based on its relative proportion and that in this zone changing ground water pressure would be the most influential.

My results indicate that increases in groundwater flow should have a direct positive impact on absolute soil surface elevation for the entire soil profile by expanding the bottom soil zone. Since expansion and contraction affects the water storage potential of the peat matrix it is an important consideration for studies of water balance, and nutrient fluxes (Nuttle et al. 1990). The current hydrological restoration of the Everglades and increases in sea level will directly affect this mangrove forest. Any modification to freshwater flows via the

Everglades Restoration will affect the elevation of the mangrove forest by expansion and/or shrinkage. In order to determine how other processes (bioturbation, organic production, decomposition, disturbance, and subsidence) will affect long-term change in soil surface elevation, researchers must account for this shrink and swell signal and remove it from the analysis. The influence of these hydrological processes must be taken into account in the context of monitoring the effects of hydrological restoration or sea level rise. Understanding the factors influencing the change in soil elevation as it relates to different parts of the soil profile will be critical when trying to predict long-term mangrove sustainability in an increasing sea level environment.

Acknowledgments

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Table 1. Depth of benchmark (m) for each SET and dates of establishment. Elevations for Group 3 SETs (mm) only with the first elevation on November 02, 2002 and second elevation on February 10, 2005 (NAVD 88 Geido 99).

Device Establishment Date	Group 1	Group 2	Group 3	First Elevation	Second Elevation
Shallow-RSET February 28, 2002	0.35	0.35	0.35	338	338
Original-SET July16, 1998	4.04	4.09	4.32	405	405
Deep-RSET February 28, 2002	5.47	6.08	6.57	131	131

Table 2. Regression equations and statistical results for daily rate of change (DRC) of surface elevation and DRC of best-fit hydrological parameters for the three SET types used in this study.

Y (dependent variable)	m (slope)	x (independent variable)	b (intercept)	F	df	Adj. R^2	N	P
DRC Shallow-RSET	-0.012	DRC River Stage	0.08	3.69	2,27	0.16	30	0.0383
DRC Original-SET	0.040	DRC Groundwater head pressure	-0.068	42.35	1,26	0.61	28	0.0001
DRC-Deep-RSET	0.074	DRC Groundwater head pressure	-0.067	259.7	1,28	0.90	30	0.0001

Table 3. Linear regression equations and statistical results for the absolute change in thickness of entire profile and the absolute change of each of the constituent components. Stepwise regression with p <.01 to enter and p < .9 to exit model. Overall model $R^2 = 0.85$.

Y (dependent variable)	m (slope)	x (independent variable)	b (intercept)	t	P	Proportion of R^2	Proportion of soil profile
Change in thickness of entire profile	1.74			2.349	0.025		
		Middle zone	0.812	6.843	0.0001	.22	.63
		Bottom Zone	1.197	13.340	0.0001	.63	.31
		Surface (Accretion)			n.s.		< .01
		Shallow zone			n.s.		.06

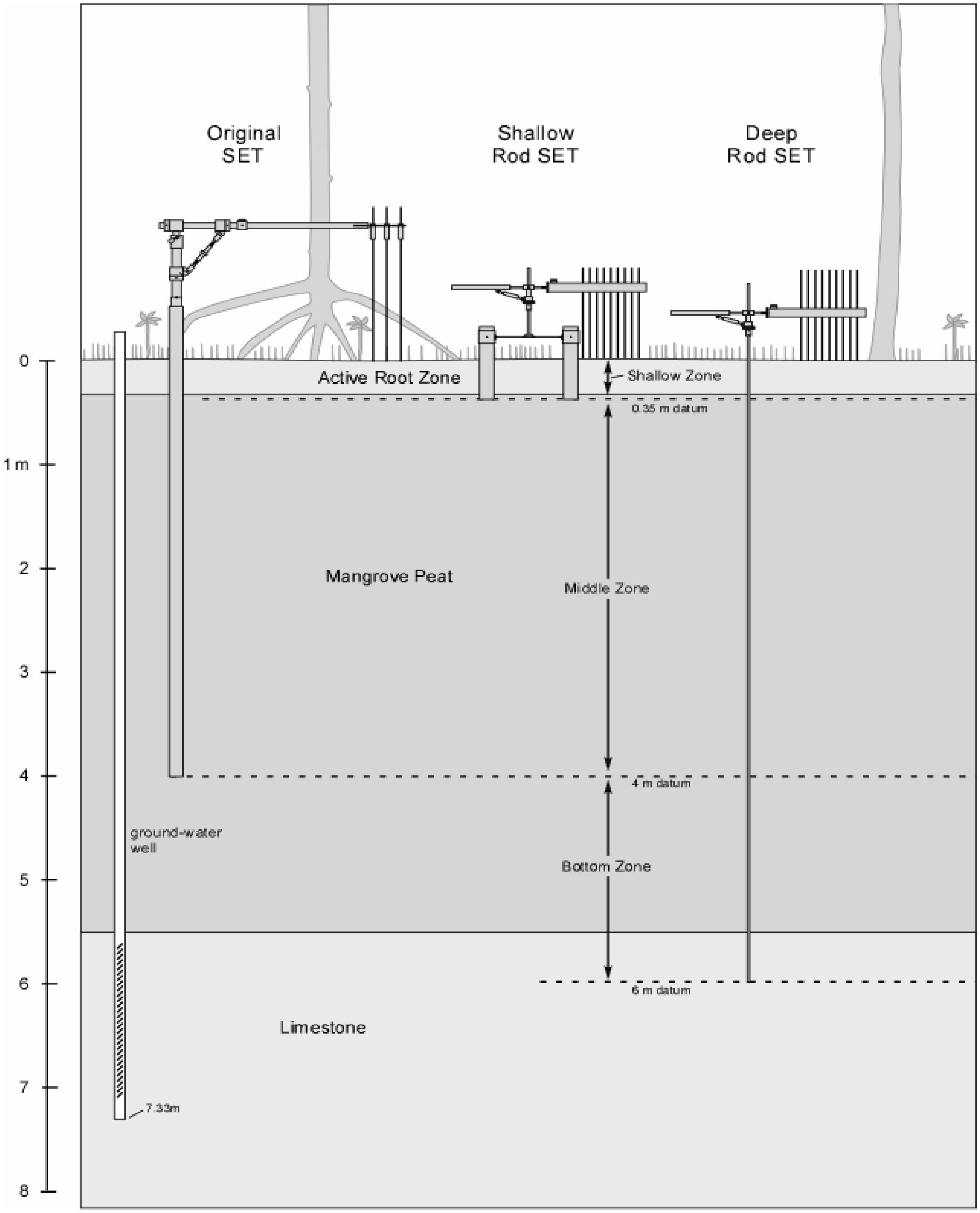

Figure 1. Profile of the substrate showing Original, Deep, and Shallow-RSETs, groundwater well and relative depth of each benchmark at Shark River mangrove site. (Adapted from Cahoon et al. 2002b with permission of the author). Drawing at 1:24 scale.

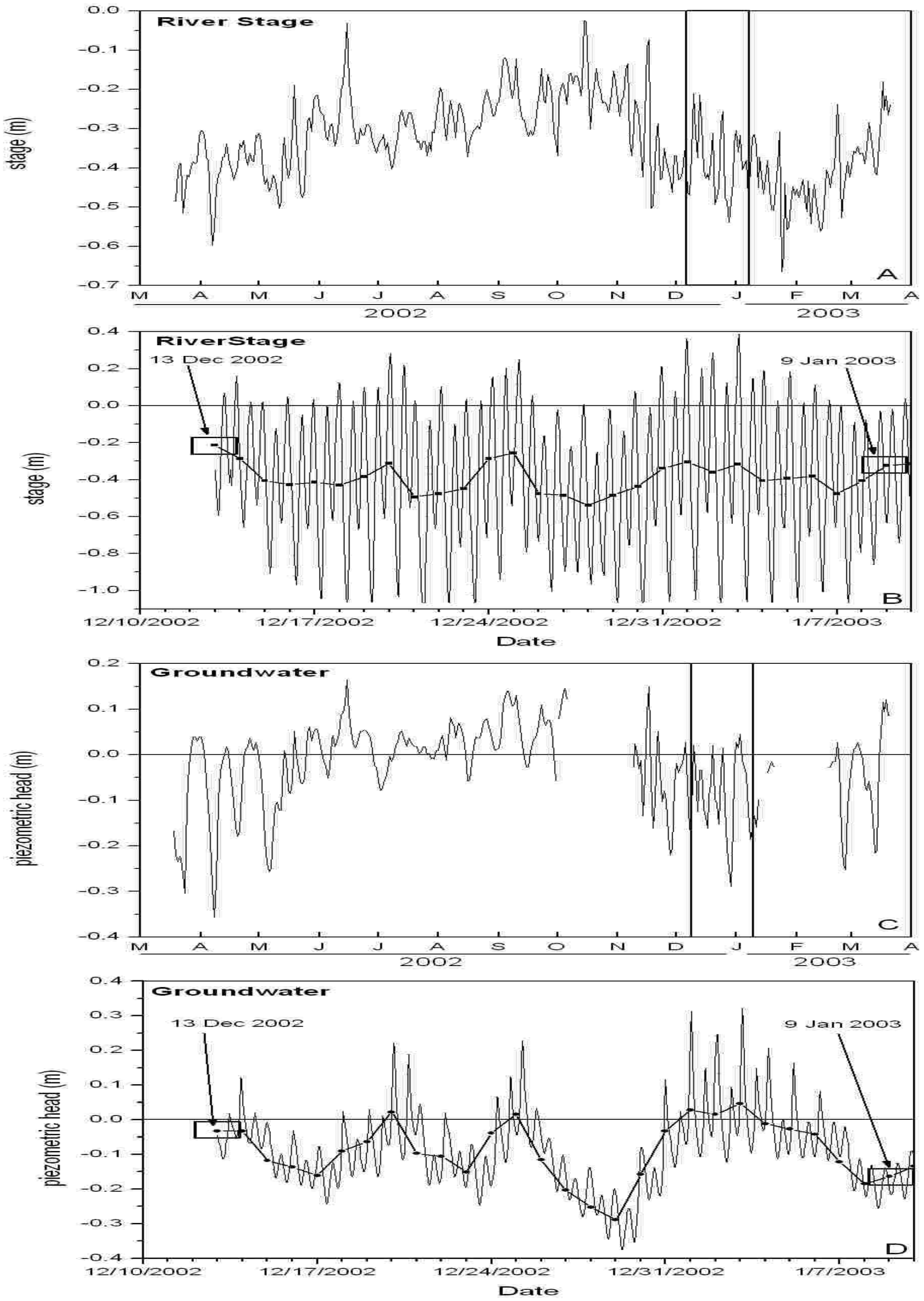

Figure 2. Hydrograph of (A) Daily averaged Shark River stage, (B) Hourly Shark River stage interval from December 13, 2002 to January 9, 2003, (C) Daily averaged groundwater piezometric head pressure and (D) Hourly groundwater

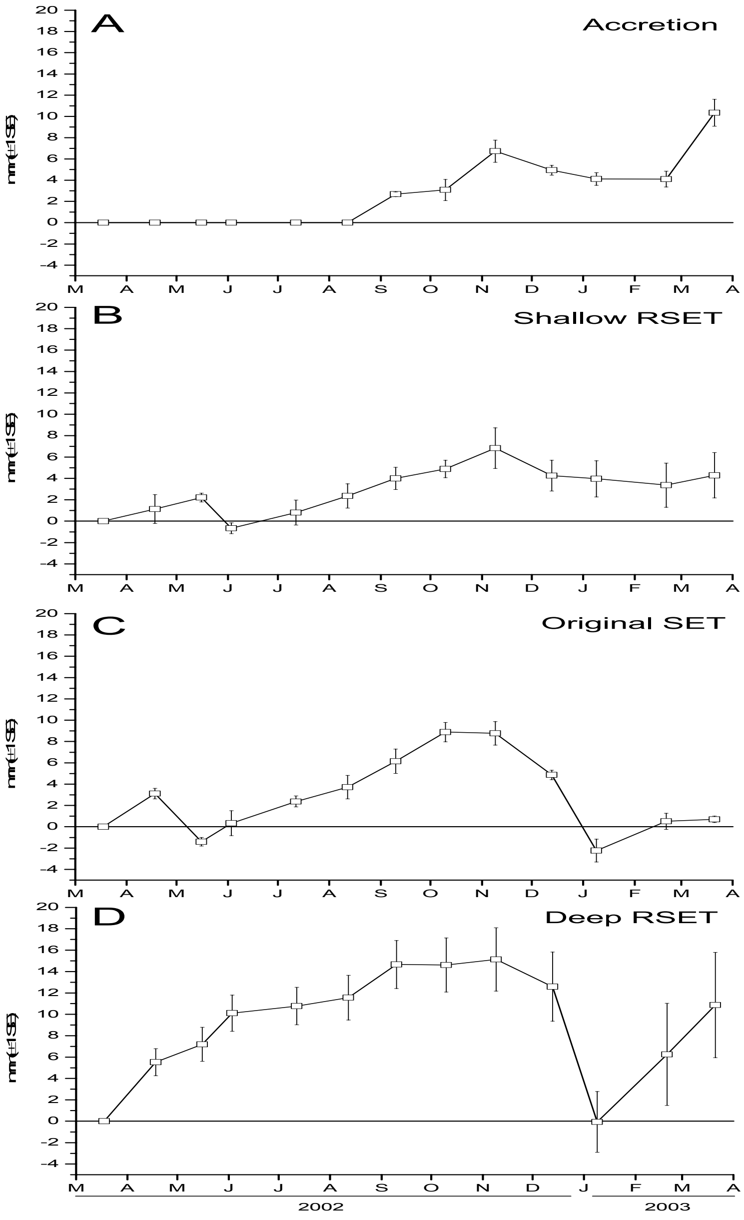

Figure 3. Mean absolute soil surface elevation (±1SD) for (A) Accretion, (B) Shallow-RSET, (C) Original-SET, and (D) Deep-RSET.

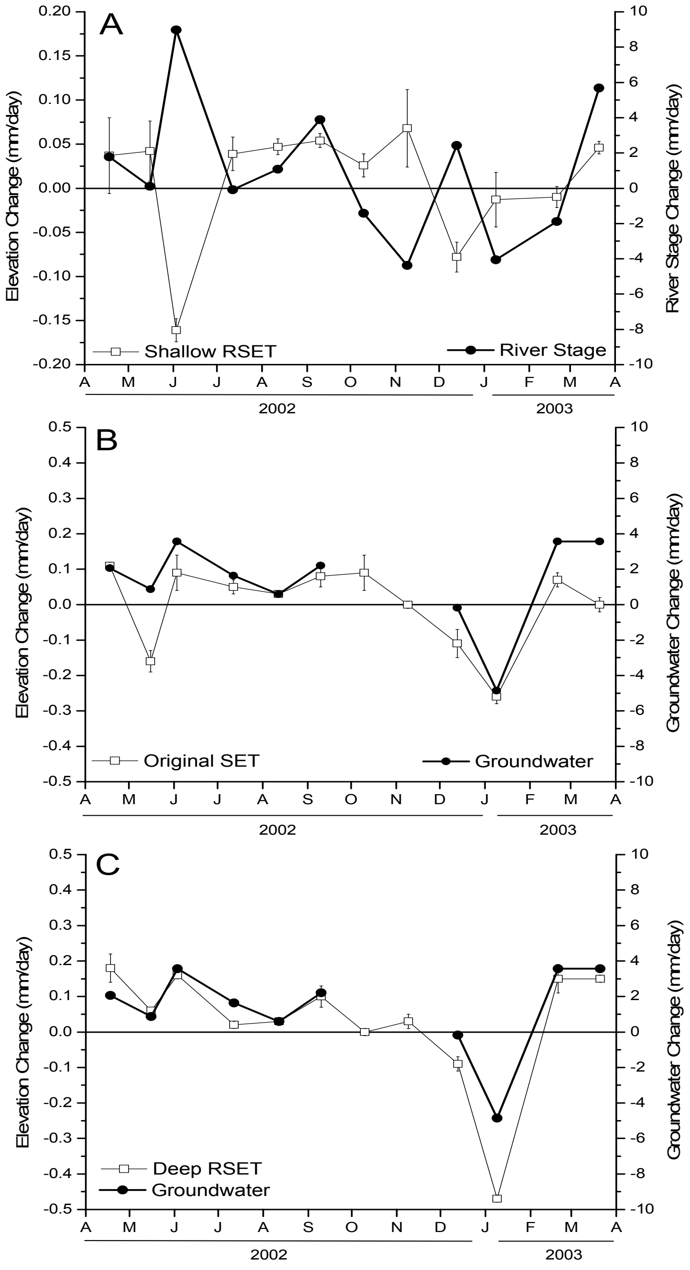

Figure 4. Mean (±1SD) rate of change for the three Shallow-RSETs and the rate of change in river stage (A), three Original-SETs and rate of change in groundwater piezometric head (B), and three Deep-RSETs and rate of change in groundwater piezometric head (C).

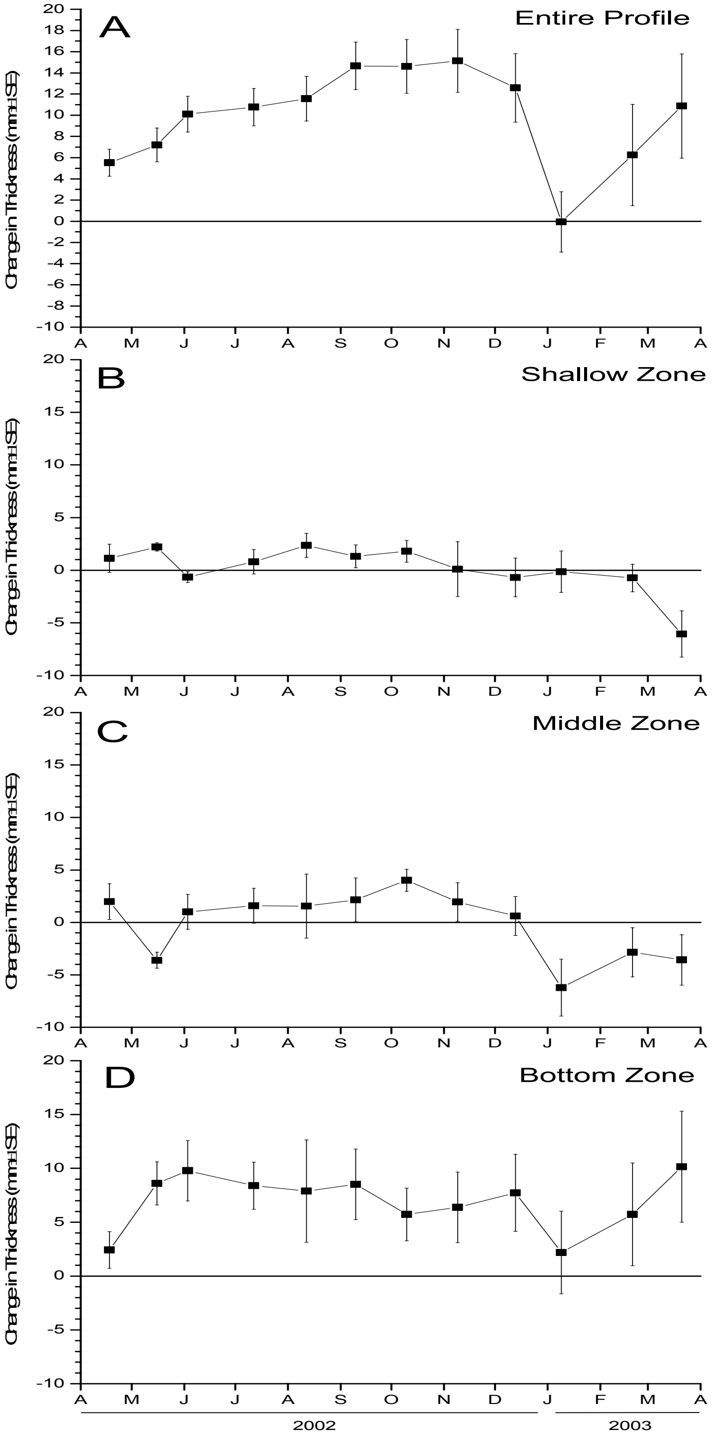

Figure 5. Mean (±1SD) Absolute change in thickness of the (A) entire profile, (B) shallow zone, (C) middle zone, and (D) bottom zone.

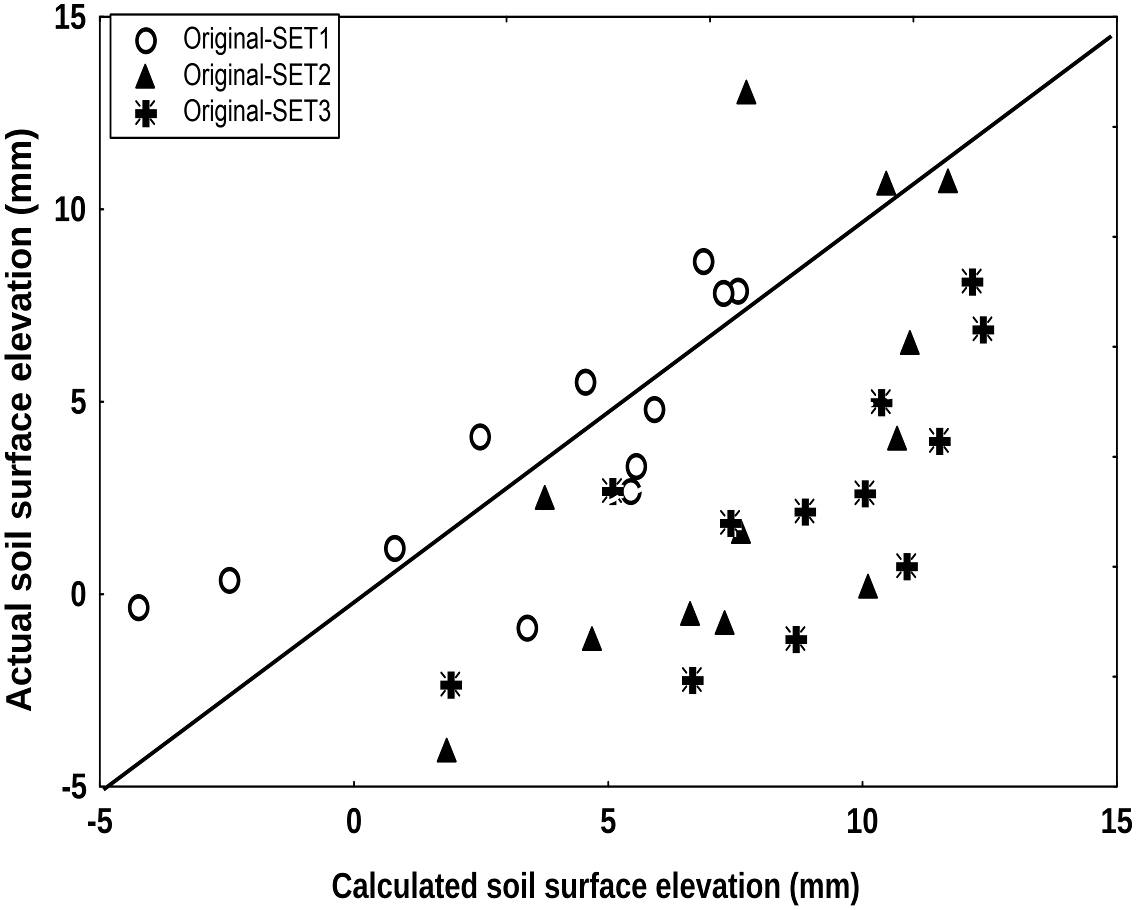

Figure 6. Actual soil surface elevation of the Original SET (mm) versus calculated soil surface elevation (mm) (proportion of the Deep-RSET). Dark solid line represents 1:1 ratio. n = 36.

Chapter VI

Conclusion

Lightning-initiated canopy gaps are an important but relatively understudied disturbance in mangrove forests around the world and are particularly important in the mangrove forests of Everglades National Park. I found that the environmental conditions within the gaps differed from the surrounding forest. The expanded gap size averaged 289 ± 20 m^2 (± SE). As gaps filled with saplings, light transmittance decreased exponentially. Overall, gaps had greater fine woody debris but less coarse woody debris than the surrounding forest. Soil torsion and soil compaction were lower in the gaps than the forest. The abundance of fiddler crab burrows decreased with distance upstream, additionally large and medium burrow abundance increased linearly with total seedling abundance. Newly formed lightning gaps had greater dead root biomass compared to the intact forest. I did not find a systematic reduction in the soil cohesiveness as new gaps aged. Soil surface elevation declined between 8.5 mm to 60.9 mm in newly formed lightning gaps; this loss was due to superficial erosion (8.5 mm) and subsidence (60.9mm). Lightning apparently kills many of the shallow surface roots and leads to a decline in the soil surface elevation in new gaps. Subsidence occurring below the shallow soil zone generated the greatest overall soil elevation loss. Recovering (Growing) gaps had lower live root biomass but similar soil surface elevation patterns as the intact forest. This study suggests that if *Rhizophora mangle* can exploit the increased flooding from soil surface elevation loss in new lightning strike gaps, then it would have to occur in the first 7 to 10 years. After this time, the soil surface elevation patterns (recovering gap) reflect the intact forest eventually removing this opportunity. I was unable to find a relationship between the change in soil elevation and survivorship, mortality rate, or recruitment in the new gaps. However, because of the small sample size (n = 3 new gaps) and the short time period of the study, this is not a unexpected result.

I found that the saplings and seedlings in new gaps survived the lightning strike, and this is the first documented evidence that in a mangrove forest a large amount of the non-canopy trees present before the lightning strike survive. This evidence comes in the form of a distinct two-cohort regeneration apparent in the seedling and sapling height distribution. The first cohort consists of the propagules and seedlings present at the site pre-strike and individuals recruiting very soon after the canopy is removed. The second group recruits into the site some number of years post strike. The high densities of *Rhizophora mangle* as seedlings and saplings in the recruiting and growing gaps stages imply that lightning strike disturbances in these mangroves favors their recruitment and does not favor *Avicennia germinans* and *Laguncularia racemosa*. However, average *A. germinans* seedling height was found to increase in later gap stages, suggesting an increase in the transition probability from seedling to sapling stage perhaps related to gap successional development.

Enumerating survival, recruitment, and growth across life stages by species is of critical importance in understanding and predicting changes in forest structure, composition, and development especially in mangrove communities. This dissertation is the first report of recruitment/mortality rates for multiple mangrove species across life stages in gaps and closed canopy forest. Survival, recruitment, and growth varied across three successional stages of mangrove forest (newly initiated lightning gaps, closing gaps, and intact forest). The life stage parameters for the three dominate life phases (seedlings, saplings, and adult) of the three dominant mangroves (*Avicennia germinans, Laguncularia racemosa, Rhizophora mangle)* differed.

The seedling and sapling recruitment rates of *A. germinans* were 1.5 times greater than mortality in new lighting-initiated canopy gaps indicating an expanding population. New gaps also had 2.6 to 10.6 times greater rate of seedling mortality for *R. mangle* and *L. racemosa* compared to the recruitment rate, indicating decreases in these populations. Seedling stem elongation was greatest in the new gaps. Taken together at least, seedling recruitment rate during my study was twice as high in new gaps, as in the other forest stages. Presumably this recruitment rate will continue to increase as the conditions within the gaps favor propagules establishment. Additionally, I conclude that new light gaps may favor *A. germinans* seedling recruitment in this initial stage of gap succession. Finally, future studies of life stage population parameters (survival, recruitment, and growth) should include recruiting gaps. From the extremely high densities of *R. mangle* seedlings and saplings in the study it must concluded that *R. mangle* recruitment and survivorship increase greatly some time after the new gap stage of succession.

At the growing gap stage of development seedling mortality rate of *R. mangle* was 10 times greater and sapling mortality was 13 times greater than recruitment. The recruitment of *R. mangle* adults was 4 times greater than mortality. The gaps have developed to a phase in which there was reduced stem elongation, sapling and adult growth, and few individuals able to recruit into the adult life stage. Sapling populations are high (~ 1 sapling m^2), and seedling populations are low (0.6 seedling m^2). *R. mangle* dominates seedling and sapling stages of the growing gaps and eventually are making the transition to the adult life stage. The end results indicate that at the growing gap stage of succession of the lightning gaps *R. mangle* stems were being favored as adult trees.

In the intact forest, *A. germinans* seedlings and sapling recruitment was 3 times greater than the mortality rate. Additionally, *L. racemosa* and *R. mangle* seedling mortality was 2 times greater than the recruitment and sapling mortality was 28 times greater than recruitment. In general, growth within the forest was low across all life stages compared to the new gaps. These population parameter results suggest that *A. germinans* becomes a co-dominant to dominant in closed canopy mangrove forest of South Florida (Craighead 1971) by having higher recruitment than mortality for the seedling and sapling stages. Given enough time the population of *A. germianans* seedlings and saplings will continue to expand whereas the populations of *L. racemosa* and *R. mangle* were decreasing.

In conclusion, this study suggest that lightning strike disturbance in these mangroves favors *R. mangle* recruitment based on densities and does not favor *A. germinans* and *L. racemosa*. Overall, vegetative dynamics in lightning initiated canopy gaps indicate that this disturbance may maintain South Florida mangroves in a cyclical or arrested successional state of development. My results provide population parameters needed to understand and predict recruitment and survivorship for each of the three dominant species (*A. germinans*, *L. racemosa*, and *R. mangle*) during the gap-phase dynamics of the mangrove forest and within the intact closed canopy forest. Additionally, I determined growth estimates enabling better understanding of intact forest and development within the stages of gap-phase dynamics. The results of this study provide new insights into the regeneration process of lightning disturbed systems and into other mangroves systems experiencing gap dynamics mechanisms.

Potential impact of Everglades Restoration on lightning gap dynamics.

I was able to show that site hydrology (both as groundwater head pressure and river stage) does have a direct impact on the soil elevation both in the intact forest (both short-term (**Chapter V**) and long-term (**Chapter IV**)) and in disturbed sites. However, I was unable to make a strong link to seedling recruitment or survival to changes in soil elevation. I found that a number of the environmental variables that varied with river location: amount of coarse woody debris, soil bulk density, soil torsion and soil compaction and fiddler crab (*Uca thayeri*) burrow densities. Additionally, river location was significant for propagule and seedling densities in *R. mangle*, propagules of *L. racemosa*, and biomass of *L. racemosa* and *R. mangle*. However, I believe that the long-term gap successional trajectory will be minimally impacted by Everglades hydrological restoration. The gap dynamics appear to have a consistent pattern regardless of river position. *R. mangle* dominates seedlings in recruiting gaps and saplings in the growing gaps at all of the sites along the river. Additionally, *R. mangle* seedlings, saplings, and adults in this forest are highly resilient to hydrological conditions (Krauss 2004). The unknown variable is the influence of hydrological manipulation on *A. germinans* and *L. racemosa* recruitment. However, since it appears that *R. mangle* is favored by lightning gap disturbance on the whole river, the impact of manipulated hydrology will be minimal on the gap successional process. The rate at which the gap transitions between forest successional stages may be affected by changes in hydrological discharge, however, and determination of changes in transition rates will have to be the subject of future studies. Sea level rise is also impacting this forest. In the short-term ecological view, the Everglades restoration will clearly influence the hydrology the mangrove forests even affecting the soil elevation. However, sea level rise will continue to modify the mangrove community by driving transgression into the freshwater marshes beyond the ability of management to mitigate the long-term impacts.

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