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Modeling gap dynamics, succession, and disturbance regimes of mangrove forests

MANDY (MANgrove DYnamics)

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Die Übereinstimmung dieses Exemplars mit dem Original der Dissertation zum Thema:

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Abstract

Despite their important ecosystem benefits for terrestrial and marine flora and fauna and the human livelihood mangrove forests suffer a high loss rate mainly due to human activity. Aside from these impacts, natural forest disturbances exist more commonly in mangroves compared to other forests as a direct consequence of their exposed coastal location.

Within this thesis I investigate the influence of natural disturbance regimes on the mangrove forest dynamics focusing in particular on the ecological role of disturbances, disturbance patterns, forest structure, succession behavior and long-term vulnerability evaluation.

The study areas were set in the Indian River Lagoon in Florida (USA) and in Can Gio an UNESCO Biosphere Reserve (Vietnam). In addition, theoretical simulation studies were carried out to complement the field studies. Thereby, in our study at the Indian River Lagoon site I investigated the ecosystem response to hurricane events of an artificially impounded mangrove forest. In Can Gio, the suitability of lightning strike – caused gaps for setting a homogenous plantation into more natural-like state according to species composition and forest structure was analyzed. Finally, a theoretical simulation study was carried out to compare lightning strike and hurricane events regarding their homogenization and heterogenization effects on the spatio-temporal forest structure.

The findings of the field study in the Indian River Lagoon indicate that hurricane events had a severe impact on forest areas in higher successional stages by creating open patches, whereas areas in lower successional stages remained largely undisturbed. Furthermore, the impoundment determines the species selection of the post-hurricane succession by favoring flooding-tolerant species. However, regeneration was found to be impaired by the artificially high inundation regime at some disturbed patches.

The lightning-strike disturbances enhance the species composition in the monospecific plantation in Can Gio by providing a sufficient light regime for entering seeds to establish. In addition, lightning-strike gaps increased the plantation structure complexity. Regenerating lightning-strike gaps remained as “green islands” within windthrow sites in the plantation due to their low stature and provided seeds for surrounding disturbed areas thereby accelerating their recolonization.

The results of the simulation analysis of a theoretical landscape showed that in the simulated highly complex natural mature forests all disturbance regimes entail homogenization on the spatial structure compared to an undisturbed scenario. The hurricane scenario showed an increased temporal variation of the forest dynamics whereas lightning-strike gaps were not able to contribute to additional heterogeneity in the simulated area, despite of having the same tree mortality probability during disturbances.

The interaction of the large-scale impoundment in the Indian River Lagoon and medium-sized hurricane events is characterized by partially impeded post-hurricane regeneration. In contrast, small-scaled lightning strikes influenced the regeneration of medium-sized windthrow sites positively within the homogenous plantation.

We therefore suggest management activities aimed at creating small clearances within the plantation in Can Gio to simulate additional small-scale disturbances in order to facilitate heterogenization of the plantation structure. Natural disturbances are found to be able to enhance the species diversity and the interactions of ecological processes. In particular, where sustainable management strategies focused on maintaining ecosystem services especially in restored sites or plantations act as a supportive part.

Natural disturbances are an integral component of mangrove forests and fulfill specific ecological functions. However, our findings indicate that these disturbances, on top of altered environmental conditions associated with climate change and direct human impacts, might jeopardize the natural development in unnatural forest structures as on plantations or restored sites. This thesis gives an extensive overview about the effect of various disturbances in different mangrove forest systems, including semi-natural forests and strongly modified plantations, on species composition and forest structure. Field studies and simulation analyses contribute in equal parts to the results of the thesis.

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II Table of abbreviations

A. germinans	Avicennia germinans
BR	Biosphere Reserve
C. equisitifolia	Casuarina equisitolia
CA	Cellular Automata
DBH	Diameter at Breast Height
e.g.	for example
FAST	Fourier amplitude sensitivity testing
FLSM	Forest Landscape Simulation Models
FON	Field of Neighborhood
GIS	Geographic Information System
i.e.	that is
IBM	Individual-Based Modeling
IRL	Indian River lagoon
L. racemosa	Laguncularia racemosa
MAD	Median Absolute Deviation
MANDY	MANgrove DYnamics
OAT	One-at-a-time
ODD	Overview Design concepts and Details
PAR	Photosynthetic Active Radiation
POM	Pattern Oriented Modeling
R. apiculata	Rhizophora apiculata
R. mangle	Rhizophora mangle
SA	Sensitivity Analysis
SELM	Spatially Explicit Landscape Models
SI	Shannon Index (here special for tree size)
SPOT	Satellite Pour l'Observation de la Terre
UNESCO	United Nations Educational, Scientific and Cultural Organization
ZOI	Zone Of Influence

III List of tables

IV List of figures

Peter J. Hogarth- Author of the book "The biology of mangrove" impressed me with his remark:

"To most people, mangroves call up a picture of a dank and fetid swamp, of strange-shaped trees growing in foul-smelling mud, inhabited mainly by mosquitoes and snakes. Mud, methane and mosquitoes are certainly features of mangrove forests – as, sometimes, are snakes. They are not sufficient to deter mangrove biologists from investigating an ecosystem of great richness and fascination."

1 General Introduction

Hurricane disturbance in a natural mangrove forest in the Everglades National Park (USA).

1.1 Purpose and Interest

Overview

Mangroves are either woody halophytes in the tropical and subtropical intertidal forest community or are defined as this community itself (Hogarth 1999, Tomlinson 1986). Further mangrove associates are plants occurring as well in mangrove habitats as in other vegetation types such as ferns and palms (Hogarth 1999). Due to the connection between the marine and terrestrial environments they provide a habitat to both aquatic and terrestrial organisms (Feller et al. 2010, Hogarth 1999).

The mangrove ecosystem is limited to the latitude of the 16°C isotherm for air temperature of the coldest month with incidentally occurring frost events (Gilman et al. 2008) and covers 137,760 km^2 in 118 countries (Giri et al. 2011). The woody mangrove plants are relatively low in diversity compared to other tropical forest systems including roughly 70 species worldwide in 17-21 families according to different authors (Feller et al. 2010, Polidoro et al. 2010, Duke et al. 1998). The biogeographical region in the Indo-West-Pacific is more diverse in species (around 62) (Spalding et al. 2010) than the Atlantic East Pacific with only 11 species (Alongi 2002). Mangroves are characterized by a great variety of structural and functional attributes including the adaptation to salinity or inundation stress which enables them to survive in a harsh environment (Duke et al. 1998).

Ecological importance

Due to their exposed location towards the sea, mangroves are important for shoreline stabilization (Duke et al. 1998). They provide protection against erosion, hurricanes and tsunamis, which can have heavy impact on human life and infrastructure (Gedan et al. 2011, Lal 2001, Hogarth 1999). The aboveground woody biomass reduces water velocities and turbulences (Gedan et al. 2011). The stabilizing root system decreases eroding processes and provides a habitat for various species by offering food and shelter against predation (Gedan et al. 2011, Nagelkerken et al. 2008, Lal 2001).

More than one third of the worldwide human population lives in coastal regions (Gedan et al. 2011). Therefore direct human extraction of wood and animals such as fish, shrimp and crabs is common (Hogarth 1999). Further benefits for local human communities include waste decontamination by filtering sediments and the reduced risk for economical damage and human life by storm protection (Gedan et al. 2011, Lacerda 2001, Lal 2001). Additionally tourism plays an important role for the local coastal economy (Gedan et al. 2011). The economical value of mangrove goods and ecosystem benefits ranges between 200,000 and 900,000 \$ ha^{-1} (Gilman et al. 2008) and worldwide value is estimated at least at 1.6 billion US \$ (Polidoro et al. 2010).

Threats and disturbances

Despite their economical and ecological importance, mangrove forests experience high yearly loss rates of 1-2% (Beaumont et al. 2011) and thus more than 50% have already disappeared in recent times (Feller et al. 2010). Reasons for this loss are for example the overexploitation such as unsustainable wood extraction; the conversion by urbanization, agriculture and aquaculture; and the pollution and alteration of the hydrological system (e.g. Lacerda 2001, Hogarth 1999). This destruction involves the deterioration of coastal water quality and elimination of nursery habitats and the subsequent decrease in fish availability (Feller et al. 2010, Gilman et al. 2008). In addition, the threat for humans is increased due to the missing protection against storm waves, surges and strong winds (Gilman et al. 2008).

Aside from the human-induced loss, natural forest disturbances exist more commonly in mangroves compared to other forests as a direct consequence from their exposed location (Hogarth 1999). O'Brien et al. (1992) describe disturbances as external catastrophes which impact the forest rejuventation and diversification. Though mangroves provide coastal protection against natural disasters, at the same time they are vulnerable to serious local damage (Hogarth 1999). For example, 55% of mangroves were directly damaged at a study site in Thailand including uprooting or washing away by the tsunami in December 2004 (Roemer et al. 2010). Hurricane disturbance patterns vary widely including defoliation, stem breakage or uprooting which is described in more detail in Chapter 2. Hurricanes can be the main shaping factor of the forest system influencing the stem size distribution, species abundance and tree density (Smith et al. 2009, Baldwin et al. 2001). Furthermore, sediment transport and subsequent erosion or sedimentation (Fromard et al. 1998) leads to local shifts of mangrove forests.

Long-term climatic change and the different interacting effects associated with global temperature increase and sea level rise are deemed as a global hazard to mangroves (Gilman et al. 2008, Hogarth 1999). Particularly the rising sea level will trigger extended loss when mangroves are not able to keep up by e.g. sediment accretion or inland forest migration, thus strongly affecting small islands or coastlines with abundant human infrastructure (Beaumont et al. 2011, Gilman et al. 2008, Duke 2001). Furthermore, the increasing temperature is assumed to increase the frequency of tropical storms and their wind and precipitation intensities (Gilman et al. 2008). A benefit of the temperature increase might be the northward migration (Doyle et al. 2010). Nevertheless, single freezing events may trigger diebacks (Doyle et al. 2003). Freezing patterns occur on local and regional scales dependent on temperature, microclimatic and topographical variations and on the mangrove structure (Olmsted et al. 1993). Damages reach from leaf browning and loss to aboveground mortality and thus leading to a patchy diversity (Ross et al. 2009, Olmsted et al. 1993).

Further local disturbing events include insect and crab herbivory, browsing either on woody plants (Feller and McKee 1999) or seeds and propagules (Duke et al. 1998). Feller and McKee (1999) noticed that in the Belizean mangroves wood-boring beetles are the major cause of small-scale gap creation, whereas in Florida lightning strikes are more important for shaping circular small gaps (Doyle et al. 2003).

The typical disturbances in mangroves are illustrated in Figure 1.1 describing the effects on the ecosystem in relation to the disturbance and recovery characteristics.

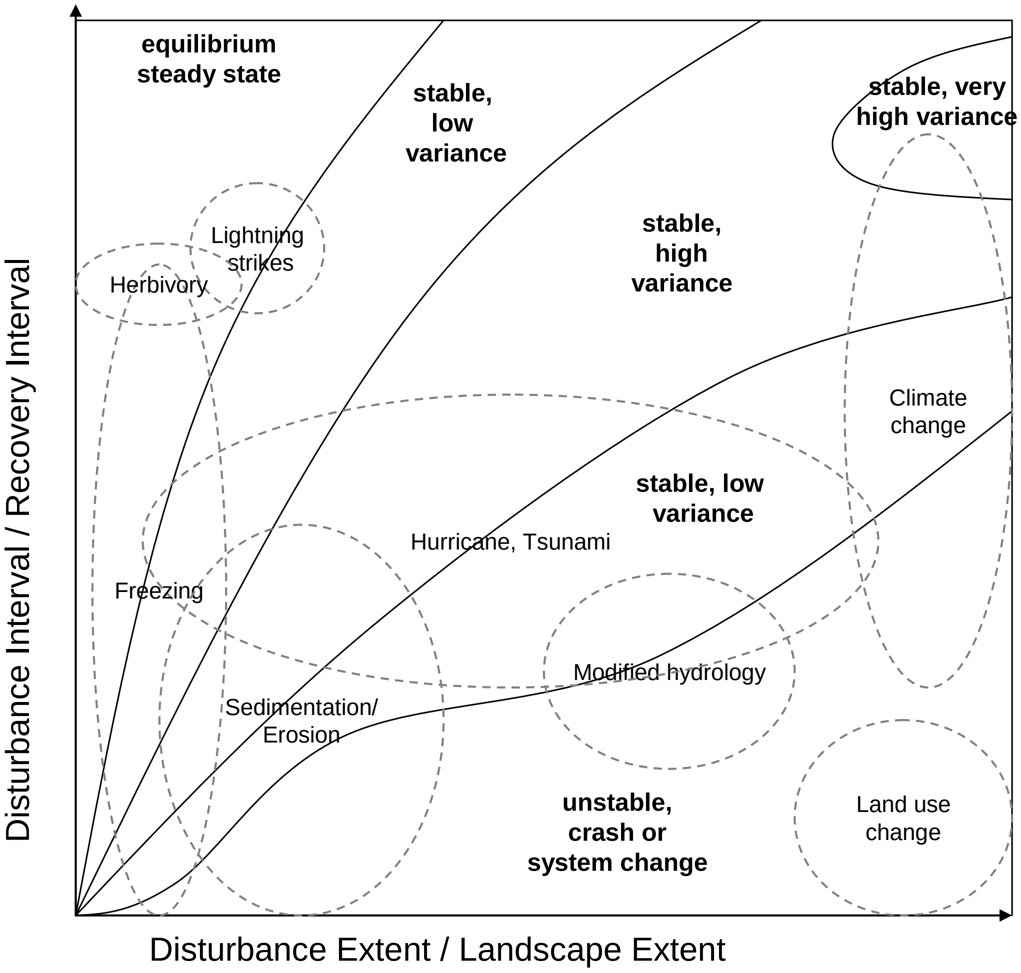

Figure 1.1: Typical disturbances in mangrove forests concerning the disturbance and recovery characteristics and the ecosystem state for a given area. The ratio between the disturbance and the landscape extent is shown on the x-axis. The size of the disturbance increases along the x-axis for a given area. On the y-axis the disturbance interval is assigned in the ratio of the recovery interval. That means for example if the disturbance interval is long having rare events and coincident a fast recovery to the pre-disturbance state (short recovery interval) the y-axis will reach maximum values. This graph was modified from (Turner et al. 1993).

Mangrove forest structures

In general mangrove forests are classified as riverine, tide-dominated, basin, overwashed or scrub forests (Hogarth 1999). These different types have certain characteristics such as basin-forests which are inundated infrequently or scrub forests which grow on extreme sites (Hogarth 1999). Monospecific zones can be formed by local topography, inundation regime, present sedimentation processes, abiotic conditions and biotic factors including propagule sorting or competition. The different tree species may respond along certain gradients and form often discrete monospecific zones (Hogarth

1999, Tomlinson 1986). Mangrove forests are relatively poor in tree species compared to tropical rain forests and do not show the typically layered structure and lacking almost entirely understory vegetation (Hogarth 1999). Clarke and Kerrigan (2000) even claim that mangrove growth and stand structure have no or only few strata and are characterized as even-aged despite the presence of canopy disturbances. This view might be too simplified considering different spatial scales. Hence, the individual tree shows complex adaption to environmental conditions and on larger scales this leads to local variations of the forest structure (Hogarth 1999). Additional disturbances are driving forces for the vegetation structure. They influence the ecosystem composition and structure across different spatial and functional scales (Jentsch et al. 2002). Therefore, mangrove forests develop zonation as well as mosaic patterns with different tree cohorts of different successional stages with distinct canopy height patchiness (Blanco et al. 2001). The structural complexity is therefore important because of its ecological role of niche requirements of wildlife species, spatio-temporal forest stand dynamics, the regeneration processes and the forest productivity (Zenner and Hibbs 2000). The measurement of the forest structure and its different aspects with sufficient structure indices enables the analysis of ecosystem processes and functions including the distribution of biomass in space or the vertical and horizontal arrangement of plant species or size classes (Zenner and Hibbs 2000). For the analysis of the spatial and temporal structural complexity poor species systems such as mangrove forests are particularly appropriate, because biodiversity is subordinate.

1.2 Goals

The overall aim of this thesis is to study different disturbance types in mangrove forests including the following four aspects: i) characterization of disturbance patterns; ii) the spatio-temporal forest dynamics; iii) the ecological role of disturbances; and iv) evaluation of their overall vulnerability to disturbances.

Three case studies were carried out to investigate disturbance regimes including impoundments, hurricanes and lightning strikes.

Research questions

1. Which characteristical disturbance patterns within mangrove forests is shown according to different disturbance regimes?

2. What is the influence on the spatio-temporal forest dynamics with regard to the disturbance regime?

3. How do the intensity and frequency of gap and patch formation influence the overall landscape pattern of the forest development?

4. How does gap turnover alter forest structure, diversity and distribution?

5. How do disturbance regimes influence the stability of natural forest dynamics and vulnerability of the mangrove ecosystem?

1.3 Approach

Within this thesis I applied different approaches to study various aspects of the mangrove forest structure according to different disturbance regimes.

Remote sensing techniques are a common tool for observing mangrove forest structure. For example, Landsat images were used to visualize the distribution of mangrove forests worldwide (Giri et al. 2011) or to investigate their dynamics according to natural and human factors (Rakotomavo and Fromard 2010). Nevertheless, remote sensing analysis often functions as a complementary approach to fieldwork and to other information sources such as expert knowledge or data about climatic and socio-economic conditions in order to calibrate and validate the findings (Omo-Irabor et al. 2011, Rakotomavo and Fromard 2010, Sherman et al. 2000). In Chapter 2 I used time series of aerial photographs to obtain an overview of an impounded mangrove coastal section disturbed by a hurricane event. The forest structure, disturbance pattern and subsequent regeneration were investigated. Furthermore, in Chapter 4 time series of SPOT images provide the main information about the size, shape and formation rate of lightning-strike gaps in a homogeneous mangrove plantation. Remote sensing analyses enable the observation of forest structures on larger scales than field studies could offer with appropriate effort. The remote sensing analyses in Chapter 4 were conducted by Markus Kautz and in Chapter 2 under my supervision by Annegret Skóra.

Based on these remote sensing studies, ***field studies*** were conducted to gather detailed information about individual plant characteristics, dead wood abundance, environmental conditions and species composition (see Chapters 2 and 4). The collected data give a very good impression of the mangrove characteristics on site and therefore deepen the understanding for the processes in the ecosystem, while enabling the statistical verification of certain processes. Moreover, the gained information forms partly the basis of the input data for the simulation study.

In addition, ***simulation analyses*** were carried out (Chapter 4 and 5) with the individual-based mangrove forest model KiWi (a detailed description is provided in Chapter 3). The previous results of forest stand and disturbance pattern characteristics serve as the base to quantify the influence of different lightning strike regimes on plantation structure in comparison a simulated randomly-established forest (Chapter 4). Furthermore, the influence of different disturbance regimes including hurricanes and lightning strikes on a landscape scale were analyzed (Chapter 5). KiWi is especially suitable for investigating the spatial forest structure according to the individual based simulation approach, including the explicit stem position in space and the size by taking into account the *DBH* and height of each tree.

The ***spatial pattern analyzes*** characterize present stand elements such as tree size and dimension, tree density, its spacing, species composition or the stand biomass (McElhinny et al. 2005). Furthermore, stand structural attributes may be used to analyze variation in size which is especially important for describing habitat heterogeneity (McElhinny et al. 2005). Therefore, I used the coefficient of variation in height (Chapter 2) and in *DBH* (Chapter 5) and the Shannon Index for height classes (Chapter 4) for analyzing the horizontal forest structure. The Clark-Evan-Index (Chapter 4 and 5) characterizes the vertical forest structure. These indices were applied to investigate mainly spatio-temporal forests dynamics (Chapter 4 and 5) and to characterize spatial heterogeneity one timestep at a time (Chapter 2). These studies enable the combination and comparison of the aforementioned methods including remote sensing, field studies and modeling approaches.

The application of the different methods provides knowledge about various aspects of the complex forest structure with regards to disturbances. The results can be used to formulate forest management suggestions (Chapter 4) or to develop an understanding of long-term processes in mangroves based mainly on the results from the simulation studies.

1.4 Thesis outline

The present thesis comprises of ***six chapters***, whereas the ***current chapter*** is an introduction to the topic of the entire work including aims, research questions and approaches.

Chapter 2 presents a field study conducted at the Indian River Lagoon in Florida USA, regarding the interaction of medium-scaled hurricane disturbances within a mangrove forest with a large-scale artificial inundation regime. Pre-hurricane forest structure, hurricane damage, subsequent regeneration and abiotic conditions were investigated. This study was published in Aquatic Botany.

In ***Chapter 3*** I address the necessity for conducting simulation analyses where field studies for investigating forest dynamics for a large time span and on medium to large spatial scales cannot be carried out with reasonable effort. The individual based mangrove forest model KiWi (Berger and Hildenbrandt 2000) is described in the context of ecological modeling approaches. It is based on a standard protocol for individual-based models (Grimm et al. 2006) and was modified according to specific aspects of this thesis. Furthermore, a sensitivity analysis of KiWi was conducted in order to provide an understanding about the sensitive input factors on the model output, particularly for the applied structural indices applied in the following chapters.

In ***Chapter 4*** I emphasize the structural and ecological benefits of small-scaled disturbances created by lightning strikes in an even-aged and size-homogenous plantation in the UNESCO Biosphere Reserve in Can Gio, Vietnam. I were able to gain knowledge of the long-term spatio-temporal dynamics of the plantation. In addition, I suggest some management activities to avoid an inadvertent dieback of larger areas within the plantation due to the homogenous structure. This study was published in Global and Planetary Change.

Consequently, ***Chapter 5*** is based on the findings of the case studies in Chapter 2 and Chapter 4. The influence of different disturbance regimes according to homogenizing and heterogenizing effects of a simulated forest were tested initially separately and then in a mixed regime. Small-scaled frequent disturbances were compared with medium-scaled infrequent ones. The publication was submitted to the Journal of Vegetation Science.

Finally, the overall discussion of the thesis is carried out in ***Chapter 6***. Main findings of this work and its contribution to mangrove research are discussed. An outlook is given, listing possible future research topics.

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2 Investigating the role of impoundment and forest structure on the resistance and resilience of mangrove forests to hurricanes

Aerial photograph of a part of the impounded studied mangrove with hurricane disturbance.

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Abstract

The present study evaluates how a prolonged artificial flooding regime in impounded mangrove forests influences the regeneration after medium-sized forest destruction created by two hurricanes in 2004 in the Indian River Lagoon, Florida, USA. Disturbance patterns, forest structure, and regeneration were investigated. We found disturbed areas, characterized by uprooted and snapped trees, and intact forests in close proximity. The canopy turnover was greater in forests in higher succession stages with median tree diameter at breast height of 7.6 ± 5.7 cm compared to the intact forest with 3.7 ± 1.2 cm. Larger trees with lower densities were more susceptible to hurricane damage. We observed that regeneration of the open patches was dominated by the flood-tolerant species *Rhizophora mangle* (89.9%) instead of the faster-growing pioneer species *Laguncularia racemosa* (7.0%). Some of the disturbed areas created by the hurricanes were not recolonized. The regeneration rate of the disturbed areas expressed by vegetation closure >50% differed between almost zero to 100% in three different impoundments. We concluded that the artificial flooding regime imposed by impoundment is the predominant selective force in the successive process according to the species composition. However, we were not able to detect the driving factors that prevented mangrove establishment in disturbed areas.

Keywords: *Succession; Disturbance; Mangrove forest dynamics; Hurricane; Impoundment; Florida; Neotropics*

2.1 Introduction

With their locations along the tropical coastlines, mangroves fulfill many important functions. They provide habitat for a diverse terrestrial fauna in the canopy and marine fauna on the mangrove roots (Nagelkerken et al. 2008). Additionally, the mangrove root system is able to stabilize shorelines and prevent erosion (Tomlinson 1986, Nagelkerken et al. 2008). Acting as “bioshields”, mangroves buffer destructive impacts of tropical storms or storm surges and protect human life and properties (Kathiresan and Rajendran 2005, Feagin et al. 2010). Nevertheless, mangroves have experienced extensive destruction worldwide due to various human impacts (Valiela et al. 2001).

In the Indian River Lagoon (IRL) along the east coast of Florida, construction of mosquito impoundments has led to long-term changes in coastal vegetation. Between the late 1950s and the 1960s, most of the salt marshes and mangroves along the central-east coast of Florida were impounded, which successfully reduced mosquito populations by flooding the substrate they required for breeding (Provost 1977). The impoundment process resulted in exceptionally high water levels, which led to a loss of *Avicennia germinans* (black mangrove) and low-profile marsh halophytes such as *Batis maritima* and *Salicornia* spp. (Rey et al. 1990). *Rhizophora mangle* (red mangrove) was the most adapted to the modified inundation regime and became dominant (Lahmann 1988).

On top of this human-induced ecosystem modification, natural disturbances occur at different spatio-temporal scales. Small-scaled gaps caused by lightning create clusters of dead trees (Smith III et al. 1994). Medium- to large- scaled killing events can happen due to freezing occurring at this latitude (Duke et al. 1998). Hurricanes and wind throws are also common disturbances to Neotropical mangroves. Hurricane impacts have been widely discussed in the literature for different forest types (Ogle et al. 2006, Imbert and Portecop 2008). In mangroves, the damage pattern caused by strong winds varies from defoliation of the canopy, to bark damage due to shredding and abrasion, and to stem breakage and uprooting (Imbert et al. 1996 Lugo 2008). Large trees generally suffer greater mortality rates because of snapping (Lugo 2008) compared to smaller ones, which may still suffer defoliation but are able to re-sprout more easily (Roth 1992). Aside from tree stature, the damage pattern and extent of a singular hurricane disturbance are also influenced by the intensity of an individual storm, topography, and historical factors (Piou et al. 2006, Lugo 2008, Canham et al. 2010).

Species-specific disturbance resistance (“survival traits”), local dispersal and seedling establishment (“competitive traits”), and species composition are the main biotic factors that contribute to the determination of the landscape structure after disturbance events (Sherman et al. 2001; Papaik and Canham 2006). Thus, hurricanes may assert selective pressure upon the forest ecosystem by increasing the heterogeneity of the landscape, changing the space available to organisms, thus resetting succession and altering species composition (Lugo 2008, Piou et al. 2008).

After severe natural disturbances, ecosystem processes are often maintained or changed only moderately in comparison to human-induced destruction (Duke 2001, Mallin and Corbett 2006). Hence, natural disturbances can result in quick regeneration. However, regeneration may take much longer after logging and transformation for different land use (Rakotomavo and Fromard 2010), water pollution (Duke et al. 2005), or oil spills (Lewis 1983). The interaction between land-use history and large-scale natural disturbances may also determine secondary forest structure and composition (Flynn et al. 2010).

Mangroves may benefit from interactions between different scales of natural disturbance. For example, after Hurricane Andrew in Florida, regeneration mainly relied on the abundance of past small lightning-strike gaps that acted as green living patches being less disturbed (Smith III et al. 1994) according to their lower forest stature (Vogt et al. 2006).

A simulation study testing the intermediate disturbances hypothesis in the species poor Neotropic mangrove system emphasized that the interplay of interspecific competition as well as abiotic conditions produced different potential vegetation dynamics dependent on the successional configurations and disturbance regime (Piou et al. 2008). Thus, the outcomes of succession trajectories can vary even in low species systems such as mangroves (Berger et al. 2006).

In the IRL, succession studies (Lahmann 1988, Rey et al. 1990) determined the effects of mosquito impoundments on vegetation structure. To complement these findings, our aim was to test the hypothesis that medium-scaled hurricane impacts are dependent on large-scale drivers (impoundment) and pre-disturbance mangrove forest structure. Thus, our plan of work was to: i) characterize hurricane damage in open patches; ii) reconstruct pre-disturbance forest structure from dead and standing plants; iii) compare the structure and resistance of open patches to nearby forests to determine the importance of pre-disturbance structure; and iv) compare the different impoundment sites to determine the effect of water management on recolonization of impacted areas. The field study was conducted 5 years (2009) after Hurricanes Frances and Jeanne made landfall (2004) along the IRL. We mapped the vegetation, measured environmental conditions, and compared the structure and species composition of gaps and closed canopy forests.

2.2 Material and Methods

2.2.1 *Study Site*

The study site was located along the IRL between Fort Pierce and Jensen Beach (27°23’00”N, 80°15’50”W) at the east coast of Florida. Hurricane Frances (category 2, with wind speeds of up to 137 km h-1) and Hurricane Jeanne (category 3, 194 km h-1) made landfall around Fort Pierce within 20 days of each other in September 2004 (Mallin and Corbett 2006). We chose three sub-sites of disturbed areas and in nearby intact forest in the recently managed impoundments (IM), IM4, IM5 and IM6. These impoundments, which were constructed to control mosquito populations, were situated in mangroves enclosed with dikes in St. Lucie County (Rey and Kain 1989). The inundation regime was artificially modified by permanent rotational flooding during the main mosquito breeding season from the beginning of May to the end of August or early September each year (see Appendix 1). During this period, the water level was maintained above the lagoon water level (about 50 cm).

2.2.2 *Aerial imagery interpretation*

Aerial photographs of May 2004, March 2005, and May 2009 provided by the St. Lucie County Mosquito Control were analyzed in ArcGIS 9.3.1 (see Appendix 2). These provided information about the vegetation cover, the size of disturbed areas, and the regeneration status 5 years after the two hurricanes.

2.2.3 *Field measurements*

Between May and July 2009, we sampled within the three impoundments along three transects of three plots each in two types of forest: disturbed areas and nearby intact forests (hence, 54 plots from 3 impoundments x 2 types of forest x 3 transects x 3 plots). Transects were at least 75 m apart and plots were measured every 25 m. In each 4 x 4 m plot, soil elevation according to the water depth [cm] (the water surface is the reference point of 0 cm), soil penetration [cm], photosynthetic active radiation (PAR [%]) at 1.6 m height, and pore water salinity [‰] were measured (see Appendix 3, Appendix 4 and Appendix 5). Each plant present in a plot was measured or categorized in term of height [m], stature [sapling (height<1.3 m or *DBH* < 2.5 cm (according to Farnsworth and Ellison 1991), and tree, respectively], species, x-y position [m], diameter (*DBH* for trees and basal diameter for saplings), and damage in the tree architecture (by visual classification of “no” (<10% broken), “low” (<40%) and “high” (>40%) damage) (see Appendix 6 and Appendix 7). Within the plots, we also collected all the dead wood and recorded species and size class based on diameter (size class1: ≥2.5-<5 cm; 2: ≥5-<10 cm; 3: ≥10-<15 cm; 4: >15 cm) of each piece. Because of the lack of pre-disturbance inventory data, we reconstructed the pre-hurricane condition of the study sites by combining the live tree measurements with dead wood analyses inside each plot (as in Imbert et al., 1996). We excluded the saplings for these pre-hurricane reconstructions based on their size in the disturbed areas. The plants that had established in disturbed areas subsequent to the hurricanes did not exceed a *DBH* of 2.5 cm. The pre-hurricane tree density was calculated as the number of living trees added to the number of rooted dead wood found in each plot.

2.2.4 Analyses

We conducted Mann-Whitney U and Students t -tests to identify significant differences in environmental conditions and plant attributes represented by medians and median absolute deviations (MAD=$\text{median}_i(|X_i - \text{median}_j(X_j)|)$) between the two treatments (“intact forests” and “disturbed areas”). To verify species-specific differences and site effects among the three impoundments, we used a Kruskal-Wallis test. A linear regression of important environmental factors such as soil elevation and salinity was applied to the sapling height of the dominant species *R. mangle* in order to understand the driving factors for the post-hurricane forest development.

2.3 Results

2.3.1 Hurricane damages in open patches

From the pre-hurricane aerial photographs, we observed that 82% of the forested vegetation within the investigated coastal section consisted of mangroves (2004 in Table 2.1) Based on ground survey, the invasive *Casuarina equisitifolia* was the dominant tree species of the other type of forest vegetation. The 2004 hurricanes created open areas of 14.1% in the mangrove area and 95.5% in the other forest types.

The results in Table 2.1 indicated that mangrove forests were quite resilient to the hurricane events, compared to the *Casuarina*-dominated forests, which had only regenerated marginally.

The vegetation inside the study area consists mainly of *R. mangle* (92.8%) as the dominant species with only few scattered *A. germinans* (2.6%) and *L. racemosa* (4.6%).

Table 2.1: The vegetation cover in the studied impoundments and the associated coastal area section of the lagoon distinguished in mangrove forests and other forests types (mainly *Casurina equisetifolia*) detected at different years by remote sensing techniques: before the hurricane 2004, the destruction during the hurricane March 2005 and the percentage of vegetation cover above 50% in spring 2009.

Sub site	**Vegetation type**	**Vegetation cover 2004**	**Disturbance 2005**		**Recovered vegetation Cover > 50% in open patches 2009**	
		[ha]	Absolute [ha]	Relative [%]	Absolute [ha]	Relative [%]
IM4	mangroves	53.14	3.46	6.5	3.46	100.0
	Other forests	1.26	0	0	-	-
	Total	54.40	3.46	6.4		100.0
IM5	mangroves	51.94	5.13	9.9	0.03	0.6
	Other forests	0	0	-	-	-
	Total	51.94	5.13	9.9	0.03	0.6
IM6	mangroves	113.39	15.51	13.7	12.49	80.5
	Other forests	15.57	15.34	98.5	0	0
	Total	128.96	30.86	23.9	12.49	40.5
Total coastal area[a]	mangroves	266.21, 82%	37.67	14.1	19.24	51.1
	Other forests	59.50, 18%	56.81	95.5	1.39	2.4
	Total	325.70, 100%	94.48	29.0	20.63	21.8

[a] including the investigated impoundments plus the adjacent areas for the total section

The field data showed balanced proportions between trees (n = 486) and saplings (n = 554) in intact forests, while the disturbed areas with few living trees (51) contained a high number of saplings (833). Damage to the tree architecture (>10% destruction per tree), such as large broken branches, twisted stems or wood damage, in general, occurred for 33% of the mangrove trees and 48% of the saplings in the intact forests. Approximately 10% of these plants were heavily damaged. In the disturbed areas, 71% of trees have been damaged. In contrast, only 11% of the saplings in the disturbed areas were damaged in their architecture, which indicated more suitable growth conditions.

Table 2.2: Comparison between intact forest and disturbed patches of measured variables including the summary of all subplots.

Variables	Intact forest			Disturbed area			Mann-Whitney U test	
							Test statistic (W)	p- Value
Environmental conditions								
PAR [%]	14.6 ± 9.3			61.5 ± 30.2			66	0.0244
Pore water salinity [ppt]	54 ± 4			47 ± 4			638	< 0.0001
Soil penetration [cm]	29 ± 19			65 ± 34			166	0.0006
Soil elevation at stem position [cm]	-21 ± 12			-30 ± 12			264232	< 0.0001
Plant measurements								
	Plants	Trees	Sapling	Plants	Trees	Sapling		
Plant height [m]	3.8 ± 1.8	4.9 ± 0.7	2.5 ± 1.6	1.5 ± 0.9	6.3 ± 3.6	1.4 ± 1.7	742208[a]	< 0.0001[a]
DBH [cm][b]	2.6 ± 1.5	3.7 ± 1.3	-[c]	0.9 ± 0.3	6.1 ± 4.2	-[c]	6539[a]	< 0.0001[a]
CV height	0.4 ± 0.1	0.2 ± 0.1	0.4 ± 0.2	0.5 ± 0.5	0.3 ± 0.1	0.3 ± 0.1	346[a]	0.7488[a]

(The values are expressed by median ±MAD.)

[a] The test statistic of the plant measurements is applied for the plants in general, containing saplings and trees. Results for the saplings and trees are separately discussed in the text

[b] The results for the mangrove plants include only plants with height of at least 1.3 m.

[c] The missing values are caused by the inconsistency of diameter measurements. The basal diameter was measured for plants below 1.3m, whereas the *DBH* was recorded for taller saplings.

Plant height and *DBH* were significantly smaller in disturbed areas because of the destruction to the canopy during the hurricanes (Table 2.2). Considering saplings and trees separately, the remaining living trees in the disturbed areas were not significantly higher (Mann-Whitney U test: W = 268, $p = 0.0877$), but had significantly larger *DBH* values (W = 307, $p = 0.0065$) than in the intact forests. Saplings were taller (W = 165, $p = 0.0016$) in the intact forests. The coefficient of variation (CV) of mangrove height showed no significant differences when all plants were included (Table 2.2). However, when subdivided into saplings (W = 563.5, $p < 0.0001$) and trees (W =37.5, $p = 0.0072$), saplings in the intact forests were more dissimilar than in the disturbed areas. In contrast, the trees in the intact forests showed more similarity to each other compared to the disturbed areas.

2.3.2 Reconstruction of the pre-disturbance forest structure

In order to reconstruct the pre-hurricane forest structure, the data of plant and dead wood measurements were combined.

The maximum tree height (intact forests: 6.8 ± 0.7 m, disturbed areas: 9.4 ± 1.9 m) and the median *DBH* (intact forests: 3.7 ± 1.2 m, disturbed areas: 7.6 ± 5.7 m) per plot were significantly higher in the disturbed areas. Median *DBH* and maximum height were highly negatively correlated ($r_S > -0.7$) with the tree number.

Figure 2.1 shows that in intact forests live trees of the smallest size class (2.5-5 cm) were by far the most abundant size class. Furthermore, we found a higher number of rooted dead wood in intact forests (182) compared disturbed areas (141), but the difference was not significant (t = 1.1, *p* = 0.2747). Both the living and the dead trees of the two smallest tree sizes were more numerous in the intact forests. In the disturbed areas, the amount of dead wood exceeded all live tree *DBH* classes, which were distributed over all size classes.

The differences in the environmental conditions between disturbed areas and the intact forests were statistically significant by Mann-Whitney U (Table 2.2). Lower light availability (PAR) due to shading of neighboring trees was measured in intact forests compared to the disturbed areas. Furthermore, the soil elevation at the tree stem position of living trees was higher in the intact forests, and the soil penetration was higher in the disturbed areas. The pore water salinity was higher in intact forests (Table 2.2). The surface water salinity (39 ± 2‰) did not differ significantly between the two forest types (t-test = -1.1, *p* = 0.29).

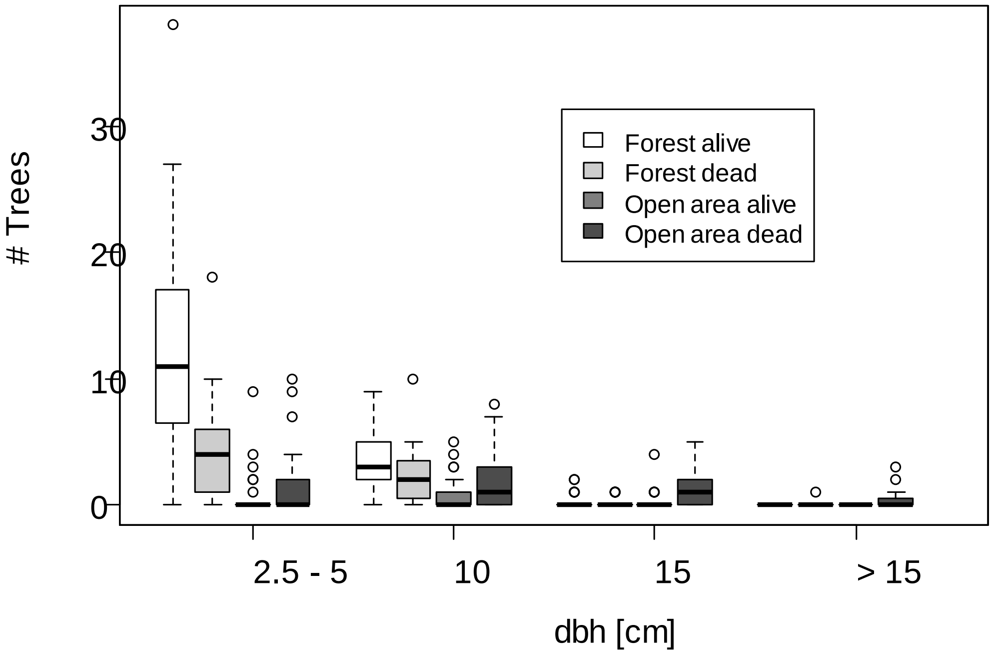

Figure 2.1: The tree *DBH* distribution per subplot illustrates the living trees and the dead rooted wood divided in the measured dead wood classes. Bars within the same classes with the same letter are not significantly different at *p* > 0.05 using pairwise Mann-Whitney U tests with the Bonferroni correction.

2.3.3 Recolonization of the three impoundments

According to the aerial photographs, the regeneration rate among the impoundments differed significantly (Table 2.1). The disturbed area at IM 4 showed a complete vegetation cover with more than 50% canopy closure. In contrast, in IM 5, almost none of the disturbed area had recovered a canopy closure of 50%. The canopy closure data for 2009 shown in Table 2.1 did not correlate with site-specific abiotic factors including pore water salinity, soil penetration, and soil elevation (Table 2.3). Additionally, the pre-hurricane forest structure of IM 5 showed lower tree densities with larger tree diameters, compared to IM 4 and IM 6.

The species dominance of the saplings within the disturbed areas remained for *R. mangle* (89.9%) with only low densities of *L. racemosa* (7.0%) and *A. germinans* (3.1%).

Table 2.3: The regeneration process of the disturbed patches expressed by the canopy closure above 50% according to environmental conditions in 2009.

Canopy closure above 50%	100% - IM 4	80% - IM 6	0.6% - IM 5
Salinity [ppt]	50.7±2.3	41.6±4.2	46.4±3.0
Soil elevation at stem position [cm]	-18.8±4.5	-24.6±19.6	-28.6 ± 5.1
Soil penetration [cm]	70.4±26.1	67.1±41.2	60.1±23.0
No. pre-hurricane trees	8.1 ± 5.0	10.3±4.1	2.9± 2.1
Pre-hurricane tree *DBH* [cm]	9.1±3.3	7.0 ± 1.9	11.3±3.7

(Values are expressed by mean ± sd)

Combining the sapling species composition according to the soil elevation at the stem position, IM 4 and IM 5 were dominated almost entirely by *R. mangle*, whereas in IM 6, *L. racemosa* and *A. germinans* occurred in higher frequencies (Figure 2.2). The three impoundments had different well-zoned abundances for *R. mangle* with the highest elevation in IM 4 followed by IM 5. IM 6 shows a separation of the *R. mangle* occurrence, divided in low elevations down to -45 cm to -25 cm and a lower abundance around the water surface (-10 cm to 5 cm). *Laguncularia racemosa* and *A. germinans* were able to establish numerous seedlings on higher spots in IM 6. Only few individuals of *L. racemosa* and *A. germinans* were found in lower soil elevation about until -30 cm from the constant level of water depth.

With respect to the overall mean values of the soil elevation at tree position (Table 2.3) for each impoundment, we found the lowest value in IM 5 despite the establishment of *R. mangle* in deeper water in IM 4 (Figure 2.1).

Our data suggest that the sapling height of the dominant species *R. mangle* was influenced negatively by the pore water salinity (R^2=0.119, F-statistic = 46, p = 0.0029) and the soil elevation ($p < 0.0001$).

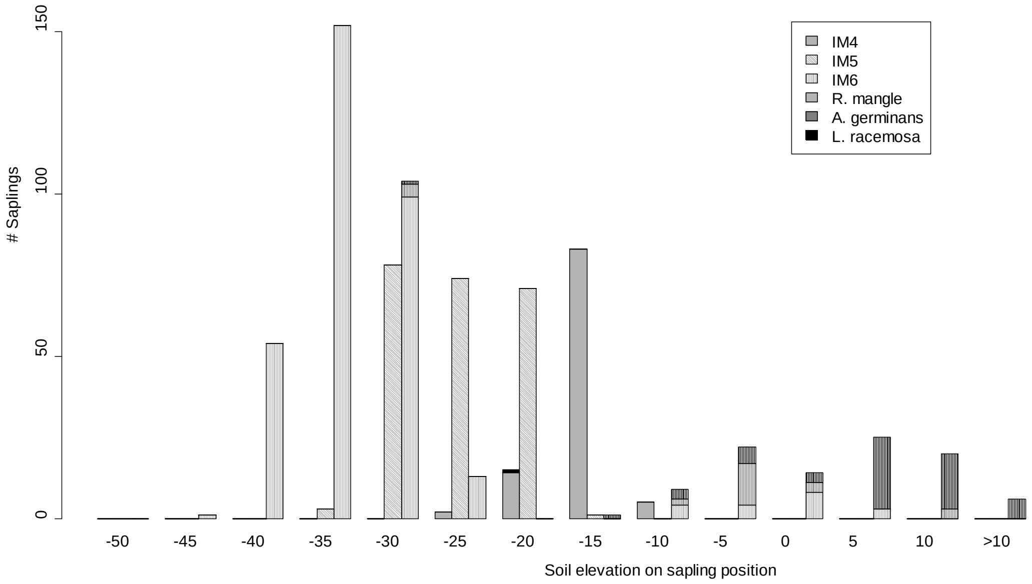

Figure 2.2: The species-specific distribution of the soil elevation at the post-hurricane established plants sapling stem position at the disturbed sites distinguished for each impoundment.

2.4 Discussion

The aim of our study was to characterize the hurricane damages in a human-modified environment and the subsequent regeneration. We found that the pre-hurricane forest structure played a crucial role for the disturbance pattern. Our results also show that the combination of two disturbance regimes might further modify the environmental conditions.

Even though the intensities of the two September 2004 hurricanes that made landfall along the IRL were moderate, they had a strong ecological effect and infrastructure damage (Mallin and Corbett 2006). The hurricanes disturbed 29% of the investigated coastal section and created considerable patches of dead trees. Hurricanes have been shown to either facilitate of the spread or accelerate the decline of introduced species (Flynn et al. 2010). In our study, the introduced species *C. equisitifolia* was more susceptible to wind damage and had a lower recovery rate than native mangrove trees, which showed a higher resistance and resilience.

Despite their close proximity and similar forest structure, the three impoundments used in this study showed large differences in the level of hurricane disturbance and the rate of regeneration. In the disturbed areas where the trees were scattered and larger, wind damage caused extensive stem breakage compared to the intact forests where the smaller trees were defoliated and recovered within a few weeks (pers. comm. James David). Similar size-dependent mortality during hurricanes was also reported in Roth (1992), Smith III et al. (1994), Imbert et al. (1996), Baldwin et al. (2001) and Flynn et al., (2010).

Lower soil elevation in disturbed areas may have been caused by the dieback triggered by the hurricanes and subsequent peat collapse (Krauss et al. 2005). Alternatively, it may have been caused by decomposition of dead root material after mass tree mortality (Cahoon 2006).

Alterations to mangrove hydrology are common and are caused by a variety of human activities such as aquaculture, road and dike construction, and, as in our study area, impoundment for mosquito control. Lewis III (2005) predicted that successful regeneration following such disturbances will occur in 15-30 yr if: 1) hydrological conditions controlling salinity, inundation, dryness, sulfide toxicity are suitable; and 2). propagules are present. In the impoundments, increased water depth after the hurricanes was not uniformly suitable and may have lead to additional stress for mangrove establishment. The propagule availability was apparently not a limiting factor since September is the main reproductive season of *R. mangle* in Florida (Rabinowitz 1978).

Our results showed that although the three impoundments had similar forest structure, they had very different rates of regeneration. After 5 yr, the recovery to a percentage of vegetation cover above 50% went from zero to entirely regenerated. IM 5 with the lowest regeneration was characterized by a pre-hurricane forest structure with the largest trees and the lowest densities of the three impoundments. Although this impoundment had the lowest soil elevation, post-hurricane *R. mangle* establishment was found in lower elevations in IM 4. Thus, neither the propagule availability nor the flooding depth explained differences in the rates of regeneration that we observed in the IRL impoundments.

The outcome of the post-hurricane species composition in the disturbed areas was mainly determined by the artificial flooding regime imposed by the impoundments. The advantages of having large propagules that can establish in deeper water (Sousa et al. 2007) and tolerate prolonged inundations (Elster et al. 1999) were crucial for the success of *R. mangle* under these conditions. Although the mangroves *L. racemosa* and *A. germinans*, which have the ability to resprout after disturbances (Duke 2001), they were a minor part of the forests at our study sites and thus were missing from the recolonization process. The pore water salinity recorded during our study exceeded the optimal conditions for *R. mangle* (Cardona-Olarte et al. 2006). Nevertheless, the hurricane disturbances in interaction with the artificial flooding regime were not able to alter the species composition. Moreover, because *R. mangle* seedlings are able to grow beneath the closed canopy, they could have survived the hurricane and therefore been established prior to the hurricanes (Baldwin et al. 2001), which could explain the rapid regeneration in some plots.

The field results showed that saplings established in these impoundments were not damaged by driftwood scouring and smothering as described in Duke et al. (1998). Instead, the numbers of damaged saplings and dead stems in small tree sizes increased in the forest, indicating suboptimal growth conditions under the closed canopy.

The unexpected negative correlation between the height of the regenerating *R. mangle* saplings and the soil elevation might be explained by the timing of the disturbance. Because September was after the main breeding season for mosquitoes the artificial pumping was stopped. Thus, the recolonization directly after the disturbance relied on a natural inundation regime for a supply of propagules. Regeneration probably started along the channels and in the low and partly inundated areas so that the saplings in those areas were older than on higher spots.

This study is another example for a succession trajectory, which differs from what was expected based on the environmental conditions and known species characteristics. It confirms the findings of Berger et al (2006) that even in relatively simple systems of three different species, human impacts may influence long-term changes in species compositions of mangrove forests.

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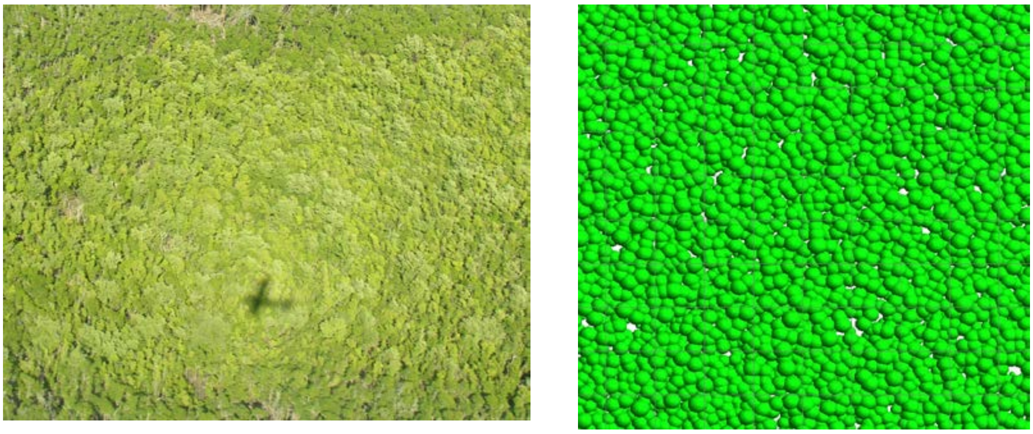
3 Simulation models for studying forest dynamics



Aerial photograph of a mangrove forest in Florida (left) and a simulated mangrove forest in the KiWi model (right).

3.1 Ecological models for forest ecosystems

Ecosystems are the products of interactions between its organisms, species and their habitat resulting in complex dynamics which makes predictions according to their behavior difficult (Green and Sadedin 2005). Additionally, the large spatial and temporal scale of ecological processes often inhibits an appropriate sampling (Green and Sadedin 2005). Ecological modeling enables experiments for specific ecosystem conditions, based on theoretical concepts or empirical data. This perceives the importance of ecological models to gain deeper knowledge in describing, understanding and even predicting (Grimm and Railsback 2005) ecological processes supplementary to the feasibility of field measurements. Thereby models do not fully represent the "real world" but simulate reproduce important aspects for a certain purpose.

Ecological models can be differentiated according to their purposes. For example analytical models based on linear equations dispose of a high amount of mathematical tractability, neglecting individual behavior of ecosystem elements (Perry and Enright 2006). In contrast, simulation models include more system specific details and non-explicit linearity, but are more difficult to extract information regarding the tractability and generality (Perry and Enright 2006). The latter enable the description of local specific behavior such as disturbances, dispersal, or differences in the life cycle which can influence the overall properties of the ecosystem (Green and Sadedin 2005, Grimm and Railsback 2005) and are therefore important tools to analyze further hypotheses for a better understanding of forest ecosystem processes. Due to the aggravated mathematical auditablility of high complex simulation models the pattern oriented modeling (POM) i.e. the reproduction of a real natural pattern should be used to understand ecological mechanisms (Grimm et al. 1996). This pattern of the simulated system is an indicator for the essential underlying processes and structures and the POM approach segregates the system information into the relevance of the single processes (Grimm et al. 2005).

The ever-increasing computer power contributes to the usage of long-term forest landscape simulations by forest ecologists and managers including e.g. ecological criteria, spatial interactions and population dynamics (Scheller and Mladenoff 2007). Within ecological processes disturbances represent a major driving force in forests influencing e.g. the mortality of organisms and the subsequent regeneration. For disturbance events often applied approaches include simulation models such as process-based vegetation dynamic models incorporating spatial-temporal interactions of disturbances with vegetation structure (Seidl et al. 2011). The spatial aspect within ecological dynamic models is substantial according to possible emergent characteristics of single elements and their interactions with the landscape (Perry and Enright 2006). Rammig and Fahse (2009) found that a non-spatial version of a grid model applied for forest succession simulation after blowndown events overestimated the number of trees and therefore distort the real measured forest structure.

Due to the importance of explicit spatial neighborhood consideration in forest systems we are going to present two spatial simulation types. Gratzer et al. (2004) distinguish between first finite state, individual orientated automata, or state-transition models which categorize the vegetation into patches with a finite number of states; and second individual-based models which track the individual life cycle including birth, growth and death in continuous states.

3.1.1 Individual oriented cellular automata and landscape models

Individual oriented cellular automata (CA) models are based on grid cells of fixed size and states considering environmental features like vegetation or topography (Green and Sadedin 2005). Spatially explicit landscape models (SELM) and forest landscape simulation models (FLSM's) belong to this model type, where patterns are described by spatial configurations and landscape elements including tree species, age classes or biomass (Scheller and Mladenoff 2007). These large-scale landscape models are derived from gap replacement models developed by the pioneers Newnham in 1964 (in Gratzer et al. 2004), Botkin et al. (1972a) with the JABOWA model and Shugart (1984) with FORET. The previous gap models uses the concept of a 'gap phase' and subsequent successional processes and not individual-based in a narrow sense possessing no spatial explicit stem position. These models work general on smaller scales of 1 ha composed of forest gap units of 0.1 ha (Shugart 1984), while the landscape models are used to simulate mostly large scale-landscape dynamics (Seidl et al. 2011) between 1 ha up to $1*10^7$ ha (Perry and Enright 2006).

The applications of landscape models in forest systems are diverse and include the modeling of disturbance patterns in general e.g. LANDIS (Mladenoff 2004), due to wood extraction FORMIND (Rueger et al. 2007) or forest fires (Perry and Enright 2006, Ratz 1995, Green 1989). Additionally they are used to analyze the synchronizing and de-synchronizing effects of natural dieback phenomena (Jeltsch 1992) or progressing waves of regeneration (Schlicht and Iwasa 2006). Furthermore, Rademacher et al. (2004) reconstructed spatio-temporal dynamics of natural European beech forest (BEFORE). They use grid cells either as a group of young individuals or as a single large tree to combine grid-based models with individual-based models described in the following section.

3.1.2 Individual-based-models

No absolute definition about individual-based models (IBM) exists (DeAngelis and Mooij 2005, Grimm and Railsback 2005) using the term as described in the following. IBMs are composed of discrete agents characterized by different traits having variations among them to simulate populations (DeAngelis and Mooij 2005). They present each plant or animal as an individual with certain characteristics of the individual's life cycle in continuous states (Green and Sadedin 2005, Gratzer et al. 2004), where the grid structure is mostly dissolved. Regarding to this definition I do not consider models as IBM which are based on units or cells compromising groups of individuals. The individuals go through time-dependent development, while characteristics like *establishing*, *growing*, *reproducing* or *dying* differ in a certain range between the individuals according to their seeking of fitness (Grimm and Railsback 2005). The individual behavior according to the environment and other individuals is an operating principle important for the questions being addressed (DeAngelis and Mooij 2005).

The consideration of space is as well advisable, because the inter-individual interactions are predominantly local in nature, and therefore individual behavior exhibits emergent characteristics on the population level thus influencing the properties of the whole system (Grimm and Railsback 2005, Gratzer et al. 2004). In this context, studying only the abundance omits structural population data and can lead to misinterpretation of the simulated system (Grimm and Railsback 2005). Therefore individual characteristics such as age, size, and location describe the system in much more details.

The first gap models by Botkin et al. (1972a) and Shugart (1984) serve as a basis for new development of subsequent individual based forest models e.g. SORTIE (Pacala and Tilman 1994) and SILVA (Pretzsch 2001). Herein, the grid structure is dissolved and the explicit tree position can be described in detail.

Traditionally the forest gap models and individual-based tree models considered relatively small areas between 0.1-1 ha. However, due to the ever-increasing computer power individual models are now applicable for larger scales than 1 ha and are suitable to investigate large natural and anthropogenic disturbances such as fire, hurricanes or land use changes.

IBM in mangroves

Three individual-based models were developed for mangrove forests in order to study their dynamics and to predict ecological behavior according to different environmental settings, natural and human-induced disturbance regimes, and management scenarios (Berger et al. 2008). They provide useful information for the mangrove protection or restoration (Berger et al. 2008). KiWi (Berger and Hildenbrandt 2000) and MANGRO (Doyle et al. 2009) use spatially explicit stem positions, while FORMAN (Chen and Twilley 1998) works with the concept of the gap models JABOWA (Botkin et al. 1972a) and FORET

(Shugart 1984). All three models were originally developed for the Neotropical mangrove tree species *Avicennia germinans*, *Laguncularia racemosa* and *Rhizophora mangle*. Resources or stress factors such as nutrients and salinity are homogeneous within the gap (FORMAN) or forest stand (MANGRO), whereas KiWi is able to use heterogeneous conditions within the simulated area and during the simulated time (Berger et al. 2008). FORMAN and KiWi analyze mainly forest stand dynamics whereas MANGRO was developed for landscape dynamics on larger spatial scales (Berger et al. 2008). Nevertheless, KiWi is suitable for simulating areas up to 1 km^2 on the individual tree level (see Chapter 4).

In addition, KiWi is the only mangrove IBM able to consider explicit sapling dispersal (Berger et al. 2008). Even though exact sapling dispersal data wasn't available, this capability of KiWi was used as described in Chapter 4, where saplings establish in a certain distance from a mother tree in regenerating lightning-strike gaps. A theoretical attempt to bypass the missing dispersal data was undertaken by Seltmann (2011), where he used Kiwi to test the recolonization of a forest stand under different dispersal strategies by applying different configurations of random versus mother-tree-dependent dispersal patterns.

3.2 Model description of KiWi

The individual-based mangrove forest model KiWi was developed by Berger and Hildenbrandt (2000) in order to simulate long-term dynamics of mangrove forests for the neotropical species *A. germinans*, *L. racemosa* and *R. mangle* influenced by environmental conditions or disturbances either naturally occurring or caused by human activity.

KiWi was successfully applied in several studies for the study of neighborhood competition and self-thinning behavior (Berger et al. 2004); for investigating recolonization of mangrove forests in abandoned rice fields (Berger et al. 2006); and testing the intermediate hypothesis on the species composition influenced by different resource and stress levels (Piou et al. 2008). Furthermore Fontalvo-Herazo et al. (2011) extended the parameterization in KiWi for one of the most common mangrove species *Rhizophora apiculata* planted in Asia for timber production to simulate sustainable harvesting strategies. This new parameterization enabled Kautz et al. (2011) and Vogt et al. (2011) (Chapter 4) to use KiWi for investigating the influences of lightning-strike gaps in an even-aged and even-sized *Rhizophora apiculata* plantation in the Biosphere Reserve in Can Gio (South Vietnam). Kautz et al. (2011) focused on the transient oscillations i.e. analyzing tree density in time series for different frequencies of lightning strikes whereas Vogt et al. (2011) investigated the transformation into a more natural-like structure.

In addition, a simulation study was carried out for the forest structure of multiple disturbed mangroves by combining the influence of small gaps and medium-sized disturbed patches on the forest structure (Chapter 5). KiWi enables the exact implementation of spatial and temporal characteristics of the disturbance regimes and the specific dispersal strategies influencing the regeneration.

Below, KiWi is described by using the ODD standard protocol (Grimm et al. 2010). Focusing on the specific research topic of this thesis, the description was modified from earlier ODD versions (in Grimm et al. 1996 and Berger et al. 2008). Additionally, a self-learning tutorial was composed, based on the ideas of Cyril Piou and modified by me and Denny Walther to enable autonomous usage of KiWi (available on request at the professorship of Forest Biometrics and Forest System Analysis, TU Dresden).

3.2.1 Purpose

KiWi was originally developed to gain knowledge about forest dynamics in Neotropical mangroves influenced by environmental settings, tree competition, management activities or natural disturbances. Temporal and spatial forest structures are analyzed considering disturbances explicitly by their type, spatial extent, intensity and frequency and others specific impacts on the mangroves such as size dependent tree mortality.

3.2.2 State variables and scales

The KiWi model is spatial-explicit for each individual tree. The trees are characterized by the species, the stem position in a coordinate system of the simulated area, the stem diameter (*DBH*), the age and the diameter increment (*Δ DBH*). These characteristics can be used to calculate further stand characteristics such as biomass.

For this thesis, species-specific parameters for *A. germinans* (sensitivity analysis performance), *R. apiculata* (investigation of lightning-strike gaps in homogenous plantations) and *R. mangle* (Simulation study of different disturbance regimes) are used for several model processes as described in the below.

The size of the simulated area varies according to the subject, using a range of 1 ha to 1 km^2 for the different simulations in this work.

Furthermore, map underlay for simulations of environmental conditions influence on tree behavior, such as stress factors (e.g. salinity), resources (e.g. nutrients), and topography (e.g. inundation regime), is possible. However, these capabilities of KiWi weren't used for the present thesis (Figure 3.1).

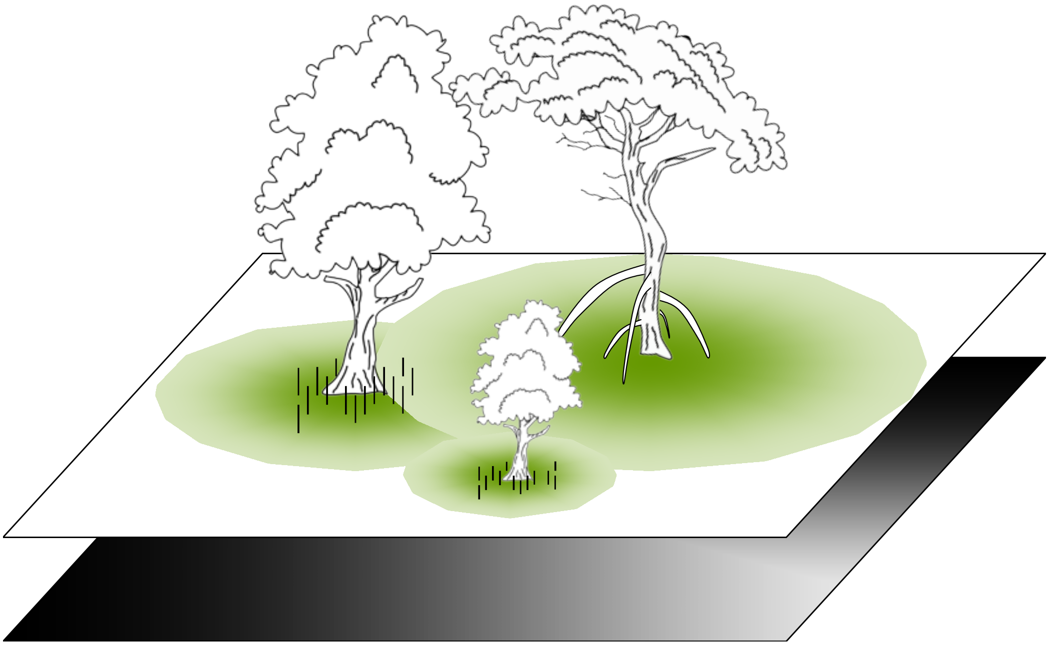


Figure 3.1: The functional principle of the KiWi model. Underlaying maps (gray layer below) representing e.g. environmental conditions differently distributed within the simulated area and influence processes within the model. The white layer illustrates the FON approach (green circles). The FON expressed by a scalar field with decreasing strength in distance to the the tree stem is species and size specific.

3.2.3 Process overview and scheduling

Tree process calculations mainly dependent on the stem diameter are accomplished and updated on a yearly base including: influence of competing neighbors; recruitment of new saplings; tree growth; and mortality. Mortality can be triggered by reduced growth of individual trees or by explicit implementation (e.g. disturbance creation), respectively.

3.2.4 Design concepts

Basic principles

KiWi is based on the idea of forest gap models (Shugart 1984) using a modified JABOWA growth function where annual tree growth depends on the species, tree size, and light availability. Botkin et al. (1972a) published the first successful reproduction of forest patterns such as species composition, individual tree suppression and release of 10x10 m field study plots with the tree growth simulator JABOWA. Moreover, in KiWi the competition with neighboring trees is defined by an overlap of individual circular zones around the stem, based on the theory that each individual consumes resources in a certain radius of its position (Berger and Hildenbrandt 2000). This implemented process in KiWi, called Field-Of-Neighborhood (FON), is based on the Zone Of Influence (ZOI) approach, but has the decisive advantage of using a scalar field influencing the competition in decreasing strength in exponential dependence from the distance to the stem (Figure 3.1).

Emergence

The annual executed tree processes result in emergent characteristics according to the explicit tree locations influencing the self-thinning behavior, size structure and spatio-temporal pattern of the forest.

Sensing and Interaction

The FON characterizes the competition between neighboring trees. Trees “sense” the influence of their neighbors via FON This scalar field is size and species-dependent and decreases exponentially with the distance of the stem position of the focal tree. The sum of FON at a specific position indicates the strength neighborhood competition. As a consequence, high total FON on a local spot will prevent saplings to establish according to the high competition pressure.

Stochasticity

KiWi includes both model-intrinsic demographic stochasticity which evolves from the IBM behavior such as the probability for saplings to establish, and environmental stochasticity which could be implemented directly by the user as needed for example by introducing disturbances.

Observation

Variables such as stem position, *DBH, ΔDBH,* age, height, competition strength of a focal tree, can be stored and used for further calculations. The graphical output of the simulated ~~forests~~ allows a visualization of its development.

3.2.5 Initialization

In this work I used single species systems for all simulation studies. The saplings are introduced at the minimal height of 1.37 m, having a minimal stem diameter of 1 cm. The sapling density depends on the simulation study by using either forest inventory data (lightning-strike gaps in the forest plantation) or data found in the literature. Simulation runs can start either with an open area or with certain beforehand simulated forest stages as described in Chapter 5.

3.2.6 Input data

Tree mortality is affected by discrete events as implemented for the lightning strike study (Chapter 4) and for the simulation analysis of different disturbance regimes (Chapter 5).The conducted sensitivity analysis (see below) does not include disturbances.

3.2.7 Submodels

Inter-individual tree competition

The FON approach describes inter-individual spatial explicit competition for focal trees sharing resources with neighbors. This FON influences directly the recruitment ability and the diameter increment and thus the individual growth and mortality caused by growth reduction of each tree. Further explicit implemented disturbances create additional mortality. Input parameters for the studied species within this work are listed in Table 3.1.

The FON intensity for each tree within its neighborhood is described in Equation 1.

$$FON(r) = \left\{ \begin{array}{l} for(0 \le r < (DBH/2)) \Rightarrow F_{\max} \\ for((DBH/2) \le r \le R_{FON}) \Rightarrow e^{c(r-(DBH/2))} \\ for(r > R_{FON}) \Rightarrow 0 \end{array} \right\} \qquad \textit{(Eq. 3.1)}$$

The *DBH* is the diameter at breast height and the size dependent FON radius *R* of a tree is calculated by:

$$R = a * \left(\frac{DBH}{2} \right)^{b} \qquad \text{(Eq. 3.2)}$$

including the FON scaling parameters *a* and *b*.

Recruitment and establishment

The spatial establishment of saplings can be implemented in different ways: First, a random distribution throughout the simulated area can be chosen (see sensitivity analyses in the current chapter and in Chapter 5). Secondly, saplings can be planted in regular tree arrangements (Chapter 4) to reproduce the spatial structure of a plantation. In addition, subsequent establishing saplings can be introduced in a certain radius of an abundant parent tree (Chapter 4). The recruiting process is an annual executed process but does not have to occur every year. The ability for saplings to establish is dependent on the species-specific competition tolerance ($F_{max\_establish}$) and the present FON intensity on the specific recruitment location. Therefore the sum of the FON intensity for the sapling position $F(x_{sapling}, y_{sapling})$ was calculated and compared with the $F_{max\_establis.}$:

$$F(x_{sapling}, y_{sapling}) = \sum_{i=1}^{n} FON(Dist_i) \qquad \text{(Eq. 3.3)}$$

The number of neighboring trees influencing the sapling stem position is expressed by n and $Dist_i$ and shows the distance between the sapling and the neighbor tree position.

Tree growth

The optimal tree growth is calculated by the stem diameter increase over time:

$$\frac{\Delta DBH}{\Delta t} = \frac{G * DBH * \left(\frac{1 - DBH * H}{DBH_{\max} * H_{\max}} \right)}{274 + 3 * b_2 * DBH - 4b_3 * DBH^2} * cF(comp) \qquad \text{(Eq. 3.4)}$$

The competition multiplier was used for the reduction of optimal growth i.e. the received neighborhood competition F_A for the focal tree factor *cF(comp)* with *n* for the neighbors of the focal tree *k*. *A* contains the FON area of *k*, and the overlap area between the focal tree and its neighbors is called *O*:

$$cF(comp) = \max\left\{0;1-2*\left(\frac{1}{A}\sum_{n\neq k}\int_O FON_n(x,y)dO\right)\right\} \qquad (Eq.\ 3.5)$$

Further correction factors on the optimal growth which are not used in this thesis are for example resource availability or stress factors as described in detail by Berger and Hildenbrandt (2000).

The tree height is calculated by the relationship

$$H = 137 + b_2\,DBH - b_3\,DBH^2 \qquad (Eq.\ 3.6)$$

(Shugart, 1984), where *DBHmax* and *Hmax* express the species-specific maximum tree size, and *G*, b_2 and b_3 are species-specific growth parameters. This output variable was used to describe explicitly the vertical forest structure (see current chapter and Chapter 4).

Mortality

Tree mortality within the model occurs according to growth repression either by achieving its maximum size or by weak competition strength compared to neighboring trees within a certain time period. Therefore, the mean *DBH* increment of each tree is calculated typically over the last 5 years and compared with the species specific threshold *critDX*. If the individual mean *DBH* deceeds this value, the trees are removed. The *critDX* value complies with the half of the potential optimal diameter increment.

Furthermore, additional tree mortality can be simulated as stochastic events e.g. by creating disturbances. In Chapters 4 and 5 I put a special focus on implementing the disturbances with explicit sizes and shapes, frequencies and severities.

Table 3.1: Species specific parameters of *A. germinans*, *R. apiculata* and *R. mangle* in KiWi used in this thesis. Sources of the parameters for *A. germinans* and *R. mangle* are Piou et al. (2008) for the parameters *a* and *b* and all other parameters Berger and Hildenbrandt (2000). For *R. apiculata* I calibrated parameters *a*, *b*, $F_{max\_establish}$ in Chapter 4 and used the parameterization of Fontalvo-Herazo et al. (2011) for all other parameters.

Parameter	**Description**	***A. germinans*** (current Chapter)	***R. apiculata*** (Chapter 4)	***R. mangle*** (Chapter 5)
a	FON scaling factor	13.7	5	18
b	FON scaling factor	0.72	0.654	0.83
F_{min}	Minimum intensity of FON parameter	0.1	0.1	0.1
$F_{max\_establish}$	Establishment threshold of competition strength for saplings	0.1	0.3	0.5
G	Growth constant	162	281.25	267
D_{max}	Maximum *DBH* (cm)	140	80	100
H_{max}	Maximum height (cm)	3500	3000	3000
b_2	Height-*DBH* relationship constant	48.04	71.575	77.26
b_3	Height-*DBH* relationship constant	0.172	0.44734	0.396
critDX	Mortality threshold of diameter increment (cm)	0.23	0.05	0.2

3.2.8 *KiWi parameterization*

Fontalvo-Herazo et al. (2011) give a very good guideline about the parameterization of new mangrove species in KiWi. Some information were adopted from this publication and additional calculation derived from Botkin et al. (1972b) are described below to receive a complete overview of the parameterization processes in KiWi for introducing new species or conducting sensitivity analyses with changing parameter ranges.

The FON radius *R* with the parameters *a* and *b* (*Eq.* 3.2) can be parameterized by using a linear regression model with logarithmic transformation of *DBH* and density data of monospecific stands with having *K* as the slope and *r* as the intercept of the regression (Fontalvo-Herazo et al. 2011):

$$a = \sqrt{\frac{21500}{e^{r}\pi\left(\frac{1}{200}\right)^{-K}}} \qquad \text{(Eq. 3.7)}$$

$$b = \frac{-K}{2} \qquad \textit{(Eq. 3.8)}$$

The species-specific growth parameters *G*, b_2 and b_3 can be calculated by the formulas of Botkin et al. (1972b):

$$G \cong \frac{\Delta D_{\max} * H_{\max}}{0.2 * D_{\max}} \qquad \textit{(Eq. 3.9)}$$

The maximum possible annual diameter increment ΔD_{max} under optimal conditions was varied to determine the growth constant G (Eq. 3.9). This relation was observed in an empirical study by Botkin et al. (1972b).

Furthermore, the parameters b_2 and b_3 are chosen for $H=H_{max}$ and $\Delta H/\Delta D=0$ when $D= D_{max}$ and 137 is the breast height [cm] (Botkin et al. 1972b):

$$b_2 = \frac{2*(H_{\max} - 137)}{D_{\max}} \qquad \textit{(Eq. 3.10)}$$

and

$$b_3 = \frac{(H_{\max} - 137)}{D^2_{\max}} \qquad \textit{(Eq. 3.11)}$$

The threshold for trees mortality events according to a growth repression *critDX* is assumed to be one half of the average increment of 5 years under optimal conditions. Lower values trigger tree death. The decline in increment is age dependent as well, according to species-specific maximum in tree size. Therefore I calculated:

$$critDX = critDX_{range} * \frac{D_{\max}}{age_{\max}} \qquad \textit{(Eq. 3.12)}$$

where age_{max} was calculated by rearranging the following formula of Botkin et al. (1972b) (see Appendix 8):

$$G = \frac{4H_{\max}}{age_{\max}}\left\{\ln(2(2D_{\max}-1)) + \frac{c}{2}\ln\left(\frac{\frac{9}{4}+\frac{c}{2}}{4D_{\max}^{2}+2cD_{\max}-c}\right) - \frac{c+\frac{c^{2}}{2}}{\sqrt{c^{2}+4c}}\ln\left[\frac{(3+c-\sqrt{c^{2}+4c})(4D_{\max}+c+\sqrt{c^{2}+4c})}{(3+c+\sqrt{c^{2}+4c})(4D_{\max}+c-\sqrt{c^{2}+4c})}\right]\right\} \quad \text{(Eq. 3.13)}$$

with $c = 1-(137/H_{max})$ which is an empirical parameter.

3.2.9 Summary of KiWi usage

The originially developed KiWi was extended for the purpose of this work. On the one hand, *R. apiculata* parametrisation of Fontalvo-Herazo et al. (2011) was adapted to a plantation system in the Can Gio region, besides the three main Neotropical model species of the initial KiWi version.

On the other hand different disturbance regimes in KiWi were explicitly implemented in shape, size and frequency for the first time in this thesis. Lightning strike gap characteristics obtained from satellite images and literature were used to simulate a realistic situation in the plantation in Can Gio. Additionally, the influence of different possible lightning strike regimes was compared to study the outcome on forest structure. Hurricane disturbances were explicitly implemented, based on field observations and used for investigating forest structure. Here the impacts of small-scale frequent lightning strike gaps and medium-sized infrequent hurricane events was shown to lead to differences in the forest structure despite the fact that the different characteristics have the same overall probability to kill trees during the simulated time.

The KiWi model is very flexible regarding various issues related to mangrove forests and could be applied for future research.

3.3 Sensitivity analysis for KiWi

3.3.1 Introduction

A sensitivity analysis (SA) was conducted for KiWi in order to obtain information about the influence of input parameters on the model results. This was achieved by calculating spatial indices for the horizontal tree arrangement and for the vertical tree height density as well as classical tree parameters such as mean *DBH* and tree density.

In general, SAs are used to detect the contribution of the input factors to the model's output regarding the total predictive variance (Cariboni et al. 2007, Saltelli et al. 2004). The most important factors as well as factors having only little effect for model calibration, validation or revision, are identified (Grimm and Railsback 2005). Therefore, the SA is applied within the modeling processes containing multiple sources of uncertainty (Cariboni et al. 2007, Grimm and Railsback 2005).

Saltelli et al. (2004) list following aspects which might be considered within the SA according to use: i) the model is adapted to a field study and specific factors are tuned; ii) most influencing factors are determined which requires additional attention; iii) input parameters with low impact might be eliminated; iv) identification of ranges of input factors for the maximum model variation; and then v) use this information for a calibration study; vi) detection of interactions between the input factors.

Hence, the SA ensures a certain quality and worthiness of the model (Saltelli et al. 2004). Different approaches toward SA can be used. A local SA, also called one-at-a-time (OAT) explores a single input factor while other factors are kept constant. The opposite approach is when all input factors are being varied simultaneously, thus identifying their total impact on model output (Cariboni et al. 2007).

3.3.2 Methods

The extended FAST (Fourier Amplitude Sensitivity Test) method for analyzing first order sensitivity indices equivalent to main effects was applied. This global SA was used according to the assessable computational effort for the amount of tested input factors (Cariboni et al. 2007). The extended FAST is a variance-based global sensitivity analysis applicable for non-linear, monotonic and non-monotonic models (Saltelli et al. 2000). The influence of each input factor is decomposed within the output variance (Cariboni et al. 2007). It is based on the functional principle which transforms a multidimensional integral over all uncertain model inputs and converts them into a one-dimensional integral via search curve scanning of the whole parameter space (Saltelli et al. 2000).

The first order effect of input factor X_i is also called the main effect S_i; where Y is the model output (Cariboni et al. 2007, Saltelli et al. 2004):

$$S_i = \frac{Var\,[E(Y \mid X_i)]}{Var[Y]} \qquad \text{(Eq. 3.14)}$$

The variance of all possible values is expressed by Var and $E(Y \mid X_i)$ indicates the expectation of the model output on the fixed input factor value. Therefore, S_i indicates which amount of variance would be removed from the total output variance if the input factor was known (Saltelli et al. 2000). An input factor X_i with a strong impact would have a high variation on the model output and thus increase the variation of the expected model output. Non-influential input factors will show relatively low constant expected variance.

The extended FAST method was conducted with Simlab (2011), a software package for global uncertainty and sensitivity analyses. Range and distribution of each input factor can be defined, and samples were generated for different combinations. Further, this selection of input factors was introduced in the KiWi model (see below for a detailed description). The model output was then reloaded to Simlab to calculate the influence of the input factors on the model output.

We tested seven input factors related to the growth and the Field of Neighborhood functions for the standard values of *A. germinans* (Table 3.2). The ranges of +/- 50% of these values were artificially chosen except for b which was varied from 0.5 to 1 due to the mathematical feasibility (see Eq. 3.2). The ranges of D_{max}, H_{max}, with $D_{max} = D_{max\ range}$ and $H_{max} = H_{max\ range}$ involve the ranges of the values of G (Eq. 3.9), b_2 (Eq. 3.10), b_3 (Eq.3.11) and age_{max} was calculated for the range of *critDX* (Eq. 3.12) deriving from Equation 3.13.

Table 3.2: Input factors of *A. germinans* for the sensitivity analysis.

Parameter	Description	Standard value	Tested range
a	FON scaling factor	13.7	6.89-15.2
b	FON scaling factor	0.72	0.5-1
F_{min}	Minimum intensity of FON parameter	0.1	0.05-0.15
D_{max}	Maximum *DBH* (cm)	140	70-210
H_{max}	Maximum height (cm)	3500	1750-5250

According to the unknown distributions of the input factors, uniform distributions were assumed. Simulations were carried out for 10,000 parameter combinations with 20 repetitions each and model outputs were stored after 100 years and averaged for the parameter combinations. The simulated size of 1 ha was initialized with 1800 saplings according to (Chen and Twilley 1998) and no further recruitment occurred during the simulation.

The model outputs include tree density, mean *DBH* and spatial structure indices such as the Clark-Evans Index (*R*) (Eq.3.15) (Clark and Evans 1954) for spatial tree arrangement with the Donnelly (1978) correction for edge effects, and the Shannon Index (*SI*) (Eq.3.16) applied for tree height (Zenner and Hibbs 2000); as well as the Coefficient of Variance (*CV*) of the tree diameter.

$$R = \frac{\overline{r_A}}{\overline{\overline{r_E}}} \qquad 0 \text{ (clustered)} \leq R \text{ (random)} \leq 2.15 \text{ (regular)} \qquad \text{(Eq. 3.15)}$$

The Clark-Evans Index is described by the distance between a tree and its nearest neighbor r_A and the expected value for a random distribution r_E, where the minimum value of R=0 shows super-clustering (all points would have the same position), R=1 a random, and the maximum R=2.15 a strongly regular distribution of the tree arrangement.

The Shannon Index (*SI*) applied for canopy height heterogeneity (Zenner and Hibbs 2000) was calculated for 6 (SI_6) and 12 (SI_{12}) size classes, respectively. These two different classifications are a methodological approach investigating the importance of the size classes for the parameter inputs. The potential maximum tree height for all parameter combinations of 52.5 m (150% of 35 m) was set as a maximum value, whereas the minimum value started with 2.5 m according to the *DBH*-height relationship of Equation 3.6. The index is based on an array of p values where p_i is the relative abundance of the height class i with (8.75 m for 6 classes (cl.) and 4.375 for 12 cl.):

$$SI = -\sum_{i=1}^{H} p_i \ln p_i \qquad 0 \leq SI \leq \approx 1.79\ (6\ \text{cl.})\ \&\ 2.48\ (12\ \text{cl.}) \qquad (Eq.\ 3.16)$$

The *CV* (Eq. 3.17) for the tree diameter characterized the size structure as well. The variation is increasing with increasing *CV* values.

$$CV(DBH) = \frac{sd(DBH)}{mean(DBH)} \qquad (Eq.\ 3.17)$$

3.3.3 Results

The results of Figure 3.2 show on the left side the distribution of the analyzed output variables for all input variable combinations. The pie charts on the right side illustrate the first order effects i.e. the influence of the input parameters on the output index (extended FAST).

The stand characteristics such as number of trees, mean *DBH*, and maximum age are influenced to a varying degree by the species-specific input parameters. The *number of trees* output ranges between zero and 2700 trees on the simulated area with a continuous decrease in frequencies with increasing tree numbers (Figure 3.2a). The major amount of the variation (79%) of the tree density is described by the input parameters. The most influencing input parameters (first order index > 0.1) are the FON parameters *a* and F_{min} and the growth parameters *G* and *critDX*.

The mean *DBH* varied widely, indicating a sensitive behavior and ranges between 0 cm (no trees left in the simulated area) to 106 cm (Figure 3.2b). This value is below the maximum possible value of the theoretical D_{max} and can be explained that after 100 years simulated time the trees did not reach their full extend. The highest frequency of mean *DBH* was found around 45 cm. The strongest influence on the mean *DBH* had the growth parameter *G* by far. Almost 50 % of the variation could not be explained by the first order effects of the input parameters.

The horizontal structure (Clark-Evans Index) values showed little variation between a random and regular distribution (Figure 3.2c). A very low amount of the variable combinations led to values below 1 indicating a clustering. By far the majority of input parameter combinations led to a regular distribution of the initially established trees. The FON parameters F_{min}

and *critDX* had the strongest influence, but 64% of the variation was not explained.

The vertical Shannon index varied for both classifications from no diversity to approximately the half of the potential maximum values, probably according to the shortage of simulated time (Figure 3.2d, e). Only a low amount of the output variation is described by the input parameters (12.5% for 6 classes and 28.9% for 12 classes). On the one hand, the high amount of no diversity in the *SI* for 6 classes indicates an even growth of the cohort. On the other hand, the distribution of tree in different height classes showed a diversification of trees of the same age but into different heights. H_{max} and *critDX* had the highest influence on this output index for both of the analyzed size classes, but still at a low level.

The *CV(DBH)* (Figure 3.2f) exhibits values below 1 for all parameter combinations indicating a low variance within the forest size structure. Almost the half of the variation was explained by the input parameters, but mainly by F_{min} and *critDX*

Out of the 10,000 variable combinations, approximately 400 simulations (cognizable by the lowest size class of the mean *DBH*) exhibit unsuitable, which lead to no trees being left in the simulated area after 100 years. The undefined variation of the model outputs were relatively high for the forest structure indices indicated by a high distribution range within the histogram in Figure 3.2. The tree density showed only a 21% and the mean *DBH* should almost 50% of unexplained variation (Figure 3.2).

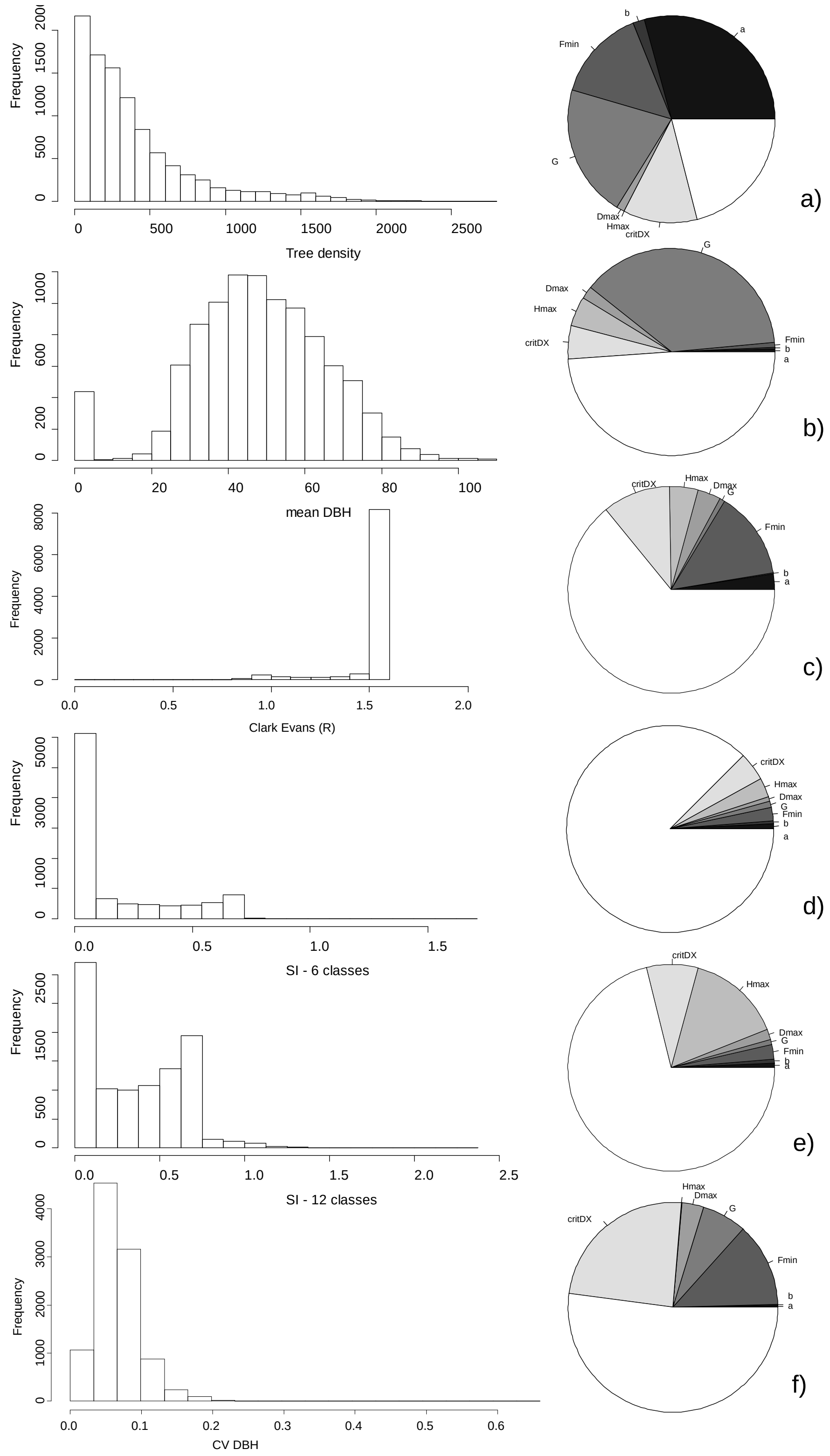


Figure 3.2: Sensitivity analysis extended FAST model output frequencies (left) and first order indices (right). a) tree density, b) mean *DBH*, c) horizontal Clark-Evans Index, and the vertical Shannon Index for d) six, and e) twelve height classes; f) *CV(DBH)*. The white segments express the amount of unexplained variation.

3.3.4 Discussion

The major variation of the classical tree parameters output (tree density and mean *DBH*) was explained by the effects of the individual tested input parameters. The growth constant *G* had a major influence on the mean tree diameters and on the tree density but not on the forest structure indices indicating that the growth has an influence of the trees, and therefore in combination with the FON an effect on the spacing between trees. The tree density was additionally influenced by the parameters F_{min} and *a* regulating directly the strength of the neighborhood. Although the structure indices showed a certain variation of their distribution regarding the single effect of input parameters, the amount of the explained variation on the model output was relatively low, except for the *CV* which is directly linked with the *DBH*. It is not possible to clearly allocate these effects, but they might be due to the influence of the interactions of these input parameters (total effects) which was not analyzed in this SA. However, Kautz et al. (2011) showed that input parameters can have different effects according to their single or interacting influence.

The SA conducted by Kautz et al. (2011) used an extended FAST and similar simulation settings to those presented in this thesis. However, there is a difference in the used species and in the implemented recruitment regimes. The sensitivity analyses of this thesis and the one published by Kautz et al. (2011) are compared in Table 3.3.

Table 3.3: Comparison of the conducted SA analysis of Kautz et al. (2011) and the current SA of this chapter.

<table>
<tr><th></th><th>SA in (Kautz et al. (2011))</th><th>SA of this Chapter</th></tr>
<tr><td><i>Simulation settings</i></td><td></td><td></td></tr>
<tr><td>Initial condition</td><td colspan="2">Open area</td></tr>
<tr><td>Spatial arrangements of trees</td><td colspan="2">Randomly distributed</td></tr>
<tr><td>Disturbances</td><td colspan="2">No</td></tr>
<tr><td>Recruitment</td><td>Yes from the 5th year (90 saplings/year)</td><td>No</td></tr>
<tr><td>Number of species</td><td colspan="2">One</td></tr>
<tr><td>Species</td><td><i>R. apiculata</i></td><td><i>A. germinans</i></td></tr>
<tr><td><i>Sensitivity analysis</i></td><td></td><td></td></tr>
<tr><td>Method</td><td colspan="2">Variance-based extended FAST</td></tr>
<tr><td>Number of tested input parameter</td><td>9</td><td>7</td></tr>
<tr><td>Input parameter range</td><td>+/- 10%</td><td>+/- 50%</td></tr>
<tr><td>Time step SA</td><td colspan="2">100 years</td></tr>
<tr><td># of tested parameter sets</td><td>657</td><td>10,000</td></tr>
<tr><td>Simulation runs per parameter set</td><td>no</td><td>20</td></tr>
<tr><td>Output variables</td><td>Tree density</td><td>Tree density, mean <i>DBH</i>, Clark-Evans, Vertical Shannon (6 and 12 classes), <i>CV(DBH)</i></td></tr>
<tr><td>First order effects</td><td colspan="2">Yes</td></tr>
<tr><td>Total effects</td><td>Yes</td><td>No</td></tr>
</table>

The total number of tested input parameters in this thesis is 7, whereby the parameter G and *critDX* depend on the values of H_{max} and D_{max} (Eq. 3.9 and 3.12), compared to 9 used independently of each other by Kautz et al. (2011). Further, the additional parameters b_2 and b_3 (*DBH*-height relationship) weren't considered directly in the present thesis, because they were kept constant related to the values of H_{max} and D_{max} (Eq. 3.10 and 3.11). From the present point of view the artificially chosen parameter range of +/- 50% of the recent study appears too broad, as in the established literature ranges of 10-20% are used (Grimm and Railsback 2005).

In Kautz et al. (2011) 657 parameter sets with no repetition of simulation runs per parameter set were tested to analyze 9 input parameters compared to the present study where 10000 parameter combinations with 20 repetitions each were tested.

The main advantages of using global variance-based methods are the independence of the model (also for non-monotonic and non-linear models) and the investigation of the influence the full range of variation of each factor and interaction between factors. However, these methods require large numbers of tested parameter sets for a reliable model evaluation (Jing 2011). For example, the variance-based Sobol method would need $N_{sim}=m*(2*n+2)$ number of simulations, where m is set as a minimum value of 100 and n is the number of input factors. Therefore a parameter set of 9 input factors would require 2000 simulation executions. Hence, 10,000 input factor combinations for 7 input factors provide a more solid base for the model evaluation.

The output variance was solely concentrated only on the tree density in Kautz et al. (2011). The current SA considered as well the mean *DBH*, and spatial structure indices (*R*, *SI*, *CV(DBH)*) which contain a major topic of this thesis. The major influence of each input parameter (first order effects) for the tree density were the FON parameters *a* and *b* in Kautz et al. (2011). This partly agrees with our results of *a* being the most influencing factor, indicating that the FON and therefore the competition is important for the spacing and consequently for the tree density. Furthermore, I found a strong influence of the growth constant G which has effects on the diameter increment and the F_{min} (trees sensing competition), which was not detected in Kautz et al. (2011). This result might be due to the influence of continuously establishing saplings throughout the simulated area in time in Kautz et al. (2011). Permanently introduced saplings could reduce the overall influence on the growth function and on the competition of the canopy trees, by having a delayed growth repression mortality of 5 years. The missing analyses of the total effects presents a disadvantage of the current SA, because the results of Kautz et al. (2011) indicate that the input parameters may have different effects if the interaction is considered. They showed that F_{min} showed on the one hand only little influence for the first order effect but on the other hand having high influence for the total order effects.

Presently, the different recruitment strategies are being omitted, and analyses regarding the dispersal strategies, e.g. random distribution within the simulated area or recruitment close to mature trees or the number of annual introduced sapling might influence the model outputs considerably.

The conducted SA provides information about the influence of the tested input parameters on several structure indices, which are an important basis for the discussion of the following chapters. Instead of using external disturbances for this analysis I concentrated on undisturbed scenarios as a reference and as a general test of model robustness and goodness. The additional implemented disturbances are already implemented in the case studies presented within the following chapters.

Therein, I address the effects of small-scaled lightning strike-induced gaps on a homogenous plantation in comparison to a randomly generated, established forest (Chapter 4). In addition, Chapter 5 expands the scope of the results from Chapters 2 and 4 by combining them in a simulation study on areas with multiple disturbances.

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4 Do canopy disturbances drive forest plantations into more natural conditions? – A case study from Can Gio Biosphere Reserve, Vietnam

Lightning strike gap in the Can Gio plantation (Photo by Uta Berger)

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Abstract

Large areas of mangrove forests were devastated in South Vietnam during the second Indochina war. After its end in 1975, extensive reforestation with monocultures took place. Can Gio, one of the biggest replanted sites with about 20,000 ha of mangroves mainly *Rhizophora apiculata*, was declared a Biosphere Reserve by the UNESCO in 2000. Although this status now enables progressive forest dynamics, there are still drawbacks resulting from the unnatural character of the plantations. For example, the homogeneous size and age structure as well as the regular arrangement of the planted trees make larger forest stands more vulnerable to synchronized collapsing which can be triggered by stronger winds and storms. A transformation into a more natural forest characterized by a heterogeneous age and size structure and a mixed species composition is of urgent need to avoid a synchronized dieback. In this study I test the capability of natural canopy disturbances (e.g. lightning strikes) to facilitate this transformation.

Canopy gaps created by lightning strikes were detected and quantified by remote sensing techniques. SPOT satellite images from the years 2003, 2005 and 2007 provided information about the spatial distribution, size, shape, and formation frequency of the gaps. Lightning-strike gaps were identified based on their shape and size. The gaps are small (mean: 0.025 ha) and their yearly probability of occurrence is approximately 0.012 per hectare. This correspond to a total area of 0.17% disturbed by lightning strikes, which is little compared to values obtained from other mangrove forest areas (1.4-4.5%). Selected gaps were additionally field-surveyed in 2008 to complement the remote sensing data and to provide information upon forest structure and regeneration.

Simulation experiments were carried out with the individual-based KiWi mangrove model for quantifying the influence of different lightning regimes on the vertical and horizontal structure of the *Rhizophora apiculata* plantation. In addition, we conducted simulations with a natural and thus randomly generated forest to compare the structure of the two different cultivation types (i.e. plantation and natural forest). The simulation shows that even small disturbances can already partly buffer the risk of cohort senescence of monospecific even-aged plantations. However, after the decline of the plantation, the disturbance regime does not play an important role for further stand development. After the break-up of the initial strongly regular structure of the simulated plantation, a vertical pattern, i.e. height distribution of the trees, similar to the one of the natural forest, emerged quickly. However, the convergence for the horizontal structure i.e. the distance of trees to their nearest neighbor, took twice as long (~ 140 simulation years) as for the vertical structure (~ 70 years). Our results highlight the importance of small disturbances such as lightning strikes to mitigate vulnerability against synchronous windfall in homogenous forest structures. Hence, creating small openings artificially may be an appropriate management measure in areas where the frequency of natural small-scale disturbances is low.

Keywords: *Lightning-strike gap; Mangrove plantation; Forest structure; Canopy disturbance; Mangrove model KiWi*

4.1 Introduction

Lightning-created canopy disturbances causing the death of small tree groups are a common phenomenon in mangrove forests worldwide (Figure 4.1) and are frequently described in the literature e.g. Panama (Sousa and Mitchell 1999), USA (Smith III et al. 1994), Australia (Smith III 1992), Dominican Republic (Sherman et al. 2000) and Papua New Guinea (Paijmans and Rollet 1977). In this study we investigate how these small canopy disturbances influence the development of a homogenous forest plantation. Our study site in the Can Gio Biosphere Reserve is situated in the Central Indo Pacific region, which is characterized by one of the highest tree species diversity of mangroves worldwide (Duke et al. 1998). In Thailand, for example, 19 mangrove tree species were recorded (Imai et al. 2006) and in the Sematan mangrove forest in Malaysia 18 species of true mangrove were found (Ashton and Macintosh 2002). In Can Gio, however, and elsewhere in southern Vietnam, large areas of the naturally diverse mangrove forests were destroyed during the Second Indochina War and extensively replanted with monocultures of *Rhizophora apiculata* in the 1970's. Today it is one of the largest mangrove plantations worldwide with about 20,000 ha. The reforestation was aimed to improve ecosystem productivity for human demands such as timber usage, fuelwood, fishery and aquaculture (FAO 1993) and to maintain major ecological functions and processes. However, unsustainable shrimp farming and ongoing transformation into agricultural land has increasingly put the mangrove plantations at risk. For this reason, in 2000 Can Gio was declared as a Biosphere Reserve by UNESCO. (FAO 1993).

Figure 4.1: Typical appearance of lightning-strike gaps in mangroves using the example of Can Gio. Source: "Title", 10°32'10" N, 106°54'40" E, GOOGLE EARTH, Date on image 14.02.10, Date on access 10.11.10.

Disadvantages of monospecific mangrove plantations, such as in Can Gio, are widely discussed. Plantations may host and nurse a less diverse marine and terrestrial fauna than more diverse natural mangrove forests, as they offer a smaller range of resources and habitats than the latter (FAO 1993, Duke et al.1998). Ecosystem functions and services, e.g. nutrient cycling, trophic complexity, fish nurseries, feeding grounds or coastal stabilization; (Rotenberg 2007, Fonseca et al. 2009) may thus be constrained in species-poor mangrove plantations. The homogeneous size and age structure of planted forests amplified by the regular arrangement of the tree cohorts can lead to uprooting with domino effects causing synchronous diebacks on stand or population level (Mueller-Dombois 1992). A loss of vitality on the stand level renders the plantations more vulnerable to physical disturbance, such as tropical storms, that are expected to increase in intensity and maybe frequency in the future (Gilman et al. 2008). When large areas of mangroves are lost, so are important ecosystem services such as stabilization of coastlines and filtration of upland runoffs.

The Can Gio mangrove plantations are highly susceptible to synchronous tree dieback, due to the unnatural even-aged, monospecific stand structure. A quantification of synchronous uprooting is not possible, but field observations indicate the beginning of that phenomenon (Figure 4.2b). When Typhoon Durian hit the southern part of the plantation in December 2006, approximately 10 ha of the plantation were deforested (see also Diele et al. this issue). The impact of storms on the forest vegetation is influenced by many different factors. These include not only the intensity of the individual storm (Foster 1988) but as well the tree stature. Taller trees are found to be more prone for uprooting and snapping (Roth 1992), and the regular distribution of the trees in a plantation can induce a domino-effect (e.g. Ennos 1997). Due to the negative effects of simultaneous collapses of monospecific plantations on ecosystem functions and services (see above), we are interested in whether the natural tree diversity can be naturally re-achieved in Can Gio. It was observed in Putz and Chan 1986 that even small canopy openings caused by single tree fall or lightning strike break up uniform forest structures and alter environmental conditions e.g. light and soil. This enhances not only the recruitment of *R. apiculata* seedlings but also of other species (Rabinowitz 1978).

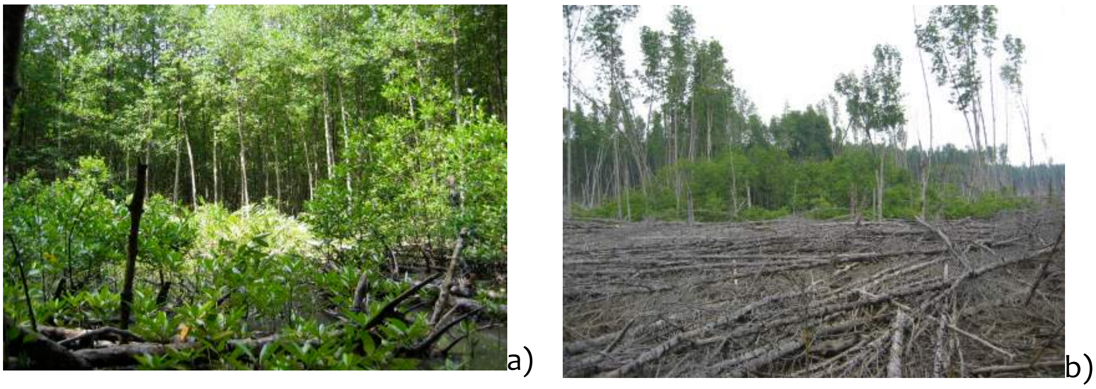

Figure 4.2: Lightning-strike gaps in the plantation a) The regenerating lightning-strike gap no. 2 in the monospecific *R. apiculata* plantation. Upcoming seedlings of different species (*R. apiculata*, *Ceriops decandra*, *Achrostichum aureum*, *Acanthus* sp.) increase the species richness and structural complexity. b) A typhoon-windthrown site inside the plantation. The vegetation patch in the centre, a regenerating former lightning gap, survived the typhoon illustrating its importance as seed source for the surrounding disturbed area.

The aim of the present study is to determine whether small canopy disturbances such as lightning-strike gaps are capable to transform the even-aged, monospecific plantation into a more natural forest and thereby reducing the risk of synchronous diebacks. The working steps to answer these questions include a satellite image interpretation (5 times 16 km² areas), data obtained during two field surveys within gaps and the surrounding plantation and a simulation study (up to 200 years on 1 km²) using an individual-based model.

4.2 Regional settings

The study site is located at the south-east coast of Vietnam in Can Gio Biosphere Reserve (10°22'-10°40' N, 106°46'-107°00'E), about 65 km south from Ho Chi Minh City. The climate is characterized by tropical monsoons with two distinctive seasons: the wet season from May to October and the dry season from November to April. The average rainfall is around 1300- 1400 mm. The size of the reserve exceeds 75,000 ha (Figure 4.3) including 4,721 ha core zone where no human activities except for research, monitoring, and education take place to enable a natural development. The buffer zone of 41,139 ha encircles the core zone. The transition zone of 29,880 ha surrounds the buffer zone. The Biosphere Reserve is accessible on land on a main road leading from the North to the Coast in the South and by boat on the large river system (Figure 4.3). Mostly *Rhizophora apiculata* was planted with a spacing of 1x1 m during the 70's. Three thinning operations have taken place during the first 15 years (FAO 1993). Since the conservation status due to UNESCO no further thinning management took place. An overall sustainable management concept in the frame of the Biosphere Reserve was necessary after conflicting interests jeopardized the reforested area due to uncontrolled exploitation such as cutting timber, transforming mangroves into aquacultures (FAO 1993). Although the sustainable usage of various timber and non-timber products should be assured by the conservation status, the simultaneous dieback e.g. triggered by wind events of the plantation may be able to compromise these resources.

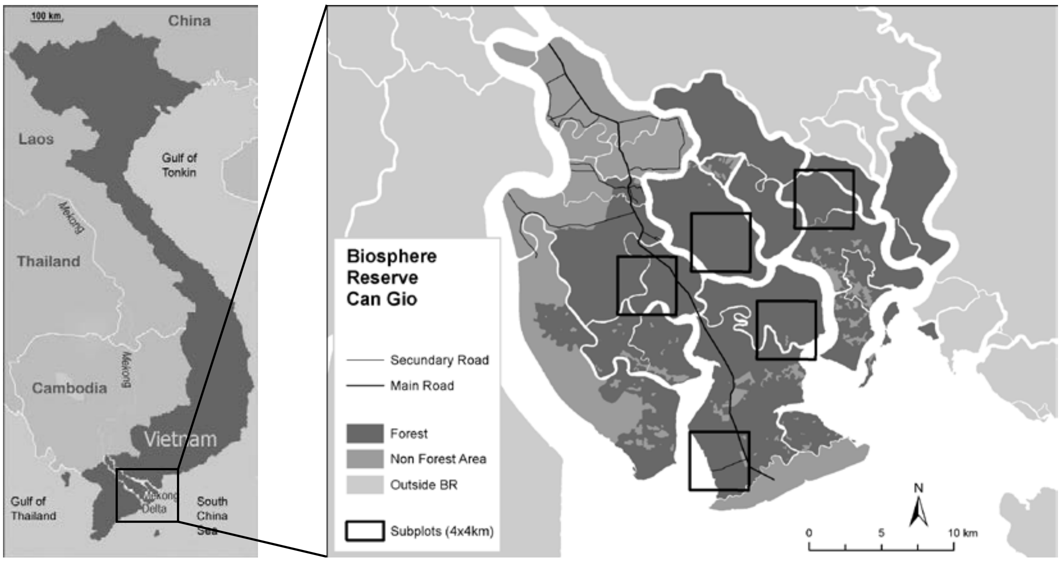

Figure 4.3: Location of the study area Land use of the biosphere reserve (BR) of Can Gio. Field work was carried out in the two southernmost subplots.

4.3 Methods and material

4.3.1 Satellite data interpretation

SPOT satellite imagery was used to quantify canopy gaps in the mangrove area. The images were chosen because of their high spatial resolution of 2.5 m pixel size, a reasonable quality with only little cloud cover, the multi-temporal availability of data: time series of 2003, 2005 and 2007, and large-scale coverage of most of the study site. Higher resolved QuickBird imagery (< 1 m resolution) from 2002 and 2006 was available only for a small section of the study site and was used to validate the size measurements of the gaps.

A supervised classification of the SPOT raster data for lightning gaps detection failed because first, the quality differences of the available images and second, the gap signatures were very complex. The gaps were identified by visual interpretation according to Read et al. (2003) and Dahdouh-Guebas et al. (2006). The latter introduced this approach to tropical forests. Five subplots of 4 x 4 km were selected to detect canopy gaps caused by lightning strikes according to the following criteria: the subplots i) had to be located inside the core zone ii) had to have high proportions of mangrove coverage, iii) should not overlap and iv) should be well distributed over the whole area to be representative. The mangrove vegetation cover was determined with a supervised Maximum Likelihood Classification (ArcGIS Spatial Analyst Tools (Liebig and Mummenthey 2005)) for each subplot.

ArcGIS analysis tools were used to determine gap size and spatial distribution parameters. Gap shape was calculated for the limited subset of QuickBird analyses with the gap shape complexity index (GSCI) according to Patton (1975), where *P* is the perimeter and A is the area of the gap:

$$GSCI = \frac{P}{2 * \sqrt{A * \pi}} \qquad \textit{(Eq. 4.1)}$$

The minimum GSCI=1 reflects the shape of a circle and a growing value indicates increasing ellipticity. The time series of our satellite images gave information about the formation frequency of gap development.

4.3.2 *Field survey*

To ground-truth the results of the satellite images analyses, field research was conducted in December 2007 and September 2008. Previously identified gaps in the two southernmost subplots from the satellite images were visited (Figure 4.2a). The selection of these gaps was done regarding the visibility in the satellite images in 2007 but not in 2005. The aim was to study the start of the regenerating process considering only gaps created between 2005 and 2007. The gaps had to be in a walking distance of up to 1 km accessible from the car or the boat. The nature of the remains of the dead trees indicated whether or not the gaps had been created by a lightning strike. Dimensions and shape of six gaps were determined on site by measuring the two longest perpendicular axes of the gap. We obtained data on tree height and stem diameter by measuring 12 trees at the boundary of the each gap as well as all trees inside two undisturbed 10 x 10 m plots which were situated between the studied gaps to be representative. In these plots, tree and seedling density were also measured.

The height measurement was conducted with a Vertex II plus transponder by Haglöf Sweden AB using trigonometric calculations which requires an adequate distance between the tree and the position of the measurement device. Out of the six gaps three gaps were selected to study the regenerating vegetation because of the abundance of mangrove trees recruits. Gaps recolonized only with herbal plants or ferns were not considered for this study. Within the three selected gaps species composition and plant height along 1 m to each side of the gaps' major axes was recorded.

4.3.3 Computer simulation

To test the impact of lightning strikes on the forest structure we used the individual-based mangrove forest model KiWi (Berger and Hildenbrandt 2000). The tree life cycle is described by growth, mortality and establishment processes. The model is spatially-explicit. The individual tree is described by stem position, age, stem diameter and annual stem increment. Introduced saplings have a diameter at breast height (*DBH*) around 2.5 cm. The influence of neighboring trees on a focal tree is described by the size and species dependent Field-of-Neighborhood (FON) approach. Overlapping areas of the circular scalar FON display the competition and therefore the growth reduction for the focal tree (see in detail Berger et al. 2008).

A density of 2270 planted saplings per hectare, which is equivalent to 2.1 m distance of neighboring plants, was used for the initial set-up of the simulation. This spacing was achieved by three thinning activities performed by the Ho Chi Minh City Forestry department in the early years of the plantation (FAO 1993) and was confirmed by our field data. The implemented lightning disturbance submodel was based on our remote sensing results. Based on the latter, we used the characteristic shape and the frequency of gap formation caused by lightning strikes. The original gap size distribution was divided into four radii range classes depending on the frequency of occurrence. The expanded gap size A_{exp} , which includes the canopy gap size A_{can}, determined from the satellite images, plus the crown radius r_{crown} was used for the simulation:

$$A_{\exp} = \left(r_{crown} + \sqrt{\frac{A_{can}}{\pi}} \right)^2 * \pi \qquad \textit{(Eq. 4.2)}$$

We simulated the following three disturbance frequencies based on a Matern cluster process: (i) no disturbances, (ii) the observed disturbance regime from Can Gio and (iii) the highest recorded rate (7 to 9 flashes km^{-2} yr^{-1}) in mangrove forests from the Everglades National Park in Florida, USA (Whelan 2005). The Matern cluster implies a point process of cluster centers, surrounded by random clusters (Illian et al. 2008) and seems to be most appropriate to simulate the observed lightning-strike gap pattern (Kautz et al. 2011).

The total simulated area was 1 km^2 for a medium-term of 200 years. To achieve repetitions we subdivided the area in 1 ha plots with a temporal replication of 50 years. New mangrove recruits have not been introduced in the simulated area in the first 4 years to take into account the time it takes until young trees first reproduce. From the fifth year we annually introduced them into the simulated area. The initial age for saplings was set to 1 year. Species-specific biological parameters of *R. apiculata* from Fontalvo-Herazo et al. (2011) (see Table 4.1) were used, except for the minimum value of the FON. The latter determines the competition strength of the species. For our simulation this value was set to 0.3 because this describes intermediate species-specific competition strength as documented for *R. apiculata* by Kitao et al. 2003. The FON scaling parameters *a* and *b* are stand-dependent and define the scale of the distance and the strength of competition of neighboring trees. We calibrated these values (a = 5, b = 0.654) according to the observed pattern in Can Gio: i) the size distribution of trees and ii) the plantation did not show extensive collapsing after 40 years but the beginning of this phenomenon was observed.

Table 4.1: Species-specific parameters of *R.apiculata* used for the parameterization of KiWi (Fontalvo-Herazo et al. 2011).

Parameter	Description	R. apiculata selected values
H_{max}	Maximum height (cm)	3000
DBH_{max}	Maximum diameter at breast height (cm)	80
∂DBH_{max}	Maximum increment *DBH* (cm/year)	1.5
φ	Resource sharing capacity	1.25
$F_{max\ establish}$	Minimum value of the FON	0.5 new: 0.3 (Kitao et al. 2003)
CritDX	Constant for tree mortality threshold	0.05

Two different spatial tree distributions were simulated: a strongly regular horizontal arrangement resulting from the initial planting and a randomly established natural forest. All other settings of the system configuration (e.g. yearly recruitment, species-specific growth parameters, the homogeneity of the environment and the disturbance regime) were kept equal (Table 4.2). The aim of considering these two forest types was to compare their forest structure development and natural regeneration.

Table 4.2: Configuration of the simulation analyses comparing the situation of the existing plantation with a random naturally-generated forest.

	Plantation	Natural Forest
***Simulation setting*:**		
Initial tree set-up	2.1 m spacing between the trees	random distribution
Initial density	2270/ha	
Age of initial trees	3 years at planting	
Yearly introduced saplings:		
Density	10/ha assuming high mortality rates at the transition between seedlings and saplings	
Distribution	Random spatial but in dependency on the competition of neighbouring trees	
Lightning-strike gap:		
Shape	circular	
Size	The gap radii were divided into 4 ranges based on the size class distribution (see Figure 4.4)	
Distribution	Based on matern cluster: Either 2 or 3 gaps depending on the occurring probability were created within two given cluster ratios at distance of a randomly picked position.	
Disturbance regime:		
undisturbed	No lightning-strike gaps occur during the whole simulation	
Can Gio	Can Gio frequency and, size of the implemented gaps are based on the satellite images results	
Florida	The frequency of the gaps is based on Whelan 2005, the size class distribution was taken from the one in Can Gio	

4.3.4 Structural indices

We analyzed two spatial indices to characterize the horizontal and vertical forest structure:

The Clark-Evans aggregation Index *R* (Clark and Evans 1954) (Eq. 4.3) including the Donnelly (1978) correction describes the horizontal forest structure. It is based on the distance to the nearest neighbor. The correction takes into account the edge effects of the simulated population.

$$R = \frac{\overline{r_A}}{\overline{r_E}} \qquad 0 \leq R \leq 2.15 \qquad \text{(Eq. 4.3)}$$

The distance between a tree and its nearest neighbor is described by r_A, where r_E is the mean expected value of a randomly distributed population. This means that a value of $R = 1$ approximates a random distribution and lower values show aggregation. A strongly regular or hexagonal pattern will be characterized by a value close to the maximum $R = 2.15$.

To characterize the vertical forest structure we calculated the Shannon Index *SI* for measuring canopy height heterogeneity (Zenner and Hibbs 2000):

$$SI = -\sum_{i=1}^{H} p_i \ln p_i \qquad 0 \leq SI \leq \text{approx. } 1.79 \text{ (for six classes)} \qquad \text{(Eq. 4.4)}$$

We used six height classes *H* (4.5 m each) equally dividing the maximum assumed tree height of 30 m (Table 4.1) and an initial height of introduced saplings of approx. 3 m. The index is based on an array of *p* values (see Eq. 4.4), where p_i is the relative abundance of the height class *i*.

The age distribution is further related to the stem diameter and to the tree abundance per age class.

4.4 Results

4.4.1 Satellite Data Analysis

We detected 348 gaps that could be attributed to lightning strikes inside the 5 subplots, which corresponds to a rate of 0.07 visible events/ha in the forest area (5100 ha). The distribution of the gap size classes (Figure 4.4) shows that approx. 50% of the openings are small canopy gaps from 150 m^2 to 250 m^2. The average gap size is 246 ± 146 m^2.

The gap shape complexity index was 1.07 ± 0.05 indicating almost circular gap shapes. In total, 0.17% (and 0.35% with QuickBird analyses) of the mangrove area is disturbed. The frequency of gap formation has a probability of $p=0.012$ ha^{-1} a^{-1}, which corresponds to one detectable lightning strike event at 83 ha per year.

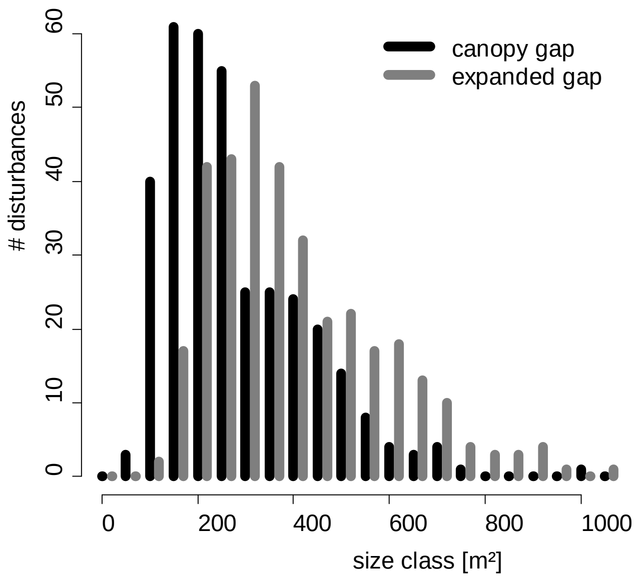

Figure 4.4: Size class distribution of all detected lightning-strike gaps inside the 5 subplots. The canopy gaps were detected with remote sensing techniques and the transformed expanded gap size classes (see Eq. 4.2) were used for implementing the gap sizes in the computer simulations.

4.4.2 Field survey

By comparing the data obtained for six gaps in the field with the satellite images an over- and underestimation of gap sizes was found with 24% deviation of the weighed harmonic mean (Table 4.3). Despite these differences the subsequent simulation analyses refer to the satellite interpretations due to the quantity of the data.

Table 4.3: Detected gap size from the field survey and satellite image interpretation. The expanded gap size A_{exp} was calculated as an ellipse and transformed to canopy gap size A_{can} (Eq. 4.2) for comparison. The measured a-axis is the major axis along the gap whereas the b-axis stands perpendicular to it. The deviation was calculated for the canopy gap size comparison between the field data and the Ikonos satellite data.

Gap	Field data				Ikonos	
ID	a-axis [m]	b- axis [m]	Aexp	Acan	Acan	Deviation
1	28.6	21.2	476.2	469.9	400	-0.17
2	19.6	18	277.1	270.8	350	0.23
3	24	16.1	303.5	297.2	400	0.26
4	33.4	18.2	477.4	471.7	600	0.21
5	14.5	12.2	138.9	132.7	110	-0.21
6	15.2	14.3	170.7	164.4	400	0.59

Figure 4.5 shows the diameter height relationship of the trees adjacent to lightning gaps with an average height of 19.26 ± 3.32 m. We excluded the trees in the undisturbed site due to the overestimation of the height caused by measuring from too small distances for the trigonometric calculation in the dense forest. The nonparametric Mann Whitney U test (W = 1463, p = 0.175) showed no significant difference between the stem diameter of the canopy trees bordering the gaps (14.9 ± 5.3 cm) and the close by undisturbed canopy trees (14.2 ± 2.5 cm).

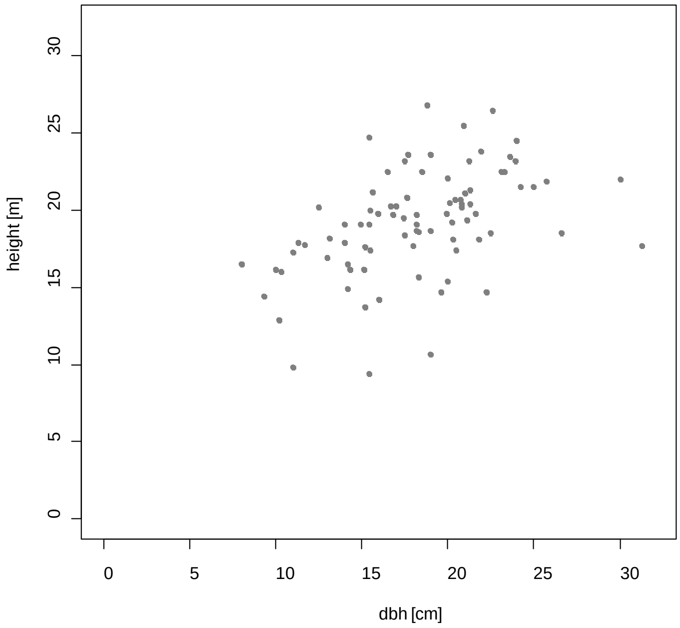

Figure 4.5: Height-diameter relationship of the gap boundary trees.

In the 10 x 10 m plots in the closed forest we counted 72 ± 29 *R. apiculata* seedlings. In three recolonizing gaps plants species such as the herbaceous *Acanthus sp.*, the fern *Acrostichum aureum*, the climbing legume *Derris trifoliata* and even a second mangrove species *Ceriops decandra* besides *R. apiculata* were detected (Figure 4.6). The three gaps were not visible in the 2003 but in the 2005 satellite images, so their formation must have taken place after 2003. Even though these gaps have a similar age, they differ considerably in terms of vegetation regeneration: Gap 1 and Gap 2 already show an increased height of vegetation, whereas the plants in Gap 3 are still small and more numerous.

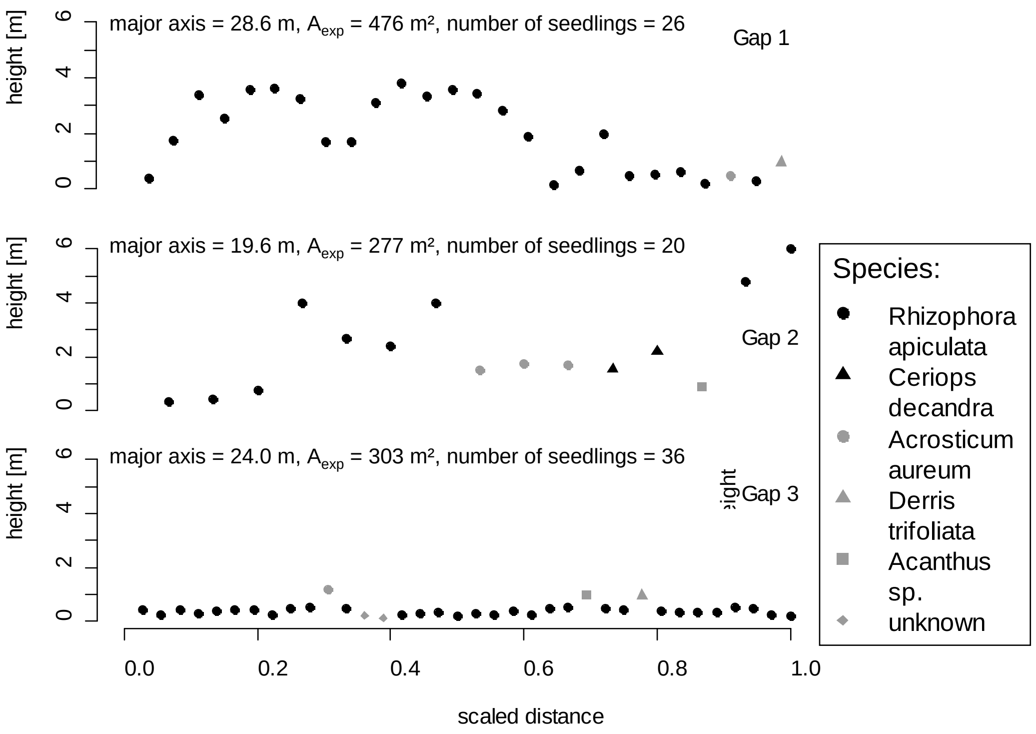

Figure 4.6: Seedling and sapling height measurements and species composition along the major central axis of three gaps. The x-axis shows a scaled distance according to the recorded plant number for comparability reasons and due to the lack of knowledge of the exact position of the seedlings/saplings.

4.4.3 Simulation experiments

Based on the results of the satellite image analysis and the field observations we simulated the regeneration of a planted and a natural and thus randomly generated forest for three lightning disturbance regimes.

The Clark-Evans Index (Figure 4.7a) shows a strong regular distribution in the initial phase of the plantation, reflecting the planting regime, with little mortality until the arrival of new saplings after 5 years. However, the latter are outcompeted by the initially planted, now canopy forming trees, so that the plantation returns to its strongly regular structure. This structure remains until competition between the even-aged canopy trees triggers natural self-thinning and disaggregation of the plantation structure. In contrast to the plantation simulation, the randomly established forest showed as a starting value of *R*=1 reflecting random distribution, as was expected. During the simulation process the trees aligned more regularly to their neighbors due to competition. The simulated horizontal structure of the randomly established and the regularly planted forest converges after approx. 70 years. From then on, both systems develop similarly.

The Shannon Index (Figure 4.7b) illustrates similar trends. Both the plantation and the randomly established forest develop from an initially homogeneous low tree height to a mixed height distribution. In the plantation, the saplings are then outcompeted and the plantation shifts back to a homogeneous tree height, while the natural forest does not show such a collapse. Later on the height diversity of the plantation increases again and finally approaches the natural forest values.

Both forest systems converge until they have a near uniform development, and the vertical structure proceeds simultaneously already after approx. 70 years. In contrast, the convergence for the horizontal structure of the plantation and the random forest takes twice as long.

The influence of the differing disturbance frequencies is reflected by both indices: the Clark-Evans aggregation Index and the Shannon Index. The undisturbed scenario returns to a strict regular plantation structure in tree position and height. With increasing disturbance probability the structure of the plantation becomes more diverse as indicated by the moderate amplitudes (Figure 4.7).

The results for the comparison of the spatial structure between undisturbed and disturbed are interesting but not as clearly visible as expected.

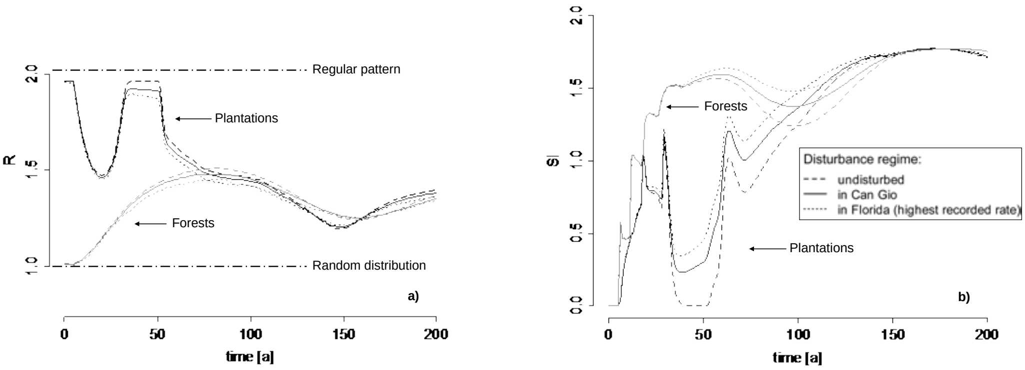

Figure 4.7: Structural parameters calculated from the simulation analyses with 50 repetitions each a) Clark-Evans Index *R* and b) Shannon tree height index *SI* shown for different disturbance probabilities per hectare and year: no disturbance (p = 0), recent disturbance in Can Gio (p = 0.012), and highest recorded disturbance rate in Florida (p = 0.1). Darker coloring indicates the plantations, lighter ones the forests.

In contrast, the age analyses show more distinctive results. For these analyses we only considered the “no disturbance”- and the “Can Gio disturbance” regime. The “Florida disturbance” regime (maximal disturbance) gave similar results on the distribution pattern as the “Can Gio disturbance” regime and was therefore not used in subsequent analyses. The age-diameter relationship per 1 km^2 shows a large number of initially planted trees (227,145 individuals (ind) at the simulated time step of 50 years (Figure 4.8). This is a critical phase of the simulated plantation as such high tree numbers increase the vulnerability to synchronous tree breakdown through storm disturbance.

Only three trees established after the initial set-up were able to survive and had relatively unproportional small diameters, indicating the suppressed situation of these individuals. In contrast, the simulated undisturbed natural forest (255,986 ind.) showed almost all ages in a wide diameter range, except for the phase right after the initial establishment due to the assumed time span of 5 years until first reproduction. 117,458 (46%) of the total number of trees established after the initialization. The “Can Gio disturbance” regime displays a distinct diverse age distribution of trees in the plantation. 10,356 individuals (5 %) out of 224,161 established after the initial set up. The high diameter values of these plantation trees indicate a better growth compared to the trees of same age in the natural forest. The forest trees (in total 224,161) arriving after the initial set-up are nevertheless more numerous (119,536 ind. equal to 53%). The influence of the regular horizontal arrangement of the plantation stems becomes noticeable in the reduced range of diameter size in the initial cohort (age of 50) independent of the disturbance regime (Figure 4.8).

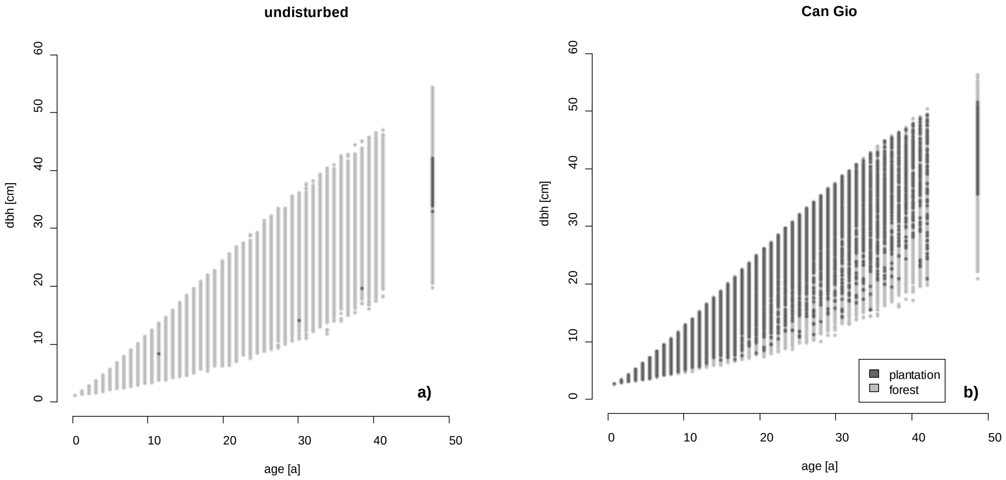

Figure 4.8: The development of diameter and age of the simulated trees at time step 50 under two different disturbance regimes a) undisturbed by lightning b) "Can Gio disturbance regime". The cohort of trees at time step 50 was established during the initial set up. Individuals with younger ages established afterwards during the simulation run.

Figure 4.9 shows the age classes at time step 70 after the horizontal convergence of the plantation and the natural forest took place. The simulated "no disturbance" regime shows a distinct separation of the age classes of plantation trees. Individuals from the initial setup were still the most numerous class followed by a big spacing of 50 years with no abundance. However, after the transformation to a more regular spatial configuration of the plantation after approx. 45 years, new individuals established in the more scattered structure of the plantation. This is visible in the two youngest age classes (Figure 4.9). Even under "no disturbance" the randomly established forest simulation at time step 70 shows trees of all age classes with a pronounced dominance of the oldest age class from the initial trees. In the same simulation with "Can Gio disturbance" regime the strong separation of plantation trees with individuals in all size classes, although not numerous, was already broken up. At time step 140, after the convergence of the vertical structure, the natural forest and the plantation have a similar age structure independent from the disturbance regime. The initial state of the plantation is only visible in the spacing between 101 and 140 years in both disturbance regimes. The age distribution between simulations tested with the Kolmogorov-Smirnov-Test differed significantly ($p < 0.0001$).

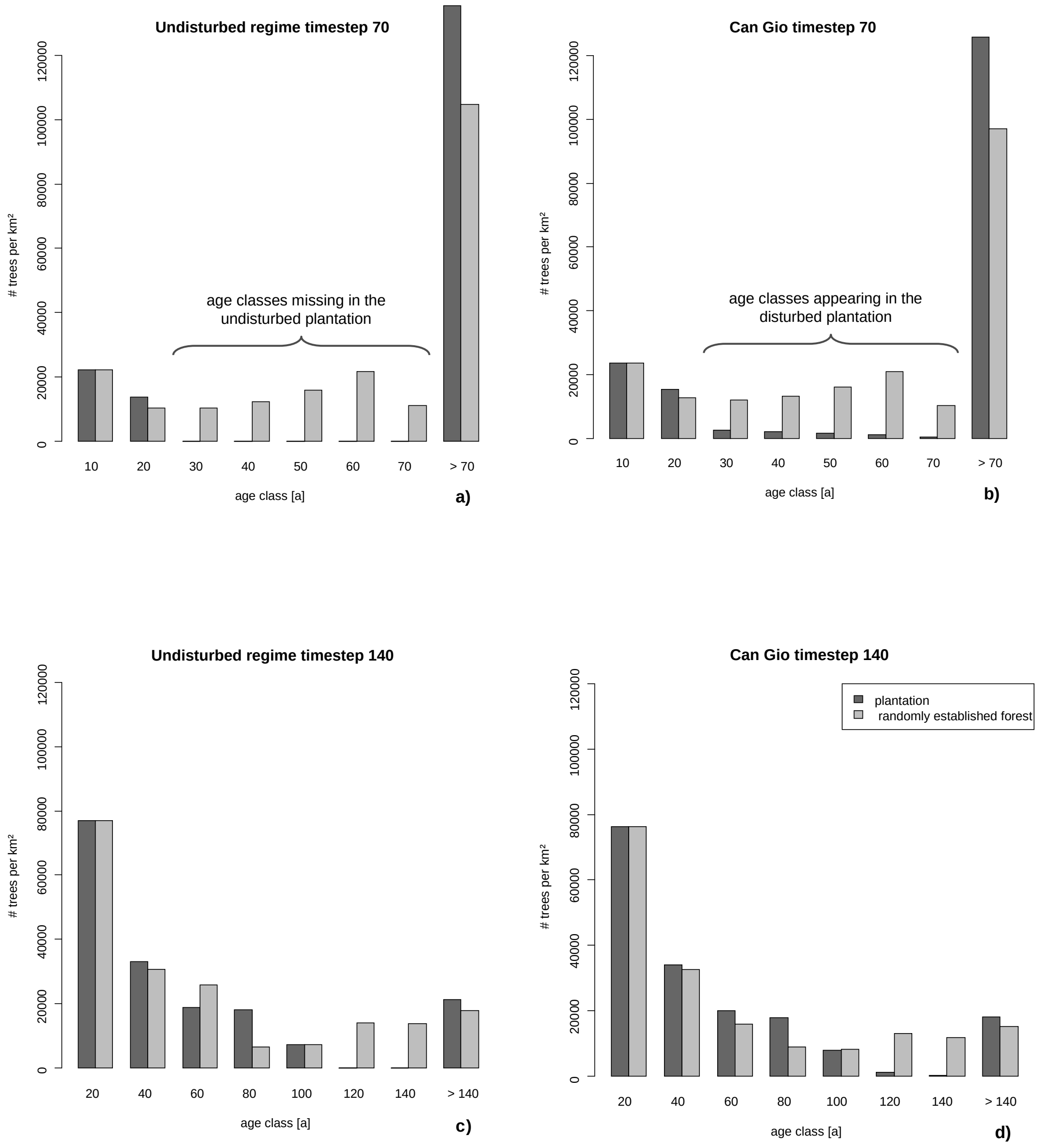

Figure 4.9: Age distribution at time step 70 a) undisturbed regime b) disturbance regime in Can Gio and at time step 140 with the disturbance regime: c) undisturbed d) in Can Gio.

4.5 Discussion

4.5.1 *Data quality*

Former studies show that SPOT satellite imagery allows confidentially classifying and identifying mangrove vegetation and its degradation (Blasco and Aizpuru 2002, Rodriguez and Feller 2004). We compared the number and size of lightning gaps detected with SPOT with those detected with QuickBird images and found that canopy gaps smaller than 50 m^2 were probably underestimated in the SPOT images, due to the low resolution of the latter. The QuickBird images revealed more gaps in the small size classes. Additionally, the gap sizes measured during field surveys showed under- or overestimations of 24% compared to the sizes obtained from the SPOT images. However, considering the coarse SPOT resolution of 2.5 m pixel size, the 24% deviation between the remote sensing interpretation and the real gap size is relatively small. A further uncertainty in our remote sensing analyses is the causer of disturbance (Zhang et al. 2008). For example, local wind-throw, single tree mortality etc. may lead to a similar gap appearance as gaps caused by lightning strikes. However, our field observations confirmed that the visited gaps had been created by lightning strikes, due to the characteristic pattern of dead tree clusters (Whelan 2005). Despite the mentioned limitations of the SPOT images, the working resolution of below 5 m is sufficient and therefore we consider the results appropriate to describe the characteristics of the disturbance regimes in Can Gio.

4.5.2 Satellite data

The nearly circular or slightly elliptic shape of the lightning gaps observed in Can Gio was also described in studies of Zhang (2008) and Whelan (2005). Average gap size in Can Gio was 246 ± 146 m^2 and was similar to the findings of Whelan (2005) in Florida, USA (202 ± 16 m^2) and half the size described by Sherman et al. (2000) in the Dominican Republic (506 m^2). The spatial distribution of gaps in Can Gio shows an inconclusive pattern in the different analyzed subplots (with 2 clustered, 2 random, and 1 regular distribution). This corresponds to the findings described in the literature. Zhang (2008), for example, observed a random distribution, whereas Sherman et al. (2000) detected a formation of gap clusters. Only 0.17% of the Can Gio mangrove area is disturbed by lightning strikes, while much higher values of 1.4% (Dominican Republic: Sherman et al. 2000) and 2.5% (Florida, USA: Whelan 2005) are known from other regions.

4.5.3 Field survey

Field data about the vegetation structure i.e. tree density, height, spatial configuration, and species composition of the plantation and the regeneration processes within gaps were obtained for three gaps. The number of *R. apiculata* seedlings found in the closed forests was considered as sufficiently high for enabling fast tree regeneration after lightning disturbance, even though high seedling mortality may occur under unfavorable site conditions (Smith III 1987). The new species found in the regeneration gaps must have arrived from areas outside the planted forest, transported by inundation, wind, or animals. These species were not present in the adjacent planted forest showing that lightning disturbance increases the floral diversity inside plantations. The regenerating gap vegetation also contributes to an enhanced structural complexity. The averaged measured height of the plantation trees were with approx. 20 m quite high and would experience higher tree mortality due to uprooting or stem breakage during wind events than smaller trees. It can withstand synchronous windfall of the surrounding forest, remaining the only green patch inside an area disturbed by windfall (Figure 4.2b). Such vegetation patches of different successional stages can play a key role for the recolonization of wind damaged sites as they serve as seed sources for the adjacent disturbed areas accelerating their regeneration, especially when tidal seed import is impeded by downed wood (Krauss et al. 2006).

4.5.4 Simulation experiments

In our simulation study we detected a transformation time of the plantation into more a natural forest structure of 50 years. Please note, that this time strongly depends on the parameterization of the FON values *a* and *b* which is uncertain. We decided to use this parameterization of the model due to the observation in the field. A change of these parameters would result in a temporal shift of the transformation, but the extent of the amplitude would remain. The canopy disturbance is able to change this amplitude of the Clark-Evans and the Shannon height index, but does not change the temporal scale of the forest transformation process. This phenomenon was already described in detail by Kautz et al. 2011).

Our results demonstrate that lightning disturbance in Can Gio Biosphere Reserve lowers the effect of cohort senescence by converting the plantation into a more heterogeneous spatial and age structure. The horizontal (i.e. spatial tree arrangement) and vertical forest structure (i.e. tree height) is more diverse in systems experiencing higher disturbance frequencies during the vulnerable transformation period of approx. 10 years, where the strong regular configuration of the plantation transforms to a more natural one, resulting from tree competition and self-thinning. The age distribution within the first 50 years shows even more distinct patterns. In the undisturbed plantation virtually no saplings were able to establish under the dense canopy of the initial planted trees. Already the low lightning strike disturbance regime in Can Gio was able to transfer the plantation into a mixed age structure. Based on these results we assume that even small disturbance frequencies (Can Gio) can contribute positively to the diversification forest structure. However, the disturbances are not strong enough to promote a full transformation into a structurally more natural forest. Our simulations further show that the lightning strike regimes tested are insufficient in buffering the swing back to the strictly uniform structure of the initially planted even-aged trees entirely. After the transformation of the plantation at approx. 50 simulation years, the frequency of disturbance does not seem to play an important role anymore for further stand development. The age distribution of upcoming saplings after the transformation showed similar high establishment rates as the natural forest ones.

We also found that the convergence for the horizontal structure between plantation and randomly established forest takes twice as long as the vertical one (tree height). This may result from different underlying ecological processes of the vertical versus the horizontal structure. The associated process determining the Clark-Evans Index (horizontal structure) is the tree establishment, the pattern of which is already transformed after the breakdown of the plantation. The height diversity (vertical structure) however, is based on growth processes, which become visible in progressing successional stages.

The risk of synchronous tree-fall was not implemented into our simulation study. However, it is clear that the structural monotony of a plantation makes it vulnerable to massive tree fall caused by strong wind or storms (see Diele et al. this issue). Larger areas of windfall, in particular, would partly set back the succession. Large areas are furthermore more difficult to recolonize e.g. due to changed salinity conditions (Clarke and Allaway 1993); furthermore sedimentation (Fromard et al. 1998) and hydrology (Elster et al. 1999) may be altered. Without synchronous massive tree-falls such as just described, our simulation clearly demonstrates that the plantation converges with the natural forest in the medium term (after approx. 140 years).

Our finding of increased species numbers in regenerating gaps underline former observations that other plant species populate and enhance their seedlings abundance under the more favorable light conditions in the created gaps (Smith III 1992). Many mangrove and mangrove associated species are able to recolonize gaps rapidly: Some studies (e.g. Ellison and Farnsworth

1996, Drexler 2001) have shown that propagules of various species have the ability to float for several months with currents and still sprout afterwards. Furthermore, the continuous production of large numbers of propagules is an important prerequisite for rapid gap regeneration (Pinzón et al. 2003). The newly established mangrove species and mangrove associates found in the lightning gaps investigated in this study were probably partly introduced from areas outside the *R. apiculata* plantation.

Our results suggest that the artificial creation of small canopy openings and subsequent planting of other native species including both mangrove and mangrove- associated species could accelerate the transformation process of the plantation into a more natural state. However, this may be difficult to realize because of the inaccessibility of core plantation areas and also because it would violate the high UNESCO protection status of the Can Gio Biosphere reserve“.

However, under certain circumstances it might be possible to allow harvesting of small clusters of trees under controlled conditions. This type of management would not contradict with the protection targets of the UNESCO to maintain ecosystem functions for long-term natural conservation in the core zones (UNESCO 2002).

4.6 Conclusion

Despite the limits of interpretation of the SPOT images used in this study, canopy gaps could be confidentially detected in Can Gio Biosphere Reserve and their size, shape and formation frequency were measured adequately. Our field observations and the simulation study showed that small canopy openings caused by lightning strikes can contribute to the conversion of the plantation into a more natural forest in terms of their spatial structure. Undisturbed plantations returned to the initial strongly monotone horizontal and vertical forest structure after approx. 40 years and were therefore more sensitive to synchronous windfall due to cohort senescence.

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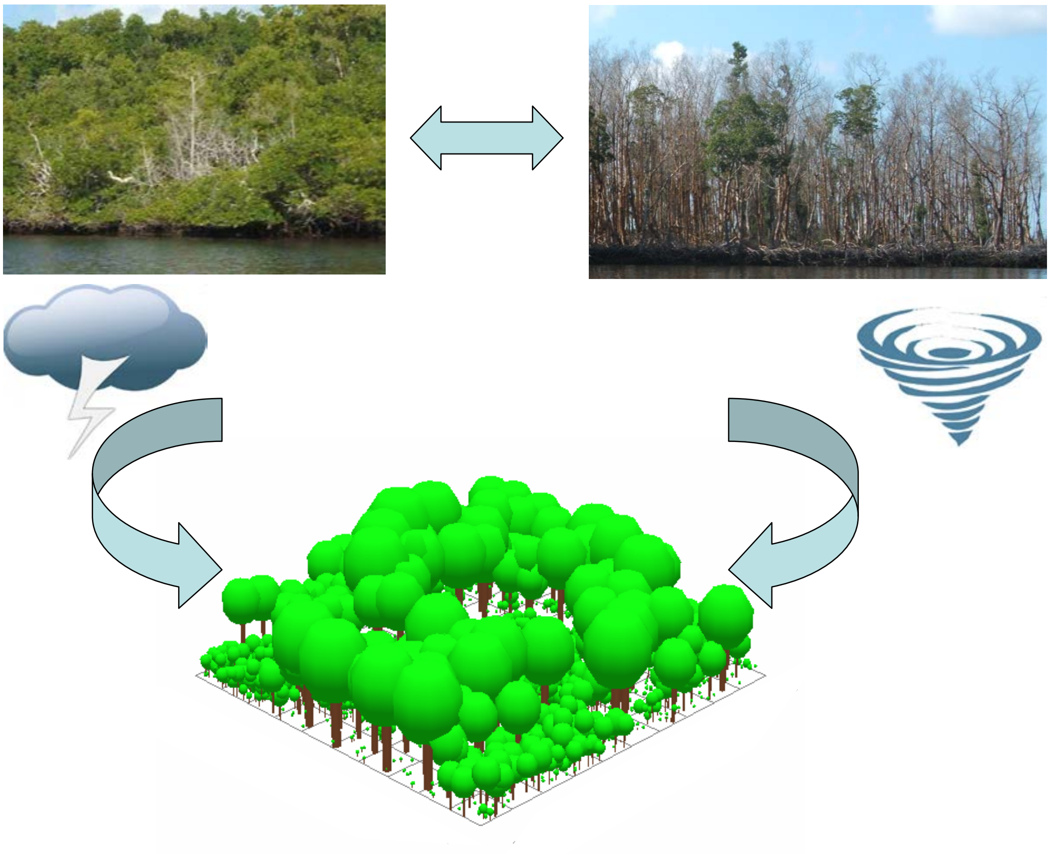
5 Testing the influence of different natural disturbance regimes on the spatio-temporal forest structure in frequently disturbed environments



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Abstract

Questions:

What effects do disturbance regimes of different frequency and extent have regarding the homogenizing and heterogenizing of forest structure? Does a mixed disturbance regime show synergistic effects on forest structure?

Methods:

We simulated different disturbance regimes with the individual-based mangrove forest model KiWi. Frequent small-scaled gaps caused by lightning strikes and rare medium-sized patches caused by hurricanes were implemented explicitly according to their size, intensity and frequency. Additionally a mixed regime was simulated including both disturbance regimes. All three scenarios had the same tree mortality caused by the disturbing events. We analyzed the temporal and spatial variations considering their homogenizing or heterogenizing effects on the forest structure.

Results:

All disturbance regimes had significant homogenizing effects on the spatial forest structure compared to an undisturbed scenario. Further, the hurricane regime entails a temporal heterogenization of the forest structure whereas the small-scaled frequent lightning-strike gaps were not able to contribute to additional heterogeneity. This shows that the explicit implementation of the disturbance characteristics generate different forest structures, despite of having the same probability for tree to die during disturbances.

Conclusion:

Spatio-temporal features of disturbances regarding to the natural heterogeneous forest structure enhancing the species richness and the interactions of ecological processes should be considered for sustainable management activities in restored sites or plantations.

***Keywords**: individual-based model; KiWi model; lightning strikes; hurricanes; mangroves; structural indices*

***Abbreviations:** CV = coefficient of variance; DBH= Diameter at Breast Height; FON = Field of Neighborhood; R = Clark-Evans Index*

5.1 Introduction

Natural disturbances can be defined as discrete events in time that disrupt either an entire ecosystem or only parts such as particular communities or population structures (Pickett and White 2005). They are common and natural phenomena in different types of forest ecosystems influencing the spatial and temporal patterns of landscapes (Seidl et al. 2011) and can take the form of e.g. fires (Ratz 1995), wind thrown (Jeltsch 1992), or calamities of insects (Coley and Barone 1996). The sum of single time-discrete disturbance events forming patches in time and space is called the disturbance regime, which affects the ecosystem at a landscape scale (Jentsch et al. 2002). In mangrove forests typical disturbing events might range from single tree fall and lightning strikes on a very local scale to medium and large scale disturbances such as hurricanes (Ward et al. 2006). Created gaps generate changes in the biomass and in environmental conditions such as in the temperature regime or the light and nutrient availability (Shugart 1984). Within forests, disturbances may act as catalysts of succession. For example, lightning-strike gaps in homogenous plantations help in the transformation into more natural conditions (Vogt et al. 2011). Disturbances may also halt the succession in any cyclic stage (Lugo 1980) as after devastating hurricane events (Smith III et al. 1994). The spatial and temporal scales of disturbances related to a studied landscape play a crucial role for evaluating the impacts to this landscape (White and Jentsch 2001, Paluch 2007). On one hand, small and frequent disturbances contribute to a diversified vertical and horizontal forest structure. On the other hand, disturbed forest patches that have been differently affected by disturbances create a mosaic of homogenous patches in different successional stages (Paluch 2007).

Interactions of different disturbance types are quite common in forest systems and have either beneficial or adverse effects. In mangrove forests, small disturbances such as lightning-strike gaps can accelerate the regenerating processes of medium sized disturbed patches created by hurricanes. The regenerating lightning-strike gaps may act as seed sources for the surrounding destroyed mangrove forest (Smith III et al. 1994). On the contrary, Vogt et al (2011) showed that impoundment perturbation on large scales interact negatively with the medium-sized hurricane disturbance by impeding recolonization.

Determining generalities of specific characteristics of disturbances on forest ecosystems is quite challenging because of i) the variations in intensity during the disturbance events even for the same disturbance types and ii) the reaction of the ecosystem itself according to the disturbance response due to a heterogeneous landscape even for rather uniform disturbances (White and Jentsch 2001). Simulation modeling can therefore be interesting tools to assess disturbances generalities. Disturbed patches can be characterized by stand volume, age and size structure, canopy openness, the regeneration or the species composition (Paluch 2007).

Furthermore, there are different ways of characterizing the influences of disturbances on the temporal and spatial forest structure. First, it is possible to distinguish disturbances into diffuse and discrete. Disturbances are defined as diffuse in space, when relatively small disturbed patches (e.g. single tree mortality) occur throughout a large area. Discrete disturbances are aggregated within an area (White and Jentsch 2001). Second, disturbances can either act as stabilizing or destabilizing forces on forest development. These effects might be difficult to detect because natural forest development includes permanent dynamic processes (Otto 1994). Disturbances might be able to put the forest system in a certain equilibrium or stable state if they occur with a constant formation rate. Lugo (1980) used the term "pulse stability" if disturbances induce a periodic setback. Third, disturbance characteristics differ in their temporal and spatial variation including homogenizing or heterogenizing and synchronizing or desynchronizing effects on the forest ecosystem. A homogenizing process put large areas of the forest in a same developmental stage. On the contrary, a heterogenizing process leads to increased different developmental stages (Otto 1994). Synchronizing processes are characterized by forces leading to the development of trees toward similar conditions. The different views of characterizing the forest structure are scale dependent and all analyzes have to be referred to a certain temporal and spatial scale.

In this study, we focused on analyzing disturbances affecting the structural pattern of mangrove forests. These forests are distributed along tropical and subtropical coastlines and experience several different types of natural disturbances e.g. lightning strikes, freezing (Olmsted et al. 1993), wind storms (Imbert et al. 1996) or tsunamis (Roemer et al. 2010). Additionally, these natural systems are interesting for generalization about disturbances on forest structure given their relatively poor tree species richness.

The worldwide distribution of lightning flashes (NASA 2011) shows that some hot spots are found along the subtropical and tropical coasts such as in the Caribbean, Central West-Africa and Southeast Asia. In mangrove forests, lightning strikes create small gaps of a dead tree cluster (Whelan 2005) and are even assumed to form the majority of small gaps in Florida in this forest system (Feller and McKee 1999).

Additionally, hurricanes which predominantly occur in sub- and tropical areas (NOAA 2011) hit coastal areas and consequently mangrove forest with their full energy. The impacts of a hurricane can range from defoliation of trees (Roth 1992) to stem breakage or uprooting of larger areas (Imbert et al. 1996). The relationship between forest damage, wind speed and duration is very complex and leads to different responses of the trees (Boose et al. 1994). The extent of the damage for forests depends on different factors such as the intensity of the disturbance (categorized by the Saffir-Simpson Scale), the distance to the eye track (Imbert and Portecop 2008), the exposition to dominant winds (Piou et al. 2006), topography, the solidity of soil layer and the forest stand response dependent on individual tree characteristics (Canham et al. 2010).

Aims

In a previous study, Piou et al. (2008) analyze the effect of perturbation frequency and intensity on species composition with a simulation model adapted to Neotropical mangroves (Berger and Hildenbrandt 2000). The individual-based spatially-explicit characteristics of this model make it a good tool to generalize understanding of effects of disturbances on spatially driven processes. Here, with this same model, we aim at analyzing the effect of different disturbance regimes on forest structure to evaluate homogenizing and heterogenizing effects of disturbances of different size and frequency. We also search in a mixed disturbance regime for potential synergisms on the forest structure. Hence, we consider two different disturbance regimes with spatially-explicit and timely differences: lightning strikes and hurricanes. We focalized on a monospecific system with homogenous environmental conditions to simplify the understanding of disturbance regimes effects.

5.2 Material and methods

5.2.1 Simulation design

To simulate the disturbance pattern within the forest structure we used the KiWi model, an individual-based spatially-explicit mangrove model developed by Berger and Hildenbrandt (2000). The model was developed to analyze neotropical mangrove forest dynamics and was already successfully applied for e.g. investigating secondary succession trajectories of mangroves in abandoned rice fields (Berger et al. 2006), species diversity according to different disturbance regimes (Piou et al. 2008) or the influence of lightning-strike gaps in a forest plantation (Vogt et al. 2011).

Every individual tree was described by its stem position (x,y) in the simulated area, age, *DBH*, height and a scalar Field of Neighborhood (FON). The radius of the area considered as FON was computed as:

$$R_{FON} = a * \left(\frac{DBH}{2} \right)^{b} \qquad \textit{(Eq. 5.1)}$$

where *a* and *b* are scaling factors (Table 5.1).The optimal tree growth was calculated by the stem diameter increase over time:

$$\frac{\Delta DBH}{\Delta t} = \frac{G * DBH * \left(\frac{1 - DBH * H}{DBH_{\max} * H_{\max}} \right)}{274 + 3 * b_2 * DBH - 4b_3 * DBH^2} * cF(comp) \qquad \textit{(Eq. 5.2)}$$

where *G*, b_2, b_3, D_{max}, H_{max} were constants (Table 5.1) and *H* was the height of the individual tree. Tree height was calculated by the relationship $H = 137 + b_2\ DBH - b_3\ DBH^2$ (Shugart 1984). The *cF(comp)* was a correction factor reducing optimal growth under the influence of neighborhood competition (F_A) and computed as follow:

$$cF(comp) = (1 - F_A / shadTol) \qquad \textit{(Eq. 5.3)}$$

where *ShadTol* was a constant representing the shade tolerance of the simulated species. A detailed description of the FON approach is given in Berger and Hildenbrandt (2000).

Natural mortality was induced to a tree when its growth was under a critical threshold during 5 years (*critDX*, Table 5.1). This could happen when the individual tree was reaching a maximum tree size or because of competition from the neighboring trees. Furthermore, tree mortality was implemented explicitly by creating disturbances.

For this simulation study the area was set to 25 ha (500 x 500 m). This size ensured the simultaneous occurrence in time and space of different disturbances considering analyses at landscape level. All simulation runs started with the same initialization set up (time = 0) of a mature forest of 700 years. This was chosen to correspond to a time when the forest development in KiWi was reaching a steady state regarding tree number and mean *DBH*. The initial mature forest was simulated beforehand 30 times for the number of repetitions of each scenario having identical initial conditions. The first 200 years of the simulated scenarios were not taken into account for calculations. Every five simulated years were recorded to analyze the forest structure. We considered a one species system using the default parameter sets of Berger and Hildenbrandt (2000) of *Rhizophora mangle* for homogenous optimal growth conditions, except for the FON scaling parameters taken from Piou et al. (2008). Yearly introduced saplings were distributed throughout the whole area and were the same for all scenarios (10,000 individuals/year).

Table 5.1: Parameter values of *Rhizophora mangle* in KiWi used for this simulation study.

Parameter	Description	Value
a	FON scaling factor	18
b	FON scaling factor	0.83
ShadTol	Minimum FON value	0.5
G	Growth constant	267
Dmax	Maximum *DBH* (cm)	100
Hmax	Maximum height (cm)	3000
b_2	Height-*DBH* relationship constant	77.26
b_3	Height-*DBH* relationship constant	0.396
critDX	Mortality threshold of diameter increment (cm)	0.2
maxtime	Time span of simulation (a)	1000
rep	Number of repetitions	30
SaplNumber	Introduced saplings per time step (individuals/year)	10 000

Disturbance regimes can be defined by four characteristics according to Papaik and Canham (2006): the type of disturbance, the spatial extent, the return frequency and the severity. We considered two different disturbance regimes: small-scaled lightning strikes and medium-sized hurricane events. Both disturbance regimes were implemented as circular. The disturbance radius of the lightning strike regime was chosen between 6 to 12 m with a mean size of 290.2 m^2 corresponding to the most frequent size class found for lightning-strike gaps in mangroves in Florida (Whelan 2005). Each simulation year, 3 gaps were created where all trees were removed, corresponding to the natural frequency found in Florida (Whelan 2005).

Although hurricane events differ extremely in the disturbance pattern they create (Gratzer et al. 2004), depending on the hurricane characteristics such as wind force and the ecosystem characteristics including tree height or soil conditions. Nevertheless, we defined a homogeneous hurricane regime. This regime simulated occurrences of hurricane destructions with random appearance at a frequency of 1 every 20 years corresponding to what can be found for mangrove areas of Florida (Blake et al. 2007). During each hurricane event 3 patches were created, corresponding to the findings that multiple patches were often created in Floridian mangroves (Vogt et al. 2011). In these patches 75% of trees equal or taller to 15 cm and 50% of smaller trees were killed. This difference was set to represent the shield effect where canopy trees prevent understory trees from heavy damage (Imbert et al. 1996). To guarantee the comparability of the two different disturbance regimes, the probability for trees to die caused by the disturbing events was equal for both regimes. Hence, we set the disturbance radius of each hurricane patch to 51 m (spatial extent 8171.3 m^2) (see Appendix 9).

Further, we used the mixture of these disturbances occurring simultaneously to analyze synergetic characteristics on the forest structure. We wanted this disturbance regime to have the same probability for trees to die due to disturbances. Consequently, half of the lightning-strike gaps and half of the hurricane patches were simulated for this scenario, i.e. one to two gaps or patches were created per year or every 20 years, respectively.

A scenario without implemented disturbances (undisturbed) was used as a reference for the forest development. There was no sapling limitation during the whole simulation; therefore all scenarios had the same ability to recover after the disturbances.

5.2.2 *Analyses*

Forest structure indices

We used classical tree parameter such as mean *DBH* and the number of trees in the simulated area for the analyses. The forest biomass was calculated using an allometric formula according to Fromard et al. (1998). Further, the horizontal structure was described by the Clark and Evans (1954) index *R* with the Donnelly (1978) correction:

$$R = \frac{\overline{r_A}}{\overline{r_E}} \quad 0 \leq R \leq 2.15 \qquad \text{(Eq. 5.4)}$$

where $\overline{r_A}$ was the average distance between a tree and its nearest neighbor and $\overline{r_E}$ was the mean expected value of a randomly distributed population. Values below *R* = 1 show an aggregation, whereas a strongly regular hexagonal pattern will be close to the maximum *R* = 2.15. The size structure was expressed by the dimensionless coefficient of variation (*CV*) of the *DBH*:

$$CV(DBH) = \frac{sd(DBH)}{mean(DBH)} \qquad \text{(Eq. 5.5)}$$

Values of *CV* < 1 are considered as low-variant while *CV* >1 is described as highly variant. We used the *CV* in two different ways: the *CV* of mean *DBH* ($CV(\overline{DBH})_t$) to analyze the temporal variation of the mean tree size and the mean *CV* of *DBH* ($\overline{CV(DBH)}$) to characterize the spatial variation within a stand.

Statistics

The analyses were carried out to identify specific forest conditions for each disturbance regime and the undisturbed scenario. The values within each repetition of each scenario illustrated by the box plots were averaged to avoid autocorrelation, whereas the figure of one simulation run especially displays the temporal characteristics of the forest biomass. In addition, only living trees were analyzed according to the forest structure.

Pairwise Mann-Whitney-U rank sum tests with Bonfferoni correction were carried out to detect differences between the simulated scenarios. All statistical analyses were conducted with the R software (2011) with the package *spatstat* (Baddeley and Turner 2005) for calculating the Clark-Evans Index *R*.

Obtained values of the Clark-Evans index *R* were tested against spatial randomness by creating random tree positions (n= 1000) for all simulated tree densities.

5.3 Results

5.3.1 Comparison of the disturbed vs. the undisturbed simulations

The lightning strike and hurricane scenarios had a significant effect on the size (*DBH*) and number of trees, and the forest biomass compared to the undisturbed scenario (Figure 5.1a, b, c). Trees were smaller and more numerous in the disturbed regimes having a reduced overall biomass. Comparing only the different disturbance regimes (lightning strike and hurricane) showed that the mean *DBH* were significantly different ($p < 0.0001$) but not the number of trees ($p = 0.28$) or the biomass ($p = 1.0$). The hurricane scenario showed a small but significantly higher mean *DBH* than the lightning strike regime.

The spatial tree arrangement showed significantly different values of Clark-Evans index (*R*) between all simulated scenarios ($p < 0.0001$). The values of *R* varied only between 1.21 and 1.23 (Figure 5.1d). These values were considered as regular after testing against randomized tree positions. The undisturbed scenario showed the most random trend followed by the lightning strike, while the hurricane regime showed the highest value indicating the most regular structure.

The temporal variation of the mean tree size ($CV(\overline{DBH})_t$) had values lower than 0.08 for all scenarios indicating low variance in general (Figure 5.1f). The hurricane regime had the highest value by far, whereas the low values of the undisturbed scenario and the lightning strike regime did not differ significantly from each other ($p = 0.46$).

The calculated $\overline{CV(DBH)}$ for the spatial size variation was seen as highly variable and significantly different ($p < 0.001$) for all scenarios (Figure

5.1e). The undisturbed scenario was the most variant scenario followed by the lightning strike scenario while the hurricane regime showed the lowest values.

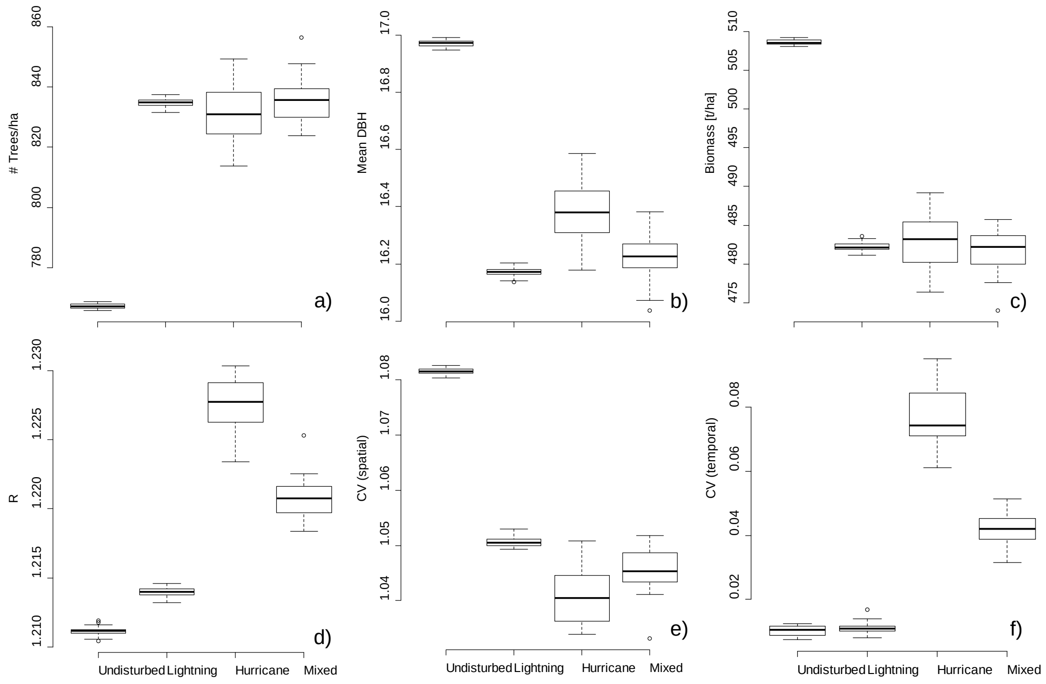

Figure 5.1: Calculated indices for the different simulated scenarios: a) tree density per ha, b) mean *DBH*, c) Biomass [t/ha], d) Clark-Evans Index R, e) *CV* of spatial variation, f) *CV* of temporal variation.

Figure 5.2 showed the forest biomass for one repetition of each scenario. The hurricane scenario was the most variable through time with the highest amplitude. The biomass of the lightning strike regime was constantly smaller compared to the undisturbed regime, whereas the biomass of the hurricane scenario could even exceed temporally the one of the undisturbed scenario. The hurricane events clearly decreased forest biomass. But on this scenario, long periods without hurricane events could lead to a biomass exceeding the one of the undisturbed scenario. A long lack of hurricanes (from year 876 to 982) showed first an increasing biomass indicating that trees in the simulated monospecific landscape were growing and competing. In this specific case, after few decades, the biomass was then oscillating at the level of the undisturbed regime.

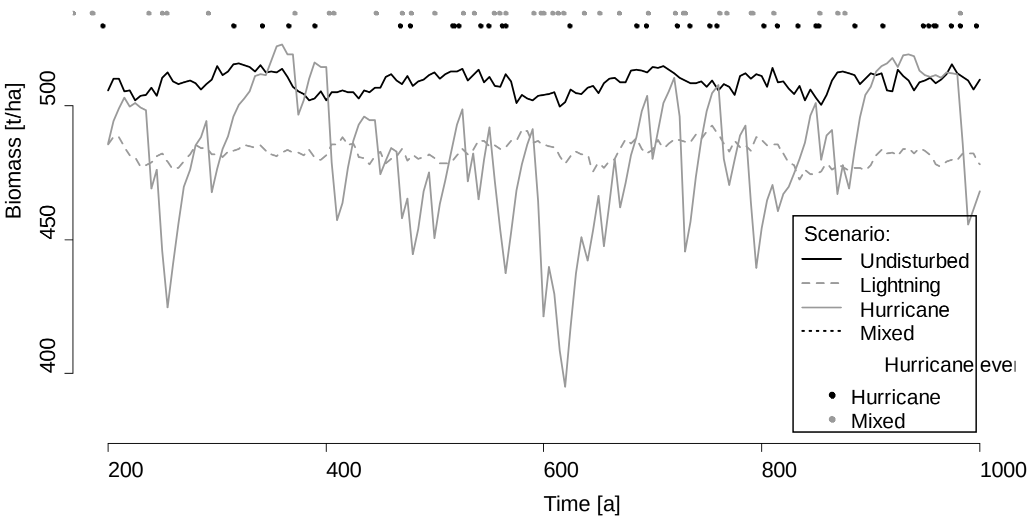

Figure 5.2: The forest biomass for one simulation run of each scenario. Please note that all hurricane events are illustrated whereas the biomass calculations were carried out every five years.

5.3.2 *Mixed disturbance regime*

For the mixed scenario the number of trees and the biomass was not significantly different from the other disturbance regimes (*p* = 1.0) while the mean *DBH*, the horizontal distribution and the temporal and spatial variation showed differences compared to the lightning strike and the hurricane scenario (Figure 5.1). These four variables were at intermediary levels between the lightning strikes and hurricanes regimes. The mixed scenario presented the second highest variation of biomass in time (Figure 5.2) after the hurricane scenario indicating the influence of the hurricane disturbances on the temporal variation.

5.4 Discussion

The simulated disturbances showed both homogenizing effects on the spatial forest structure compared to the undisturbed reference scenario. This is caused by growing up cohorts having a limited age and size variation (Paluch 2007), which create homogenous structures within disturbed patches (White and Jentsch 2001). However, the simulations were conducted on a landscape scale and disturbances are expected to create increased complex forest structures by the existence of different successional stages (White and Jentsch 2001). This additional heterogenization in the disturbed scenarios was not found in our simulation because the mature undisturbed forest presented a very high heterogeneity of the tree size structure.

Comparing the effects of disturbance regimes on forest structure it is apparent that hurricane events set back forest succession by opening large spaces and subsequently creating a more regular spatial tree arrangement. This leads to an increased homogenization compared to lightning strikes effects. Despite these large openings the hurricane regime was characterized by higher averaged tree size. This can be explained by the incomplete tree removal in disturbed patches, leading to an overall decrease in neighborhood competition, which triggers a growth release for the remaining trees. By comparison, entire tree removal in lightning-strike gaps induced only decreased asymmetric competition for trees at gap borders. Triggered growth release immediately after the disturbances might be an artifact of the KiWi model to a certain extend. Instead, an immediate growth reduction of the surviving trees would be expected due to the damages to tree architecture. Following a recovery by stem sprouts or layered branches (Johnson and Miyanishi 2007), a time-delayed growth release is expected due to the reduced competition within the disturbed patches.

With regard to the temporal dynamics, only hurricane events had heterogenizing effects. The hurricane regime had strong temporal fluctuations with a noticeable decrease in biomass after disturbance events and a subsequent fast regeneration showing “pulse stability” (Lugo 2008). Despite the same mortality rate by disturbances, the lightning strike regime did not lead to an additional heterogenization of tree sizes compared to the undisturbed regime. The small frequent lightning-strike gaps produce a stable amount of patches of various successional classes in time. Therefore, the lightning strike regime entails relatively uniform and homogenous conditions in large areas by behaving similarly in time as small intrinsic variations such as single-tree mortality of the reference scenario. The biomass values of the undisturbed and lightning strike scenario are predictable on a landscape scale, both are considered in a “steady state” (White and Jentsch 2001).

The absolute values of the spatial variations of tree size are multiple times higher than the temporal variation for all scenarios (see Figure 5.1).

The biomass of the hurricane scenario showed high variations in time. It even exceeded the high values for the biomass of the undisturbed scenario for short periods of time confirming as well the strong impacts of hurricane events on the temporal forest dynamics. The high biomass values in the hurricane scenario can be explained by the synchronous growth of even-aged cohorts reaching a maximum before obtaining a “steady state” forest stage (Shugart 1984). Subsequently, the biomass would oscillate to the same level as forests without disturbances given that no further disturbance occurs. Nevertheless no significant differences in biomass of the two disturbance regimes are found when comparing the overall forest biomass for the simulated time-span.

The results show that the often considered biomass (Shugart 1984, Fromard et al. 1998) is not sufficient to characterize spatio-temporal patterns of forest structure in detail in front of disturbance regimes. We suggest to apply structural indices that are taking the variation in time and space into account for receiving a deeper understanding of the forest dynamics. However, the spatial observation scale must not be ignored to characterize forest dynamics. Resulting disturbance effects are always strongly dependent on the size of the regarded area. To assess homogenizing and heterogenizing characteristics it is important to consider the scale of the disturbed area versus the size of the analyzed forest area. For example, when using a too small observation area to assess the effects of lightning strikes this can result in the observation of temporal heterogenization compared to the undisturbed area. Our simulations showed that the contrary should be observed.

In this study, the simulated area of 25 ha was kept constant for all simulated scenarios creating a multi-patched landscape for the disturbance scenarios, containing a range of different successional stages due to disturbed patches of various ages.

Usually, grid-based models are widely applied to analyze spatio-temporal dynamics for large areas and time horizons, whereas our study was conducted with an individual-based model. Grid-based models represent cell units considering certain conditions of an ecosystem, while often neglecting the properties of the individuals. Typical applications are studies of synchronizing and desynchronizing effects on the forest structure e.g. Ratz (1995) for fire disturbances, Jeltsch (1992) for natural die-back phenomena or Rademacher et al. (2004) who developed BEFORE to simulate the mosaic structure of beech forests. In BEFORE (Rademacher et al. 2004), storms support synchronization on local scale, but disrupt the regional synchronization by mixing successional stages of undisturbed and disturbed forest patches, which was also found for our implemented disturbance regimes. The undisturbed scenario showed in BEFORE an entire synchronization of the grid cells in time and space, whereas in our simulation study the highest spatial tree size heterogeneity and expected desynchronization was achieved. This effect can be affiliated by the different starting conditions and would not contradict each other. (Rademacher et al. (2004) started with a blank area, while we used mature forest in a desynchronized stage as a reference and initial state for the disturbed simulation regimes. One advantage of an individual-based model approach is that ecological processes can be described in more detail. Beside the disturbance-induced tree mortality, the model-intrinsic competition mortality leads to a more realistic behavior of forest dynamics.

The simulation runs were conducted under the assumption of unlimited sapling availability. However, propagule and subsequent sapling supply strongly depends on the intensity and spatial extent of disturbances (Turner et al. 1998) and the presence and accessibility for them to reach disturbed patches (Price et al. 2001, Gratzer et al. 2004). Therefore, explicit consideration of seedling availability and dispersal would influence the post-disturbance succession patterns. By assuming unlimited sapling availability the elasticity, i.e. the ability of regeneration after disturbances, was kept constantly optimal and was comparable for all disturbance regimes. As a result, the implemented mixed scenario might have not shown any emergent characteristics. However, this view might be too simplified, due to diverse functional interactions regarding the regeneration, growth and death in multiple and mixed disturbed areas (Jentsch et al. 2002). For example, regenerating gaps would have a particular role in terms of providing seeds for newly created patches according to existing species communities and stand structures (Shugart 1984, Jentsch et al. 2002).

Each forest patch, regardless of whether it is undisturbed or disturbed, is characterized by specific ecological functions carried by functional traits of different plant species (Jentsch et al. 2002). Hence, besides causing heterogeneity in the spatial structure, multiple disturbances enhance the diversity of species as well. The increased habitat heterogeneity entails reduced vulnerability to breakdown during catastrophic events (Drever et al. 2006).

On the one hand when the disturbances are too small in size no niche formation is observed (Jentsch et al. 2002). On the other hand in case of having only large-scale disturbances the forest structure would be set in an unfavorable uniform forest stage, with jeopardized regeneration when sapling supply is not adequate. Therefore, a regime of mixed disturbances would be the most preferable, where regenerating gaps and patches of different sizes and successional stages are interacting with each other providing various habitat conditions for different populations. This beneficial interaction was found after a windthrown event in a mangrove plantation in Can Gio Vietnam (Vogt et al. 2011). The disturbed patches of the windthrown sites characterized by only little regeneration benefit from the seed supply of regenerating lightning-strike gaps left unaffected by the wind storm (Smith III 1994).

Drever et al. (2006) developed a similar reasoning for promoting a heterogeneous natural forest structure characterized by different age and size classes for commercially used forest by applying natural-disturbance-based management.

In conclusion, we were able to show that different disturbance regimes, although characterized by the same tree death probability by different disturbing events, affect the spatio-temporal forest dynamics in various ways. The differences in frequency, size and intensity of disturbances determine heterogenizing and homogenizing processes in space and time. These effects were not detectable by analysis of classical forest characteristics such as tree number and biomass. On the other hand, structural indices incorporating temporal and spatial variation reveal that both the lightning-strike and hurricane disturbance scenarios homogenized.

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6 General Discussion and outlook

6.1 Discussion

This thesis gives an extensive overview about various disturbances in different mangrove forest systems, where field and computer simulation analyses are equally important. Additionally, mangrove species of different biogeographical regions were studied, including the Neotropical species *R. mangle*, *A. germinans* and *L.racemosa,* as well as the Centro Indo Pacific species *R. apiculata*. Disturbance regimes of different spatial scales and origins involving different impacts on mangrove forests were investigated. The broad view of this thesis permits conclusions especially for the protection and restoration strategies of mangroves. It is shown that management activities are strongly dependent on the respective mangrove system. The broad range of the considered mangrove forest types from monospecific plantations lacking in natural species diversity and forest structure in Can Gio; human-influenced still semi-natural forests in the Indian River Lagoon; as well as simulated natural forests, need a separate consideration regarding the response to disturbances. Thus, this thesis makes a significant contribution for the mangrove ecology with focus on disturbances and mangrove forest development.

6.1.1 Major findings

Disturbance patterns

The influence of different disturbance regimes including human-induced impoundment characterized by an artificial prolonged inundation regime, hurricanes and lightning strikes on the mangrove forest were investigated. I found that the different disturbances act as selective forces according to the biodiversity and forest structure. Hence, the impoundments in Florida promote a monospecific forest development where *R. mangle* is better adapted than *L. racemosa* and *A. germinans* (Chapter 2). Furthermore, the hurricane events showed tree-size dependent mortality where larger trees were more prone to death by uprooting or stem breakage. Furthermore, the mangrove species are well adapted to hurricanes compared to the non-native *C. equisetifolia*. The mortality during the hurricanes of *C. equisetifolia* exceeds those of the mangrove species multiple times and almost no post-hurricane re-establishment was found.

On the other hand, canopy gaps created by the lightning strikes were found to be tree size-independent by killing all trees within a certain radius (Chapter 4). No records of species-dependent mortality within these gaps were found in the literature. Although lightning strike disturbances affect all tree sizes and species equally, they play an important role for increasing the structural heterogeneity and the floristic composition in homogenous plantations. Regenerating gaps have a lower mean tree size than the surrounding plantation and the light gaps enable shade intolerant species to establish. No restrictions according of a fast subsequent regeneration of these small gaps were found due to the small size of the disturbance and therefore having an adequate provision of propagules from the surrounding forest.

Interaction of disturbances

Positive interactions between these small-scaled gaps and medium-scaled disturbances such as windthrow events may occur. The simulation study in Chapter 5 has shown that the explicit size and frequency of disturbances matters, despite causing the same probability for tree death, and therefore have different ecological influence on mangrove forests. Within a windthrown site at the plantation in Can Gio which killed almost all trees, impeded recolonization was observed except for the abundance of “green islands” (Chapter 4). These green spots were formed by former lightning-strike gaps which are now in the regeneration phase. The trees were smaller in size which provided resistance against uprooting during storms. Now these islands provide the surrounding disturbed areas with seeds and hence facilitate and accelerate their recolonization. For all the above-mentioned reasons small-scaled gaps are an important ecological factor for forests dynamics in mangroves.

In contrast, interactions between medium-scaled and large-scaled disturbances may lead to deteriorated conditions for mangrove establishment or growth. Hurricane events in the impounded mangrove forests along the Indian River Lagoon could entail peat collapse including root decomposing of dead trees. The increased water depth may cause further abiotic changes and thus create additional stress for the mangroves especially for their establishment.

Concerning the different natural disturbance regimes in mangrove forests, management strategies for restoration or maintenance efforts should be guided by their natural dynamics. Therefore I suggest the creation of small clearances within the plantation in Can Gio for enhancing its structural and floristic composition. I conclude that this type of management would not contradict the protective regulations and goals of the UNESCO biosphere reserve.

6.1.2 Contributions of this work to mangrove forest ecosystem

This thesis is embedded in the general framework of the study of mangrove forest dynamics. Due to the challenge for understanding the immense complexity of the interacting processes that determine and maintain biodiversity and productivity of mangrove ecosystems (Feller et al. 2010), this thesis is only able to address parts of these complex processes. In particular, I investigated the characteristics of spatio-temporal forest structure processes by focusing on their behavior against disturbances and its regeneration behavior under different environmental conditions. Single aspects such as i) the ecological role of disturbances, ii) the forest structure and succession behavior, iii) restoration efforts and management, iv) long-term changes are discussed within the context of the current scientific research.

The ecological role of disturbances

As discussed before, disturbances do not always have a negative impact on a forest system. On the one hand, mangrove ecosystems in some areas might be highly dynamic naturally, for example due to extensive sedimentation processes (Proisy et al. 2009). On the other hand, mangrove forests have a pronounced adaption capability even to severe natural disturbances either through resistance mechanisms or by having the ability to regenerate after the disturbing event. For example, during hurricane events trees lose their foliage, but this prevents stem breakage and increases the individual survival rate (Roth 1992), or in case of stem breakage some species e.g. *L. racemosa* and *A. germinans* are able to resprout (Baldwin et al. 2001).

Disturbed patches within a forested area help to maintain biodiversity especially for light-demanding species (Brokaw 1985), they reset successional processes (Fromard et al. 2004) and therefore increase the heterogeneity at a landscape scale. Therefore, natural disturbances of different origins are an integral part of the mangrove ecosystem. Seidl et al. (2011) emphasize the important role of disturbances in ecosystem dynamics, while noticing the challenges to receive the acceptance of the local inhabitants to these disturbances, especially when human infrastructure is threatened.

In contrast, artificial disturbances may lead to long-term transformation and destruction of mangrove forests, a scenario where potentially valuable ecosystem services provided by mangroves are lost. The long-term influencing climate changes might increase the risk of economically damaging storms or increase the overall damage extent (Gedan et al. 2011). In this case, the natural disturbance regime might change dramatically and the subsequent mangrove adaptation may be jeopardized. Even though long-term impacts are hard to predict, it can be expected that the resistance, the buffer capacity and the resilience might be negatively affected. I found aggravated post-hurricane establishment conditions in the impoundments indicating already a decreased regenerating ability in this artificial modified system interacting with hurricanes (Chapter 2).

Forest structure and succession behavior

Usually mangroves are either distinguished by their forest forms shaped by e.g. shore morphology, inundation regimes, salinity and nutrient availability or by their successional stages (Hogarth 1999). In this way, Hogarth (1999) differentiates between riverine, tide-dominated, basin and other forest forms.

Fromard et al. (1998) uses successional stages such as pioneer and young mangrove, mature mangrove declining or dead mangroves to describe forest dynamics. Every successional stage is characterized by certain processes: within early developmental stages inter-tree competition is high and leads to pronounced self-thinning, while by obtaining the mature phase the competition, growth and mortality is decreasing and mortality will increase again during the senescence phase (Fromard et al. 1998).

Besides these classifications, the ecosystem complexity can be characterized by different aspects such as species composition as well as disturbances and the spatial arrangement of various components e.g. height of different canopy levels and tree spacing (McElhinny et al. 2005).

The biodiversity aspects in mangroves were considered by several authors such as Duke et al. (1998) who correlate the diversity of mangrove plants with the diversity of structure in mangrove habitats for the associated fauna. Furthermore Piou et al. (2008) conducted simulations testing the influence of abiotic conditions on species diversity. The current thesis examined the floral composition of the impounded forests and it was found that the subsequent post-hurricane regeneration is dependent on the inundation regime. In addition, field studies in Can Gio clearly showed an increase in species within the lightning-strike gaps compared to the surrounding plantation.

Nevertheless, the main focus remains on the structural description of forest dynamics in space. Within the case studies comprising this thesis this classical distinction of successional stages is dissolved into single-tree consideration within a forest stand in order to describe spatio-temporal mangrove dynamics. The single known study which explicitly describes spatial forest structure in mangrove forests according to disturbances was conducted by Blanco et al. (2001). They applied the universal complexity index for different mangrove forests which characterizes the forest state within a single value:

$$CI = s*d*b*h* 10-3 \qquad (Eq.\ 6.1)$$

with the number of species *(s)*, stand diversity *(d)*, basal area *(b)*, and height *(h)*. This index is commonly based on the three tallest trees of the investigated area describing the maximum forest development, which is a suitable approach in the absence of disturbances but would otherwise be an overestimation (Blanco et al. 2001). McElhinny et al. (2005) point out that this index is strongly influenced by the number of overstorey species and lacks information about inner stand variation. Therefore Blanco et al. (2001) suggest mean and mode values for calculations. However, even these parameters might not be able to represent entirely the very dynamic and successional mangrove structures with their wide range of tree sizes.

Further, this stand level index summarizes effects of different structural attributes in a single value and bears the risk of masking or even losing important information about forest stands (McElhinny et al. 2005). Thus, two different stands may have the same index value derived from different input variables.

For this reason I took into account the variation considering the entire forest structure by applying either the coefficient of variation or the Shannon height Index (*SI*) for tree sizes. Additionally, the horizontal tree arrangement was calculated when information about stem position was abundant. As a consequence, by applying these indices I was able to compare different forest stands and were able to identify specific characteristics such as tree size structure and arrangement important for forest dynamics. To ensure the comparability between different forests the study area and the number of chosen size classes has to be constant.

Restoration effort and sustainable management

In light of the high loss rates of mangrove forests (Beaumont et al. 2011) it is of urgent need to restore mangroves in affected areas to re-establish the important ecosystem functions along the coasts. It is rather important to create an adequate hydrological regime and not only provide plant saplings in these areas, where the establishment success might be doubtful (Lewis III 2005). The flooding depth, duration and frequency are crucial factors for the survival of the mangrove seedlings (Bosire et al. 2008). For example, the restoration of mangroves in abandoned shrimp farms often fails due to unsuitable hydrological conditions (Lewis III 2005) or sapling planting was unsuccessful on destroyed mangrove areas because of the cut off from the natural inundation regime (Elster 2000). The analysis of the artificially impounded mangroves in the Indian River Lagoon indicates stress for the post-hurricane establishment in some parts and a successful regeneration might be jeopardized.

Presently, no attention has been drawn to natural disturbances in the context of mangrove restoration projects. Natural disturbances might be able to influence abiotic components and thus impair establishment and growing conditions.

Previous mangrove restoration was mainly focused on optimizing the production of timber, on increasing the fishery productivity or on recreating protective coastal barriers (Bosire et al. 2008). Restored sites were characterized by monotone plantations with very few species or even by monocultures. Often the forest development takes place very homogenously in respect of the spatial structure, age structure and species composition such as found in the Can Gio plantation. However, (Bosire et al. 2008) highlight the importance of assessing structural and functional characteristics of restored mangroves including vegetation structure, the ability of natural regeneration and socio-economic values. These current restoration activities are aimed at re-establishing ecological processes in order to receive a self-sustaining ecosystem (Jentsch et al. 2002). Restoration plans should therefore include a mosaic of all age stages and species and thereby maintain dynamic processes (Jentsch et al. 2002). This can not be achieved with an one-time planting, instead, continuous management activities are necessary. This task is partly performed by the lightning strikes in the plantation in Can Gio. These disturbances create gaps of different developmental forest stage within the homogenous structures and support the transformation to natural condition including risk reduction of synchronous windfall. However, due to the relatively low formation rate of these gaps it would be advisable to create additional artificial small clearings.

Jentsch et al. (2002) highlight that the influence of disturbance events on the spatial and temporal restored forest development can act initiating and stabilizing for natural ecological rhythms. However, unfavorable changes in natural disturbance regimes might be as well able to destabilize successional processes. Therefore I emphasize the necessity for considering natural disturbance regimes as well as hydrological conditions for obtaining successful restoration efforts.

Long term changes

Besides, direct mangroves destruction due to land transformation and climatic changes jeopardize these forests in a way which is difficult to predict. As mentioned before, devastating wind storms such as hurricanes are assumed to increase in frequency as well as intensity (Webster et al. 2005). Predicted sea level rise would entail direct negative impacts such as catastrophic floods for coastal inhabitants (Gedan et al. 2011). Especially fringe mangroves, most important for coastal stabilization, would be threatened by rising sea levels. Their resistance and resilience against storms and subsequent buffer capacity for coastal protection might be further constrained by negative interactions of wind storm events and the additional increased inundation regime. Although it is not possible to compare impounded areas and sea level rise directly due to the missing natural tide cycles, certain parallels can be drawn. The sea level rise involves the increase of inundation according to duration and depth leading to additional waterlogging stress for fringe trees. The study results of the impounded forest showed that the flooding-tolerant species *R. mangle* is adapted to some degree to high inundation regimes, but after disturbance events establishment was partly impeded. This leads us to conclude that even when mature trees are able to adapt to higher inundation regimes, establishment might not take place. The impounded mangroves in Florida might have advantages from the surrounding dikes where the artificial water regulation could be used to keep the inundation depth lower than the natural regime. Even so, I would not suggest a wide application of this management: the economical costs and ecological impacts of constructing the dikes and maintaining the management activities to ensure the ecological functioning of impounded areas are exceptionally high. For example, the exchange marine fauna dependent on mangroves has to be ascertained to maintain breeding places. Furthermore the simulation of water movement and the permanent exchange of sea water is required to obtain the required water quality for the majority of organisms. These management strategies demand high investments and running costs (pers. comm. James David –head of the Mosquito control in St. Lucie County). Additionally, impoundment efforts changed the hydrology in an undesirable way, involving a massive dieback of mature mangrove trees, which is understandable in light of the fact that the mangrove impoundments in Florida were constructed as a mosquito control measure and not for counteracting changing inundation regimes.

6.1.3 Methods evaluation

Multiple methods are often necessary for the analysis of complex conditions. By conducting field measurements, simulation studies, and calculations of different spatial pattern indices and by applying remote sensing techniques I received an eclectic picture of our study topic. Especially gap creation by disturbances activates a set of ecological processes including biotic changes such as removal of overstorey trees and the subsequent change in vegetation structure which influences abiotic factors, including an increased light availability or changes in the microclimate (Johnson and Miyanishi 2007).

Field measurements and ***remote sensing techniques*** are widely applied important tools in mangrove ecology and are often used complementarily (Zhang 2008, Sherman et al. 2000). Remote sensing techniques give a general overview about certain characteristics of the vegetation structure e.g. species composition (Satyanarayana et al. 2011), disturbance pattern (Zhang 2008), forest distribution (Kovacs et al. 2011), loss rates (Giri et al. 2011) and temporal development (Omo-Irabor et al. 2011) on a larger scale than field studies are able to supply. The derivable information strongly depends on the quality of the images as well as on other knowledge including various data sources e.g. climatic, socio-economic information or expert knowledge (Omo-Irabor et al. 2011) of the considered system. The SPOT satellite images used for the study in Can Gio have a sufficient resolution for detecting lightning-strike gaps. Furthermore, the quality of the aerial photographs used for the study areas of the IRL permitted even the detection of the starting regeneration of the hurricane patches and the distinction between mangrove species and *C. equisitifolia.* Nonetheless, field studies are irreplaceable for validating the observed image structures with the actual vegetation structure and to obtain further information about the ecosystem, which can only be collected through direct measurements.

Structure indices based on field data (Chapter 2) or simulation analyses (Chapter 4 and 5) were used to characterize the spatio-temporal dynamics of the forest structure. Most comparisons of mangrove forests are based on biomass calculations or basal area (Sherman et al. 2000, Imbert et al. 1996). The study in Chapter 5 indicates that these approaches are insufficient for the in-depth characterization of the complex forest structure. Blanco et al. (2001) used the Holridge complexity index (Eq 6.1) to describe and compare mangrove forest structure in different transects. The disadvantages of this index include the overemphasis of large trees, no information about inner variation or the masking of important aspects (McElhinny et al. 2005). For these reasons I calculated the Shannon Index for the tree size which represents a diversity measure permitting direct comparison between diameter and height distributions expressed in a single value (McElhinny et al.

2005). This index is applicable for different management strategies (McElhinny et al. 2005), or as in our case, suitable for comparing different disturbance regimes. Still, I have to point out that the outcome value is dependent on the classification of the size classes (Chapter 3, sensitivity analysis). Thus, for comparison purposes this index requires an identical amount of size classes. In order to avoid the arbitrary distinction between size classes, the coefficient of variation for tree sizes might be used as a further measure of heterogeneity.

In addition to the vertical description of the forest structure I address the importance to investigate the horizontal forest structure which is determined by ecological processes such as thinning according to competition (regular tree arrangement) or facilitation (clustered distribution). A widely applied method to describe spatial structures are marked point pattern analyses including the characterization of both horizontal tree arrangement and horizontal tree size (Illian et al. 2009). As a consequence of the difficulty of describing temporal dynamics of forest development, I abstained from conducting such measurements. The graphical output is very suitable for snapshots comparing different forest systems at certain time steps but not for monitoring the development over a period of time.

Instead, I applied the Clark Evan Index using one single value to describe the spatial tree arrangement. The disadvantage of this index is the difficult determination of the horizontal tree arrangement within the transition from randomly to regularly or clustered.

The ***individual based mangrove model KiWi*** used for the simulation analyses was already successfully applied to study mangrove forest dynamics (see Chapter 3). The simulation approach is essential for gaining knowledge about the ecosystem as a whole, while large-scale field experiments require a huge financial and work effort and could have disastrous consequences on the ecosystem functions (Green and Sadedin 2005). A great advantage of simulation studies is the readily available information on ecosystem responses under controlled conditions on large temporal and spatial scales. Structural characteristics can be easily derived from this data. Besides calculating vertical structural indices, the exact description of each stem position enables us to use the widely applied aggregation Clark-Evans index, which requires the nearest neighbor distance of each tree.

In KiWi, disturbances are implemented by the resulting tree mortality of the particular disturbance regime. Consequently, hurricane wind forces or directions are not simulated but rather the amount and size of expected dead trees where size-dependent tree mortality can be considered. These assumptions might be very simplified because of the complex impacts of the hurricane events. A tree might survive the disturbance but damage to tree architecture may alter its growth rate (Johnson and Miyanishi 2007). Presently these considerations are neglected in KiWi simulations: either a tree was killed by the disturbance or survived undamaged without any slowdown in growth.

Furthermore, KiWi allows explicit spatial sapling dispersal. I introduced saplings either randomly (Chapter 5), regularly (initially planted saplings in Chapter 4) or with an establishment pattern close to existing trees (yearly recruitment, Chapter 4). I estimate that having detailed data about the establishment process could improve the quality of simulation results. (Turner et al. 1998) notice that propagule availability is a driving factor for successional patterns. They noticed that within small disturbed areas within an intact forest sufficient propagule supply exists, whereas the amount of propagules decreases with the distance to seed trees. Therefore, the propagule availability in disturbed areas is dependent on the intensity and the spatial extent of the disturbances.

Though KiWi considers the sapling dispersal explicitly, entire processes from propagule dispersal to growth into the sapling stage are missing and should be investigated in future studies. Especially for post-disturbance regenerations dispersal, establishment and seedling growth are crucial processes determining subsequent succession. Additionally, gap-filling processes as vegetative regrowth of damaged trees or lateral crown development from edge trees (Johnson and Miyanishi 2007, Duke 2001) are presently not possible to implement within KiWi. Mangroves show a highly variant trait plasticity related to the adaptations to salinity, flooding and nutrient regime (Feller et al. 2010). For example the mature size of *R. mangle* might vary between 0.5 and 40 m which is a very pronounced plastic response compared to many terrestrial species (Feller et al. 2010). Currently, KiWi is able to calibrate maximum tree sizes and the increment of growth to specific study site, but it is not possible to apply the existing growth function with a minimum input height of 1.3 m (see Chapter 3) on dwarf individuals. In the following section I want to elaborate on potential future studies aimed at gaining a better understanding of mangrove dynamic processes.

6.2 Outlook

This thesis gives insight about the spatio-temporal forest dynamics under different disturbance regimes, considering the ecological role of disturbances, the disturbance patterns on the forest structure and succession behavior and sustainable management strategies. However, interesting aspects were only touched briefly and are discussed in the following. I would like to point out further applications and development of the KiWi model for the simulation of important ecological aspects of forest dynamics which are presently not well understood. One example would be the consideration of dead wood: In its current development state, KiWi uses only tree mortality as a tree removal factor. Several studies have pointed out the importance of dead wood within the nutrient cycle (Krauss et al. 2005) and as a mechanical barriers for propagules for entering disturbed sites (pers. obs Uta Berger in Vietnam at a windthrow site), thereby influencing both seedlings dispersal and regeneration in multiple ways. One way to implement dead wood effects is to create underlaying maps based on tree size, stem position and assumed fall direction in case of uprooting.

Berger et al. (2008) point out that none of the existing individual-based mangrove models include recruitment processes explicitly. In KiWi, saplings are introduced into the simulated area with mostly simplified assumptions. In particular, recruitment processes including water dispersal (Duke et al. 1998) and lack of seed dormancy and consequently the importance of reseeding (Feller et al. 2010) play a fundamental role for subsequent succession processes. A seedling model integrated in KiWi would enable the simulation results to account for these processes (see Appendix 10).

While regeneration is initialized by seedlings, vegetative regeneration might be occur by damaged or surrounding trees due to resprouting or lateral growth (Baldwin et al. 2001). KiWi considers symmetric tree crowns of single stemmed individuals, but resprouting trees are often multi-stemmed trees (pers. obs. in Florida) and are characterized by asymmetric growth using open space effectively (Duke et al. 1998).

Furthermore, tree characteristics are dependent on tree architecture. For example, trees growing along margins have more prostrate statures, with a small height-diameter relationship and as a consequence are less vulnerable to wind and waves than trees within the forests of upright architecture with little support structure (Duke et al. 1998). Wild and Winkler (2008) applied the

FON for asymmetric clonal plants, which could be adapted for KiWi. Using an asymmetric FON and tree crown shape would fulfill the requirement for the high plasticity and common asymmetric growth of mangroves.

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Conclusion

Research questions

1. Which characteristical disturbance patterns within mangrove forests is shown according to different disturbance regimes?

Disturbances of different origins are a common phenomenon in mangrove forests. These disturbances can be described according to their cause, spatial extent, return frequency, and intensity. Thus, the resulting disturbance pattern may range widely from few impacted individuals to large-scale forest destruction. The different disturbance regimes affect the forest in various ways. For example, impoundment promotes mangrove species with a higher flooding tolerance (*R. mangle*). In contrast, hurricane events appear to damage all mangrove species to the same extent, but clearly cause higher damage within the non-native *C. equisetifolia* population. The mangrove tree species exhibit a good site adaptation. Within the mangrove forests hurricanes are selective forces regarding tree size, where larger trees are more prone to death due to stem breakage or uprooting. However, small lightning-strike gaps are characterized by non-selective tree mortality irregardless of species composition and tree sizes.

2. What is the influence on the spatio-temporal forest dynamics with regard to the disturbance regime?

Different disturbance regimes influence the forest dynamics in different ways. Small lightning-strike gaps were found to create structural tree-size heterogenization in homogenous even-aged plantations, but lead to homogenization in a simulated mature undisturbed forest with a high structural complexity. This homogenization was found for hurricane events as well, which set back large areas of the forest into a young successional stage. Inside the impounded area, hurricanes create heterogeneous structures by opening patches within the closed canopy. The large scale impoundment initially led to an extensive death of the dominant non-flooding tolerant *A. germinans* and herbaceous halophytes and therefore succession was restarted from an almost unvegetated area with *R. mangle*. This cohort growth and the constant high water depth and flooding duration which is only suitable for very few plant species lead to a homogeneous forest structure and species composition.

Considering temporal forest dynamics, small-scaled gaps do not create any temporal variation in simulated large areas. On the one hand, they might be able to buffer the effects of synchronous diebacks in an even-aged homogenous plantation to a certain extent. On the other hand they are not able to accelerate a conversion into more natural forest structure. In contrast, hurricane events have a strong impact on the temporal variation on the simulated forest dynamics due to the caused large-scale impact. Impoundments are a long-term ecosystem change, but in case of the absence of additional disturbances may be considered as an undisturbed regime with altered species composition and homogenous forest structure due to the cohort behavior.

3. How do the intensity and frequency of gap and patch formation influence the overall landscape pattern of the forest development?

Lightning-strike gaps are known to kill all trees within a certain area, but differ in the radius of the circular dead tree clusters. The frequency differs geographically. For example, lightning strikes in Florida are supposed to be the major factor for creating small gaps in mangrove forests. They occur in Can Gio as well but have a lower frequency. Therefore, lightning-strike gaps are similar according to their intensity and shape but differ in their formation rate.

Hurricane events strongly differ in their impacts according to the nature of the storm and the ecosystem characteristics. Therefore the single events vary strongly in their extent and intensity and consequently in the landscape pattern. I studied hurricane events in Florida and used their characteristics as an example for simulating the hurricane impact on the forest structure. With the given disturbance regime these events created open patches within the mangrove forests, setting back especially forest areas of higher developmental stages into an almost entirely open area. Hence, the senescence phase within forests might not be abundant in areas with a high hurricane frequency. It is even assumed that these regions hardly reach the senescence stage within mangrove forests.

4. How does gap turnover alter forest structure, diversity and distribution?

The studied disturbances affect the forest structure in various ways. One important aspect is the relation to the characteristics of the undisturbed forest. Hence, lightning-strike gaps involve a heterogenization within a homogenous plantation, whereas a homogenizing effect was found compared to a simulated structurally complex and undisturbed forest. Considering the disturbance itself there was no change in tree-size distribution by affecting all tree sizes equally, but regenerating small gaps caused by lightning strikes are characterized by small tree sizes. Furthermore, the lightning-strike gaps increased the species composition in the monospecific plantation in Can Gio by providing a sufficient light regime for seeds and propagules which can not establish under the dense canopy of the plantation.

Hurricane events alter the tree-size distribution due to the size dependent mortality where larger trees are more prone. In addition, the regenerating patches create large areas of identical young developmental stages. This cohort growth leads to an extensive homogenization within the patches and thus on a large forest scale. At the same time the forest might be more structured due to the presence of disturbed and undisturbed areas.

Generally there is a typical post-hurricane species selection. The most benefiting species are *L. racemosa* and *A. germinans*. Possibly due to the rare occurrence of these species within the impoundment that could not be confirmed at our site in Florida The post-hurricane regeneration was dominated by the flooding-tolerant *R. mangle*. I also found that the impoundment in combination with the hurricane events partly deteriorate the conditions in a way that even R. mangle was unable to establish throughout after disturbances.

The velocity of the regeneration is related to the size of the disturbed area and to the availability of propagules. The latter is dependent on multiple factors such as the time of the disturbance event in regard of the fruiting season or the survival of seed trees within disturbed areas. The dispersal by water currents could be partly interrupted by blocking dead wood. I found that the regeneration in the plantation in Can Gio on a windthrow site relied on previously created, regenerating lightning-strike gaps which remained as “green islands”. These islands are characterized by having a lower forest stature and remained unaffected during the wind event. Currently, they act as seed sources for the surrounding hurricane-disturbed plantation, thus accelerating the regeneration process.

5. How do disturbance regimes influence the stability of natural forest dynamics and vulnerability of the mangrove ecosystem?

Natural disturbances are an integral part of the spatio-temporal forest dynamics and intact forests show adaptation mechanisms according to resistance and resilience. However, non-intact forests or restored sites, which are characterized by non-natural species composition or forest structure might be more vulnerable to natural hazards. Here the disturbance events may destabilize successional processes. The results from our studies suggest that the homogenous plantation in Can Gio and the impounded forest in Florida suffer from an impaired regeneration after windthrow or hurricane events. Prospectively, these areas will be even more threatened by altered disturbance regimes associated with climate change which could involve sea level rise or increased storm intensity and frequency. Furthermore, even in intact forests the altered disturbance regime might exceed their adaptability and therefore jeopardize their important ecological benefits such as coastal stabilization. However, the direct forest destruction by human activities poses the most severe threat to the mangrove ecosystem. Even in case of restoration efforts, there is no guarantee for a successful reestablishment of the components of this complex ecosystem.

Zusammenfassung

Diese Doktorarbeit untersucht die Auswirkung verschiedener Störungsarten auf die Entwicklung von Mangrovenwäldern. Mangroven sind einerseits Gezeitenwälder entlang sub- und tropischer Küsten, andererseits bezeichnet man sie als holzige Halophyten die speziell auf dieses Ökosystem angepasst sind. Weltweit bedecken sie eine Fläche von 137,760 km^2.

Mangroven sind ein wichtiger Bestandteil des natürlichen Küstenschutzes und können Schäden, verursacht durch Erosion, Tsunamis oder Hurrikans, abmildern. Außerdem beherbergen sie eine Vielzahl von marinen Lebewesen, die teilweise auch eine große ökonomische Bedeutung für die Fischerei besitzen.

Trotz ihrer wichtigen Ökosystemfunktionen für Land- und Wasserlebewesen sowie für die Sicherung der menschlichen Lebensgrundlage, haben Mangrovenwälder hohe Verlustraten, welche hauptsächlich durch menschliche Aktivitäten verursacht werden. Des Weiteren treten in diesen Wäldern auch besonders häufig natürliche Störungen auf. Dies ist mit der exponierten Lage entlang der Küstenregionen zu erklären.

Der Schwerpunkt dieser Arbeit liegt auf dem Einfluss der oben genannten natürlichen Störungen auf die Mangrovenwaldentwicklung, insbesondere hinsichtlich der folgenden Aspekte: die Beschreibung i) der Störungsmuster; ii) der raumzeitlichen Walddynamik; iii) die ökologische Rolle der Störungen; und iv) die Abschätzung der Anfälligkeit gegenüber Langzeitstörungen.

Die Untersuchungsgebiete für Feldstudien lagen in der Indian River Lagoon in Florida (USA) und im UNESCO Biosphärenreservat in Can Gio (Vietnam). Des Weiteren wurden theoretische Simulationen komplementär zu den Feldarbeiten durchgeführt.

Die Feldstudie in der Indian River Lagoon beschäftigt sich mit der Frage, wie Hurrikanstörungen die dynamischen Waldprozesse künstlich überfluteter Mangrovenwälder zur Mückenbekämpfung beeinflussen. In Can Gio wurde der Frage nachgegangen, ob Blitzschlagstörungen geeignet sind, um eine struktur- und artenarme Plantage in naturnahe Zustände zu überführen. Abschließend wurden in einer theoretischen Simulationsanalyse Blitzeinschläge und Hurrikanstörungen hinsichtlich homogenisierender und heterogenisierender Einflüsse auf die raum-zeitlichen Walddynamiken untersucht.

Die Ergebnisse der Felduntersuchung in der Indian River Lagoon zeigen, dass Teile des Waldes in einem höheren Sukzessionsstadium von den Hurrikanereignissen besonders betroffen waren. Ein großer Teil der Bäume war am Stamm gebrochen oder entwurzelt. Dagegen blieben Waldgebiete mit kleineren Bäumen und einer höheren Stammzahl weitgehend ungestört. Die großflächige künstliche Überflutung bestimmt die Artenselektion auf den hurrikangestörten Flächen und fördert *R. mangle*, welche am besten an das hohe Überflutungsregime angepasst ist. Allerdings wurde innerhalb dieser Aufstauungen auch verminderte Wiederbesiedlung mit Keimlingen in einigen Gebieten nachgewiesen.

Störungen können die Biodiversität der Mangrovenwälder ganz unterschiedlich beeinflussen. So führen großflächigen Aufstauungen zu einer Artdominanz von *R. mangle* in naturnahen Wäldern. Wohingegen kleinflächige Blitzeinschläge die Artenvielfalt in der monotonen Plantage in Can Gio erhöhen. Zusätzlich wurde eine Zunahme der strukturellen Komplexität innerhalb der Plantage festgestellt. Wiederbesiedelte Blitzeinschlagslücken, die durch geringere Baumhöhen gekennzeichnet sind im Vergleich zu der umgebenden Plantage, bleiben auf Windwurfflächen als „grüne Inseln" bestehen. Ausgehend von diesen Inseln können sich Samen ausbreiten und beschleunigen somit eine Widerbesiedlung auf den gestörten Flächen.

Die Simulationen ergaben, dass die untersuchten Störungsregime eine Homogenisierung in einem reich strukturierten, natürlichen gut entwickelten Wald nach sich zogen. Hinzu kommt, dass das Hurrikanszenario neben der Homogenisierung der räumlichen Struktur auch eine erhöhte temporäre Variation in der Walddynamik im Vergleich zu einem ungestörten Wald zeigte. Im Gegensatz dazu führten simulierte Blitzeinschläge nicht zu dieser zeitlichen Erhöhung der Schwankungen, obwohl beide Szenarien die gleiche Wahrscheinlichkeit des Baumabsterbens durch die Störungen aufwiesen.

Das Wechselspiel zwischen den einzelnen Störungsregime kann ganz unterschiedlich sein. So zum Beispiel haben großräumige Aufstauungen einen negativen Effekt auf die Wiederbesiedlung von hurrikangestörten Flächen in der Indian River Lagoon. Jedoch zeigen kleinflächige Blitzeinschläge einen positiven Einfluss auf die Regeneration von mittelgroßen Windwurfflächen in einer monotonen Plantage.

Basierend auf diesen Ergebnissen müssen geeignete Managementmethoden immer unter Beachtung von strukturellen Waldeigenschaften erfolgen, um die Artenvielfalt und Vernetzung ökologischer Prozesse, insbesondere auf renaturierten Flächen oder in

Plantagen, zu erhöhen. So könnten sich kleine Abholzungen innerhalb der Plantage in Can Gio als sinnvoll erweisen, um eine größere strukturelle und Artenvielfalt zu erlangen.

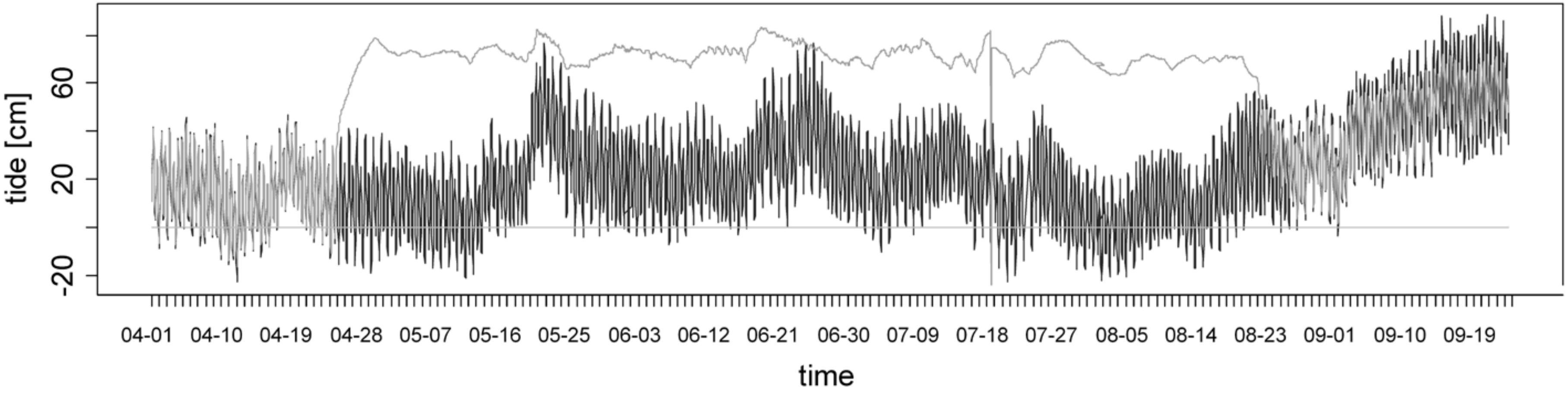
Natürliche Störungen werden als ein wesentlicher Bestandteil von Mangrovenwäldern angesehen und erfüllen spezielle ökologische Funktionen. Nichtsdestotrotz können Störungen zusätzlich zu veränderten Umweltbedingungen im Zusammenhang mit Klimawandel und direkten menschlichen Eingriffen die natürliche Entwicklung besonders in unnatürlichen Waldstrukturen wie in Plantagen oder Renaturierungsflächen gefährden.

Diese Arbeit gibt einen umfangreichen Überblick über verschiedene Störungsarten und deren Einfluss auf jeweilig betrachtete Mangrovenwaldsysteme. Hinsichtlich der Störungen wurden vom Menschen beeinflusste aber dennoch naturnahe Wälder, sowie angelegte Plantagen mit einer unnatürlichen Artenzusammensetzung und räumlichen Strukturierung untersucht. Dabei haben Felduntersuchungen und Simulationsanalysen zu etwa gleichen Teilen zu den Ergebnissen dieser Arbeit beigetragen.

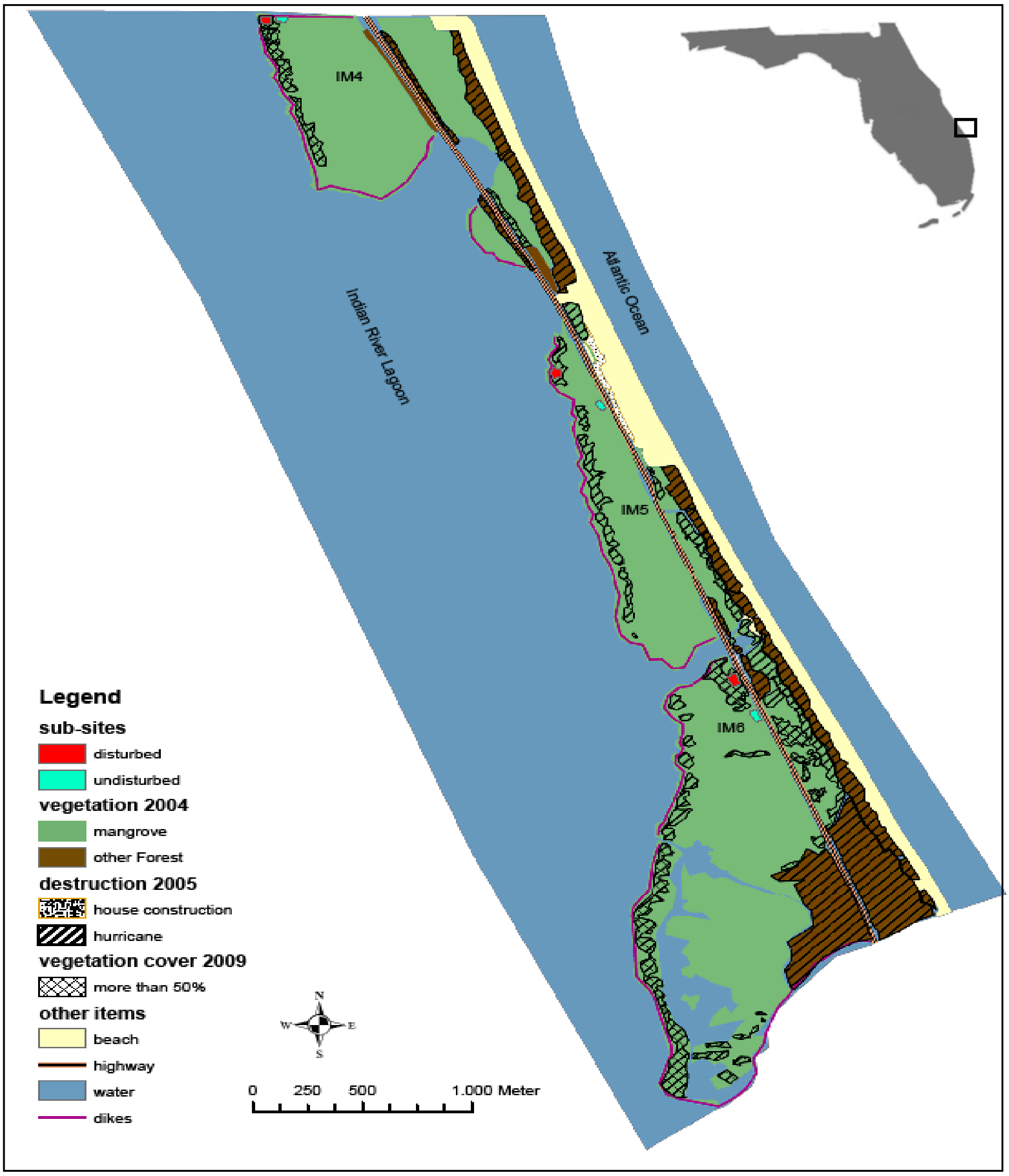
7 Appendix

List of appendices

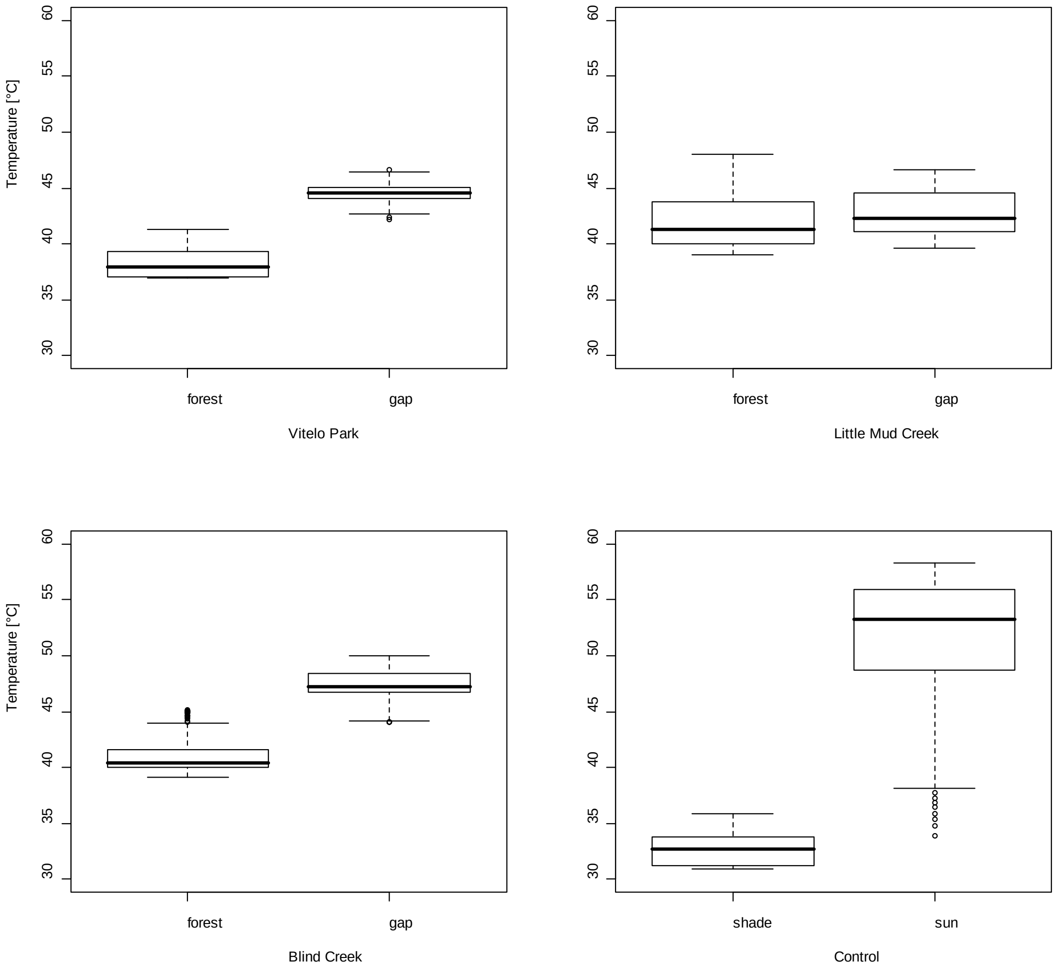
Appendix 1: Tide regimes of the Indian River Lagoon (dark gray line) and within the impoundments (light gray line) exemplarly illustrated for the Impoundment 5. The pumping within the impoundments started at 29th of April and stopped at the 22th September.



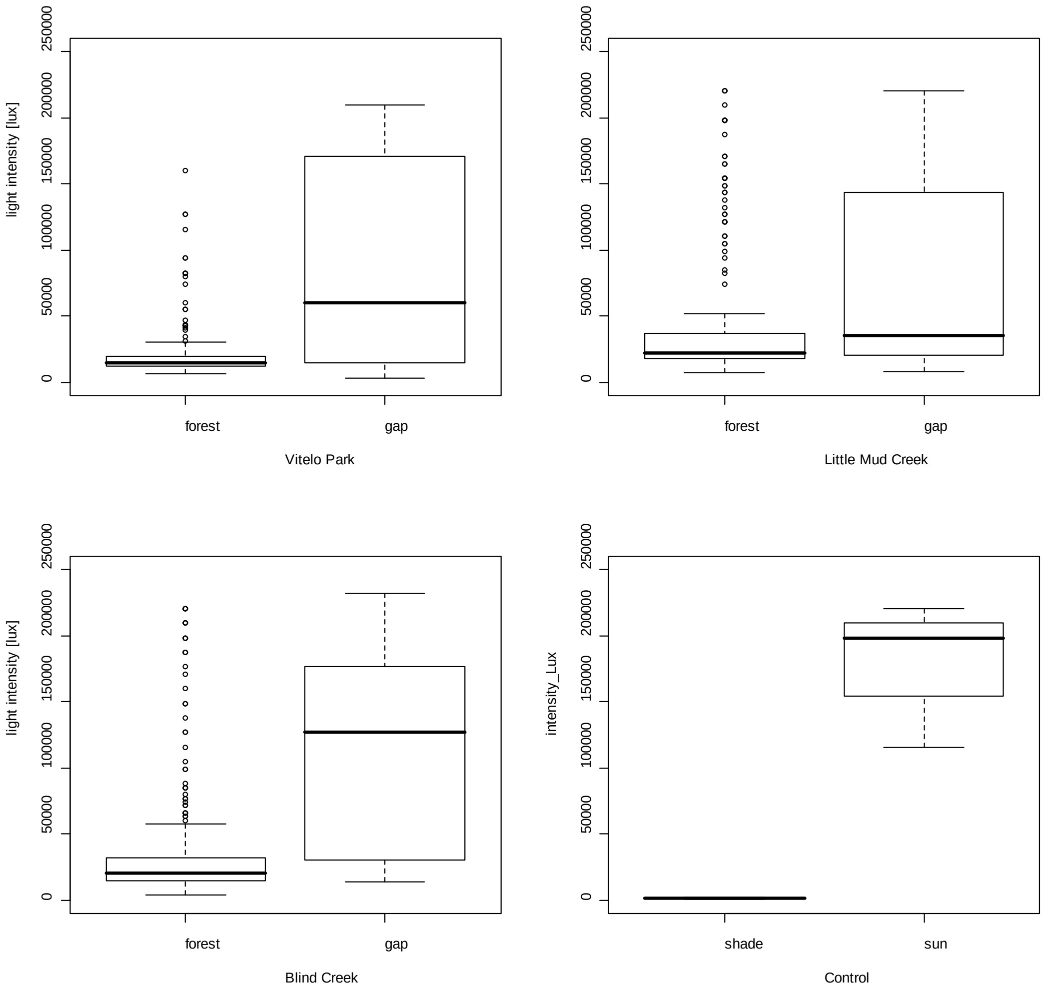
Appendix 2: Map of the study areas in the Indian River Lagoonbased on aerial photographs and compiled in ArcGis.



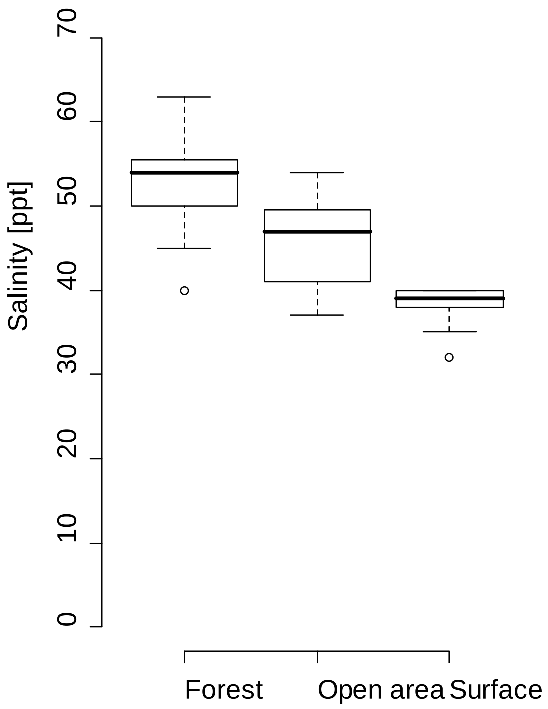
Appendix 3: Temperature measurements in 1.6 m height from the ground within the impoundments recorded on data logger.



Appendix 4: Light regime measurements in 1.6 m height from the ground within the impoundments recorded on data loggers:



Appendix 5: Pore water salinity measurements sampled in the intact forest, disturbed open areas and in the surface water within the impoundments.



Appendix 6: Field protocol of the Indian River Lagoon.
The tree data were used in this thesis and and the seedling data were used in the diploma thesis of Annegret Skóra.

Subplot tree protocol: Gap / Forest

Site: Transect ID: subplot ID: :

Date:………………….. time: ……………

worker: ……………

Site

GPS coord: x ……………….. y…………………..

Exposition……………

Distance to prior subplot:……… Distance to next subplot:……….

Distance to prior transect……… Distance to next transect……….

Photograph ID ……………

Dead woody debris (Shoots without roots):

Id										
Size class										
Length class										
…										

Dead woody debris with roots (4m x 4m):

Root id	Shoots	spec	condition	Bark y/n	Size class	height	Length class	expostion
…								

Subplot tree measurements (4m x 4m):

ID	Spec	x	y	height	10cm	dbh	damage	Fruit/flo	shoots	U dead	Crown1	Crown2	Condition
…													

Subplot seedling protocol: Gap / Forest:

Site: Transect ID: subplot ID: subplot tree ID:

Subplot seedling: (1m x 1m):

ID	Spec	x	y	height	Basal dmeter	Dbh 10cm	twig	Lnumber	Nr of interno	Distan interno	mix	Lshape
…												

Seedling (predation)

ID	Lcolor	stem	growth	shade	necrosis	herbivory	fungus	Wood damage	General health
…									

remarks:……
…

Appendix 7: Identification key for the field protocol.

Dead wood:
Condition:
1 – uprooted
2 – standing death
3 – root crown
Size class (DBH):
1 – (2.5 – 5 cm)
2 – (5.1 - 10 cm)
3 – (10 – 15 cm)
4 – (>15 cm) measure)
Length class:
1 – (0.5 - 1.5 m)
2 – (1.6 – 3 m)
3 – (3.1 – 5 m)
4 – (5.1 – 7.08m)
Tree plot:
Damage:
0 – no
1 – low
2 – high
Under the shade of dead wood/ roots:
0 – no
1 – yes
2 – roots
Seedling:
Mix:
Gf – over the hole area
Gw – in groups
Ew – single tree
Leaf shape:
1 – normal
2 – abnormal
3 – atrophy
Leaf color:
1 – green
2 – green yellow
3 – yellow
Stem:
g – straight
z – two or more shoots
v – shrub

Seedling:
Growth:
g – straight
k – kink
b – arch
Shade:
1 – sunshine
2 – half sunshine
3 – shade
4 – under water
Necrosis:
0 – no
1 – low
2 – high
3 – letal
Herbivory
0 – no
1 – low
2 – high
3 – letal
Fungus:
1 – yes
2 – no
Wood damage:
1 – yes
2 – no
w – top
z – twig
Leaf damage:
0 – no
1 - <10%
2- 11-50%
3 - 50-75%
4 - >75%
General health:
0 – good
1 – normal
2 – bad
3 – lethal

Appendix 8: Converted age calculation for parameter selection based on Shugart 1984 used for the sensitivity analysis of KiWi

$$age_{\max} = \frac{4*H_{\max}}{G} * \log\left\{ 2*(2*D_{\max} - 1)) + \frac{c}{2} * \log\left(\frac{\frac{9}{4} + \frac{c}{2}}{4*D_{\max} * D_{\max} + 2*c*D_{\max} - c} \right) - \left(\frac{c + \frac{c*c}{2}}{(c*c + 4*c)^{0.5}} \right) \right.$$
$$\left. * \log\left(\frac{3 + c - (c*c + 4*c)^{0.5} * (4*D_{\max} + c + (c*c + 4*c)^{0.5})}{3 + c + (c*c + 4*c)^{0.5} * (4*D_{\max} + c - (c*c + 4*c)^{0.5})} \right) \right\}$$

with c = 1-(137/H_{max}) which is an empirical parameter.

Appendix 9: Equating the tree mortality of two different disturbance regimes.

Probability for trees to get killed by lightning strikes:

$$P(die_{lighting}) = \frac{A_{lightning}}{A_{simulation}} = \frac{freq_{lightning} * radius_{lightning}^2 * \pi}{width_{simulation} * height_{simulation}}$$

where $A_{lightning}$ is the area of the lightning strike gaps, $A_{simulation}$ is the total simulated area expressed by the $width_{simulation}$ and $height_{simulation}$, $freq_{lightning}$ is the frequency of lightning strike occurrences, $radius_{lightning}$ is the radius of one circular lightning strike gap.

Probability for trees to get killed by hurricanes:

$$P(die_{hurricane}) = \frac{A_{hurr}}{A_{simulation}} * freq_{hurr} * \left(P(DBH \geq DBH_{hurr}) * mortality_{hurr1} + P(DBH < DBH_{hurr}) * mortality_{hurr2}\right)$$

$$= \frac{number_{hurrpatches} * radius_{hurr}^2 * \pi}{width_{simulation} * height_{simulation}} * freq_{hurr} * (p * mortality_{hurr1} + (1-p) * mortality_{hurr2}$$

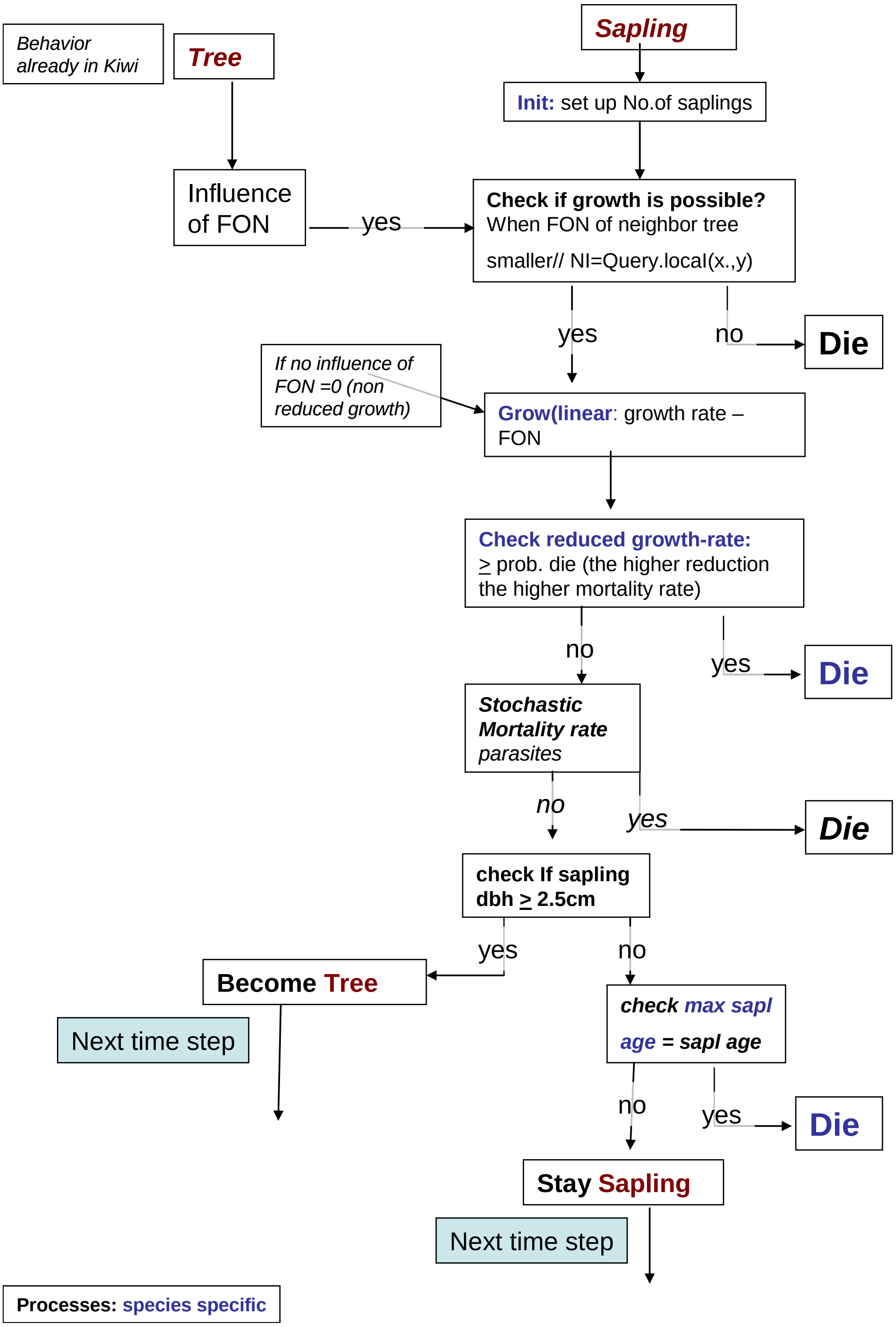
where A_{hurr} is the area of the hurricane patches consisting of $number_{hurrpatches}$ – the number of patches created by one hurricane event and the $radius_{hurr}$ – radius of one hurricane patch. $Freq_{hurr}$ is the frequency of hurricane occurrences. The following expressions are for the size dependent mortality caused by hurricanes, where larger trees (above the threshold DBH_{hurr} have a higher probability to die with the $mortality_{hurr1}$ and smaller trees with the $mortality_{hurr2}$.

The previous mentioned equations are equated to determine the $\text{radius}_{\text{hurr}}$:

$$P(die_{lightning}) = P(die_{hurricane})$$

$$radius_{hurr} = \sqrt{\frac{freq_{lightning} * radius_{lightning}^{2}}{freq_{hurr} * number_{hurrpatches} * (p * mortality_{hurr1} + (1 - p) * mortality_{hurr2}}}$$

Appendix 10: Flowchart of a seedling model concept
which could be integrated in the KiWi model.



Erklärung:

Hiermit versichere ich, dass ich die vorliegende Arbeit ohne unzulässige Hilfe Dritter und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt habe; die aus fremden Quellen direkt oder indirekt übernommenen Gedanken sind als diese kenntlich gemacht worden. Bei der Auswahl und Auswertung des Materials sowie bei der Herstellung des Manuskriptes habe ich Unterstützungsleistungen von folgenden Personen erhalten:

Kapitel 2: Investigating the role of impoundment and forest structure on the resistance and resilience of mangrove forests to hurricanes:

Zusammen mit Uta Berger, Cyril Piou und Ilka C. Feller wurden konzeptionelle Ideen zu dem Thema und die Struktur des Manuskriptes diskutiert. Annegret Skóra und Glenn Coldren unterstützten mich während der Feldarbeit. Des Weiteren erfolgte die Auswertung der Luftbilder durch Annegret Skóra unter meiner Anleitung im Rahmen eines studentischen Hilfsvertrages. Ilka C. Feller und Glenn Coldren waren wichtige Kooperations- und Ansprechpartner vor Ort in Florida. Alle Autoren waren an dem Korrekturlesen des Kapitels beteiligt.

Kapitel 4: Do canopy disturbances drive forest plantations into more natural conditions? – A case study from Can Gio Biosphere Reserve, Vietnam:

Uta Berger und Karen Diele waren an der Entwicklung der Thematik und der Strukturierung des Manuskriptes maßgebend beteiligt. Des Weiteren übernahmen sie die Leitung während der Feldarbeiten in Vietnam und erhoben die Felddaten zusammen mit vietnamesischen Studenten der Vietnam National University in Ho Chi Minh City. Markus Kautz übernahm vollständig die Analyse der Satellitenbilder. Martha Liliana Fontalvo-Herazo entwickelte eine Methode für die Parametrisierung der dominanten Mangrovenart im Modell. Zusammen mit Denny Walther wurden geeignete Indizes für die Strukturanalyse der Plantage und des Waldes diskutiert. Ulrich Saint-Paul und Tran Triet waren wichtige Kooperationspartner u.a. für die Unterstütung vor Ort und die Bereitstellung von Ressourcen, welches die Bereitstellung der Satellitenbilder und die Unterstützung bei den Feldarbeiten beinhaltet.

Kapitel 5: Testing the influence of different natural disturbance regimes on the spatio-temporal forest structure in frequently disturbed environments:

Zusammen mit Cyril Piou und Uta Berger wurden das Konzept und die Struktur des Manuskriptes entwickelt bzw. mögliche Analysen diskutiert. Alle Autoren waren an dem Korrekturlesen des Kapitels beteiligt.

Weitere Personen waren an der geistigen Herstellung der vorliegenden Arbeit nicht beteiligt. Insbesondere habe ich nicht die Hilfe eines oder mehrerer Promotionsberater(s) in Anspruch genommen. Dritte haben von mir weder unmittelbar noch mittelbar geldwerte Leistungen für Arbeiten erhalten, die im Zusammenhang mit dem Inhalt der vorgelegten Dissertation stehen.

Die Arbeit wurde bisher weder im Inland noch im Ausland in gleicher oder ähnlicher Form einer anderen Prüfungsbehörde zum Zwecke der Promotion vorgelegt.

Ich bestätige, dass ich die Promotionsordnung der Fakultät Forst-, Geo- und Hydrowissenschaften der TU Dresden anerkenne.

Dresden, den 31.01.2012,

Juliane Vogt