A Contemporary Approach to a Classic Model: Exploring the Influence of Local Interactions and Disturbance on Mangrove Forest Dynamics with a Spatially-Explicit Version of FORMAN

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A CONTEMPORARY APPROACH TO A CLASSIC MODEL:
EXPLORING THE INFLUENCE OF LOCAL INTERACTIONS AND DISTURBANCE ON
MANGROVE FOREST DYNAMICS WITH A SPATIALLY-EXPLICIT VERSION OF
FORMAN

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ABSTRACT

The mangrove forest gap dynamic model, FORMAN, was the first individual-based model (IBM) to simulate the long-term successional dynamics of three Caribbean mangrove species, *Avicennia germinans*, *Laguncularia racemosa*, and *Rhizophora mangle*. Assumptions under the spatially implicit approach of gap dynamic models limit their application to small-scale simulations. An expanded, spatially-explicit version of FORMAN was developed to allow for simulations of larger spatial grids, through the inclusion of localized soil conditions and neighborhood-based light resource competition. This expanded model was used to investigate the influence of localized interactions and disturbances of varying size on forest dynamics. A data-model comparison using field data from the Shark River Estuary in the Florida Coastal Everglades (FCE) tested the model’s ability to predict spatial relationships (inter-tree distances) based on tree size and species. The structure and function of the simulated mangrove forests were sensitive to complex interactions between localized soil and light competition based on neighboring trees. Under spatially varying soil conditions, neighborhood-based light competition limited tree growth (especially that of *A. germinans* and *L. racemosa*) in favorable soil zones, while allowing for sapling establishment in less optimal habitats. Forest recovery rates following disturbance were sensitive to both soil stress and disturbance size. *L. racemosa* experienced the greatest increase in annual productivity following disturbance, and exhibited a positive relationship between post-disturbance structure (biomass and basal area) and disturbance size. There was good agreement between the model and field data for frequencies of inter-tree distances and for the distribution of inter-tree distances when examined by size-class and by each species within sizes classes. However, there were no consistent differences or
trends in inter-tree distance probability distributions observed across size-classes or for species within size-classes. The expanded FORMAN model, while still limited to the km² scale in scope, is a very first step in increasing its spatial capability beyond the gap scale. This expansion potential is important in the context of climate change, as IBMs have been suggested as potentially useful tools in identifying and minimizing inaccuracies resulting from current methods of scaling biomass and productivity estimates from site to continental scales.
1. **INTRODUCTION**

Mangrove forests are highly productive intertidal wetland ecosystems located in tropical and subtropical regions between approximately 30°N and 37°S (Feller et al. 2010, Spalding et al. 2010, Mukherjee et al. 2014). Current estimates of the number of mangrove species worldwide range from 57 to 70 (Duke 1992, Ricklefs et al. 2006, Feller et al. 2010, Spalding et al. 2010, Mukherjee et al. 2014), representing 21 families (Feller et al. 2010). Mangrove ecosystems are found in a variety of geomorphological settings that vary in their climate, soil fertility and salinity, tidal amplitude, freshwater input, and other hydrological factors (Twilley et al. 1999, Feller et al. 2010). Despite inhabiting a wide geographic area and range of conditions, mangrove forests share a common trait – the presence of environmental stressors that typically include prolonged flooding, high salinities, anoxia, and toxic soil compounds (Lugo 1980, Ball 1996, Twilley & Rivera-Monroy 2005, Berger et al. 2008).

A suite of structural and physiological adaptations has allowed mangroves to cope with these stressors and has enabled them to establish in a variety of coastal landscapes with highly varied physical and chemical environments (Twilley et al. 1999, Feller et al. 2010). Soil conditions vary greatly between and within mangrove forests (Feller et al. 2010). Spatial differences in soil factors arise due to the combined effect of influences such as local topography and tidal gradients (Thom 1982, Twilley et al. 1996, Chen & Twilley 1998). Temporal differences in the soil environment are influenced by tidal cycles and seasonal changes in the balance between precipitation and evaporation (Provost 1973, Chen & Twilley 1998, Feller et al. 2010). Observed salinities in mangrove forests range from freshwater to hyper-saline conditions, which may be three times as concentrated as seawater (Feller et al. 2010). While
early literature widely regarded mangroves as salt-tolerant facultative halophytes, more recent studies show certain species to be obligate halophytes requiring salt to complete crucial life processes (Ball 2002, Feller et al. 2010, Wang et al. 2011). Mangroves show wide range of tolerances to salinity among species (McKee 1993, Chen & Twilley 1998). A greenhouse study by McKee (1993) found mangrove propagules of three species, *Rhizophora mangle*, *Laguncularia racemosa*, and *Avicennia germinans*, to have fairly equal growth rates in salinities up to approximately 45 g kg\(^{-1}\), with differential tolerance among the species beginning at 45 to 60 g kg\(^{-1}\) (Chen & Twilley 1998). Models (Chen & Twilley 1998) and field studies (Cintrón et al. 1978, Odum et al. 1982, Castañeda-Moya et al. 2006) have suggested maximum tolerated salinities for *R. mangle*, *L. racemosa*, and *A. germinans* to be 70 g kg\(^{-1}\), 85 g kg\(^{-1}\), and 100-140 g kg\(^{-1}\), respectively.

Nutrients associated with mangroves also vary spatially, ranging from oligotrophic conditions observed in some marine settings to highly concentrated conditions in areas receiving enriched effluent (e.g., agriculture and aquaculture - Alongi 2009, Feller et al. 2010). Temporal variation in nutrients arises from the cyclical and seasonal patterns in nutrient inputs and rates of cycling (Feller et al. 2010). Nutrient use efficiency among mangrove species spans a wide range, due to differences in both physiology (Naidoo 2009, Feller et al. 2009, Wanek et al. 2007, Lovelock & Feller 2003, Martin 2007, Lovelock et al. 2006, Feller et al. 2010) and structure (Duke 1990, Suárez 2003, Feller & Chamberlain 2007, Feller et al. 2010). *R. mangle* and *L. racemosa* possess adaptations that allow them to persist despite poor nutrient conditions (Feller et al. 2010). These differential tolerances to environmental stressors, which occur at the individual plant level, have been implicated as a driver of large-scale patterns in forest zonation,

Mangrove species also exhibit differential tolerance to flooding, with many species possessing specialized structures such as aerial roots and aerenchyma (Naidoo 1985, Feller et al. 2010) that allow them to persist despite potentially stressful soil chemical conditions that may develop following extensive periods of flooding (Gibbs & Greenway 2003, Feller et al. 2010). A key characteristic of many highly flood-tolerant species is vivipary (Farnsworth & Farrant 1998), in which reproduction occurs via the release of buoyant, photosynthetically-active propagules (Rabinowitz 1978, Stieglitz & Ridd 2001, Feller et al. 2010). Vivipary allows for dispersal of propagules over considerable distances (Nettle & Dodd 2007, Feller et al. 2010) acting as buffer for locally poor conditions.

The unique root structures found in mangrove forests create significant and diverse habitat that spans vertically from sublittoral through supralittoral regions and horizontally across the terrestrial-marine interface (Nagelkerken et al. 2008, Feller et al. 2010). The complex root systems, coupled with mangrove forests being located at the intersection between marine, freshwater, and terrestrial environments, results in very complex biological interactions and food webs associated with the habitat created by the roots (Feller et al. 2010, Mukherjee et al. 2014). Mangroves provide extensive habitat for many commercially important fish and invertebrates (Nagelkerken et al. 2008, Feller et al. 2010), and serve as nurseries (Nagelkerken et al. 2008, Feller et al. 2010) and rookeries (Feller et al. 2009, Mukherjee et al. 2014) for many species.
In addition to habitat to many fish and shellfish species, mangroves also contribute to other crucial ecological functions in coastal zones. Mangroves filter out sediments and pollutants (Feller et al. 2010, Mukherjee et al. 2014), which contribute to the low turbidity conditions required by photosynthetically-dependent neighboring seagrass and coral communities (Feller et al. 2010). Mangroves also contribute to shoreline stability and storm buffering through wind and wave attenuation (Feller et al. 2010, Mukherjee et al. 2014); an increasingly important function as climate change is expected to increase storm intensity (Doyle 1997) and increase coastal vulnerability to flooding due to sea level rise (Doyle 1997, Doyle et al. 2003). The role mangroves play in the global carbon cycle has potential implications on climate change (Feller et al. 2009, Mukherjee et al. 2014, Rovai et al. 2015). Recent studies suggest that mangroves forests contain more carbon per unit area than any other type of tropical forest (Donato et al. 2011, Mukherjee et al. 2014), and are substantial contributors to the pool of oceanic dissolved organic carbon (DOC) (Dittmar et al. 2006, Bouillion et al. 2008, Feller et al. 2010). Feller et al. (2010) state that mangroves are the source of an estimated 10% of total land-based oceanic DOC (Dittmar et al. 2006) and 15% of all stored carbon in oceanic sediments (Jennerjahn & Ittekkot 2002). On average, mangrove peat sequesters atmospheric carbon at a rate of 10.7 mol carbon m\(^{-2}\) yr\(^{-1}\) (Jennerjahn & Ittekkot 2002, Feller et al. 2010).

The complex interactions and rich life associated with mangrove ecosystems and the many roles they play in coastal ecosystems make them extremely valuable both ecologically and economically (Alongi 2008, Feller et al. 2010). However, these systems are highly susceptible to anthropogenic and natural disturbances, and losses of critical ecosystem services have occurred due to the alteration and loss of forest structure and function following
disturbances (Primavera 1997, Alongi 2008, Feller et al. 2010). Globally, it is estimated that the areal extent of mangrove forests has declined 30-50\% during the past half century (Balmford et al. 2002, Mukherjee et al. 2014). A survey of 106 mangrove experts conducted by Mukherjee et al. (2014) cites coastal development as the greatest threat to global mangrove forests, with tourism, the timber industry, aquaculture, natural disasters, climate change, oil spills, and infestation and disease cited as the other major threats.
2. MODELS OF MANGROVE COMMUNITIES

Simulation models are regarded by many to be essential to effective mangrove management and restoration efforts (Twilley et al. 1999, Doyle et al. 2003, Field 1998 & 1999, Duke et al. 2005, Twilley & Rivera-Monroy 2005, Berger et al. 2006, Poiu et al. 2006, Fontalvo-Herazo et al. 2011, Berger et al. 2008). Ecological models are important and powerful tools that can provide insight into the dynamics of complex systems, such as mangrove forests. Through simulation, models allow for experiments that would otherwise be impractical or even impossible in field conditions, and allow for the identification, investigation, and prediction of specific processes that are not well understood or are difficult to measure in the field (Berger et al. 2008).

Mangrove models, like all ecological models, also have disadvantages and potential weaknesses. Models are over-simplified representations of complex systems and can therefore be missing important processes. A current major challenge in mangrove modeling is the ability to accurately simulate forest processes at large spatial scales, for example at the continental level (Rovai et al. 2015, Shugart et al. 2015). This limitation is due to uncertainties about how local and meso-scale interactions combine to form large-scale dynamics and the present limited availability of large-scale data with which to validate such model predictions (Rovai et al. 2015, Shugart et al. 2015). This challenge is further compounded by a lack of understanding of forest response to global-scale climate change (Shugart et al. 2015).

The earliest mangrove forest models were functional models (e.g., Odum & Heald 1975) that represented energy flow in detrital food webs. Following these functional models, came the development of the first simulation model by Lugo et al. (1976), which investigated the
response of mangrove primary productivity to various hydrological scenarios (Berger et al. 2008). Later models further focused on the geomorphology (Thom 1982, Semeniuk 1985, Woodroffe 1992) and hydrology (Twilley & Rivera-Monroy 2005) of mangrove forest systems (Mukherjee et al. 2014). Feller et al. (2010) explain that while these process-based models have been used for a variety of applications, their ability to explain the emergence of large-scale forest structural patterns is hindered by a lack of explicit consideration of individual trees’ interactions with their biological, physical, and chemical environment (Rivera-Monroy et al. 2004). Unlike functional and process-based models, individual-based models (IBMs) explicitly include the characteristics and behaviors of each individual through time, providing greater insight into how individuals combine to result in the system’s higher-level emergent properties (Feller et al. 2010).

Early forest growth dynamic IBMs modelled relatively small (typically a few hundred square meters) forest gaps, in which openings in the canopy developed as the result of a disturbance such as a treefall or lightning strike (Botkin et al. 1972, Shugart 1984). Among the earliest of such models were JABOWA (Botkin et al. 1972) and FORET (Shugart 1984) that simulated growth dynamics for multispecies temperate forests in the northern and southern United States. FORMAN, a gap dynamic model which utilizes the general design of JABOWA and FORET, has been applied to mangrove species dynamics (Chen & Twilley 1998).

The FORMAN model of Chen & Twilley follows the general JABOWA-FORET approach and represents the annual reproduction, growth, and mortality of individual trees of three species, *Avicennia germinans*, *Laguncularia racemosa*, and *Rhizophora mangle*. In FORMAN, soil salinity and nutrient availability are homogeneous within the modelled gap (spatial domain),
light resource availability is calculated per height class, and individual tree location is implicit (Chen & Twilley 1998). Applications of the FORMAN model include investigating forest growth under various conditions of environmental stress and resource availability (Chen & Twilley 1998), projecting forest recovery following hurricane disturbance in southern Florida, USA (Chen & Twilley 1998), and comparing various restoration scenarios of mangroves in the Ciénaga Grande de Santa Marta estuary at the mouth of the Magdalena River in Colombia (Twilley et al. 1999).

Berger & Hildenbrandt (2000) stressed the importance of considering the inherently spatial nature of ecological processes, stating the spatially implicit approach of gap style forest models as their major limitation. This lead to the development of KIWI (Berger & Hildenbrandt, 2000), an IBM in which tree location and competition are modelled explicitly. This spatially explicit consideration is achieved through the “field of neighborhood” (FON) concept, in which each individual tree is encircled by a zone within which it competes for resources (Berger & Hildenbrandt 2000). While light resource availability is not explicitly modelled in KIWI, general competition is calculated as a function of the degree of overlap of neighboring trees’ FONs (Berger & Hildenbrandt 2000). The FON approach is based on the “zone of influence” (ZOI) concept (Czárán 1998); however, in contrast to ZOI, the intensity within the FON is not constant, accounting for the decreasing influence of competition with increasing distance from a tree’s stemming point (Berger & Hildenbrandt 2000). Since its inception, KIWI has been used in a variety of applications, including predicting succession in a Brazilian forest following clear-cutting and agricultural usage (Berger et al. 2006). KIWI has also been used to investigate a variety of theoretical concepts (Berger et al. 2008), including asymmetric competition (Bauer et
al. 2004), self-thinning (Berger and Grimm 2004, Khan et al. 2013), and the intermediate disturbance hypothesis (Piou et al. 2008).

A third mangrove IBM (MANGRO - Doyle 1997, Doyle & Girod 1997, Doyle et al. 2003) focuses on the three-dimensional consideration of individual trees’ aboveground structures (Doyle 1997, Berger et al. 2008). MANGRO was designed to investigate the response of mangroves in the Everglades of southern Florida to climate change, sea level rise, and various water management scenarios (Doyle 1997, Doyle & Girod 1997, Berger et al., 2008). This spatially-explicit model is typically run at larger spatial scales (1 ha or greater), and can be run in conjunction with SELVA, a higher-level model which predicts and sets landscape variables and environmental conditions for the modeled forest stand (Doyle 1997, Berger et al. 2008).

These models, as well as others, have become important tools in predicting mangrove responses to both natural and anthropogenic alterations, and it has been recommended that such models be utilized to help understand mangrove dynamics and to aid in the design of management and restoration plans (Twilley et al. 1999; Doyle et al. 2003; Twilley & Rivera-Monroy 2005; Berger et al. 2008). In this thesis, I use an expanded version of the FORMAN model that accounts for the explicit spatial location of trees within the model domain to explore mangrove responses to variation in environmental conditions (light, nutrient availability, and salinity), disturbances, and compare predictions of inter-tree distances to a detailed field dataset.
3. RESEARCH OBJECTIVES AND THESIS ORGANIZATION

It has been suggested that in order for models to most effectively simulate the major processes that govern forest structure and function, they must take into account the spatial nature of the system (Berger et al. 2008). Berger & Hildenbrandt (2000) state the need for "[...] explicit consideration of the continuous space" as a major driver for developing their mangrove model KIWI. A key assumption of many forest gap dynamic models is that in a relatively small forest gap (a few hundred square meters), trees shade all other trees shorter than themselves and experience the same nutrient availability and salinity conditions (Chen & Twilley 1998, Berger et al. 2000). This restricts the application of these models to small-scale systems, as this assumption would become increasingly unrealistic at larger spatial scales.

The first objective of this research was to develop a spatially explicit version of the original mangrove model FORMAN, in which the exact location of individual trees of three species (*Avicennia germinans*, *Laguncularia racemosa*, and *Rhizophora mangle*) is simulated. This would allow application of the model to geographic areas larger than a forest gap. Keeping track of the spatial locations of individual trees enables representation of the localized (within grid) interactions between trees (i.e., shading by neighboring trees) and between individual trees and their soil environment (Ellison 2002, Clarke 2004, Berger et al. 2008). I used the model developed by Chen & Twilley (1998) and expanded it to simulate the continuous locations of individual trees on a rectangular spatial grid with the capabilities of only some trees shading others and with trees experiencing different nutrient and salinity conditions. The expanded model incorporates both the ZOI (Czárán 1998) and FON (Berger & Hildenbrandt 2000) approaches, allowing for explicit consideration of light competition among neighboring
trees, and by assigning nutrient availability and salinity unevenly across the cells of the grid, also allows for the representation of localized soil conditions.

Three simulation experiments were performed using the spatially explicit version of Chen & Twilley’s mangrove FORMAN model. First, the expanded version was used to investigate the influence of localized effects (salinity, nutrients, light) on the overall structure and function of the resulting forest. The model was run under varying combinations of localized effects of soil and light ("new" expanded spatially-explicit version of the model) and "original" gap version of the model in which all trees affect each other and soil conditions are uniform. I refer to the version with localized soil effects as gradient (versus uniform for the original version), and with the neighborhood effects on shading as distributed (versus lumped for the original version). Model predictions of species-specific and total forest basal areas, biomass, annual productivity, and size class distributions were compared between the localized (gradient soil and distributed shading) and original (uniform soil and lumped shading) versions.

The second simulation experiment focused on the effect of various-sized disturbances on forest structure and productivity during recovery. The ability to model disturbances at different spatial scales has been identified as another essential capability of forest dynamics models (Ellison 2002, Clarke 2004, Berger et al. 2008). Because the new spatially-explicit version allows for localized effects, a wide range of disturbances (beyond gap sized) were able to be simulated. Model predictions of species composition, productivity, and biomasses in and outside of the affected areas were compared at various time points after the disturbances were imposed.
The third simulation experiment tested the model using field data of spatial relationships among trees of the three species. The model simulated very roughly the conditions in the Shark River Estuary in the Everglades of Florida, and predicted probability distributions of inter-tree distances were compared to measured values (Rivera-Monroy, unpublished data) from multiple sites. Because the areas monitored were small (gap-sized), I used uniform soil conditions with the distributed shading approach of the new model.

This thesis is organized as follows. I next present a description of the expanded (spatially-explicit) version of the FORMAN model of Chen & Twilley (1998). The majority of parameter values utilized in this research are those reported in Chen & Twilley (1998) to simulate forests of the Shark River Estuary located in the Everglades of Florida, USA. All parameter values, including deviations from values reported in Chen & Twilley (1998), are reported in Table 5 of Appendix A. This is followed by a summary of the design of the three simulation experiments, including the grid dimensions, nutrient availability and salinity values assigned to the cells on the grid, disturbance effects (experiment 2), and the timing of model outputs related to forest composition, biomasses, and (for experiment 3) spatial arrangement. Model results are then presented for each of the experiments. I conclude with a discussion about the implications of the simulation results, strengths and caveats of the modeling, and areas for future modeling and data collection.
4. MODEL DESCRIPTION

4.1 Overview

The model is a spatially-explicit version of the FORMAN model developed by Chen & Twilley (1998) for mangroves. The model simulates mangrove forest succession through the yearly reproduction, growth, and mortality of individual trees of three species, *Avicennia germinans*, *Laguncularia racemosa*, and *Rhizophora mangle*. Two life stages are delineated: sapling and adult. Reproduction is represented as the number of saplings of each species that are added to the simulated model spatial grid per year, which is dependent on the available light beneath the forest canopy. Surviving saplings become adults. Growth of adults is simulated as species-specific optimal annual growth, adjusted for salinity, temperature, and the availability of nutrients and light. Annual mortality of adults is represented by two sources: species-specific maximum age and growth suppression. Individual trees (saplings and adults) are located in continuous space on a horizontal grid of square cells.

A new feature of the model is the ability to represent localized soil and shading effects. Explicit locations of each tree allow for subsets of trees (rather than all trees) to affect each other via shading (distributed), and for individual trees to experience the local environmental conditions as defined by the nutrient availability and salinity values assigned to their cell (gradient). I used the label “gradient” because the nutrient availability and salinity values were assigned to cells with monotonically changing patterns (e.g., high to low from the left edge to right edge). When the new version of the model is set-up to have all trees shading each other (lumped) and nutrient availability and salinity is uniform across the grid (uniform), the new version defaults to the original Chen & Twilley gap version of the FORMAN model.
Simulations use a one year time step and simulate up to 250 years. Model output variables include the species identifier and continuous and cell location of each sapling and adult tree, the diameter at breast height (dbh, cm) for each adult tree, which is determined by growth, and leaf area and height of each adult tree, which are assumed allometric functions of dbh. The model was coded in NetLogo version 5.3.1. The model description below is from the Chen & Twilley version, modified and updated for the capability to simulate the localized effects; detailed equations and parameter values are presented in Appendix A. The rationale for equations and parameter values for simulation of mangroves located in the Everglades National Park (Shark River Estuary) in south Florida, USA are described in Chen & Twilley (1998).

4.2 Grid Configuration and Environmental Variables

The modeled spatial area (domain) is represented as a two-dimensional grid of cells. Each cell is assigned a value of salinity and nutrient availability; temperature is represented as a degree-days variable repeated each year and is assumed uniform across the grid. Simulations used values of salinity between 10 and 100 g kg\(^{-1}\), based on values observed globally across mangrove forests (Feller et al 2010, Twilley et al. 1999, Castañeda et al. 2006), and in some cases, observed within forests (Twilley et al. 1999, Castañeda et al. 2006).

Relative nutrient availability (RNA) is defined as a value from 0 to 1.0; Chen & Twilley defined species-specific growth responses to RNA based on greenhouse studies by McKee (1995). Nutrient limitation of growth in mangrove forest systems has been attributed to the availability of either nitrogen or phosphorus, depending on the particular forest studied (Lugo & Snedaker 1974, Boto & Wellington 1984, Lugo et al. 1988, Clough 1992, Twilley 1995). Studies by Chen (1996) found that the mangrove forests of southern Florida, which the Chen & Twilley
version was designed to simulate, to be phosphorus-limited systems. Given the positive correlation between total phosphorus and available phosphorus in the south Florida mangrove systems (Chen 1996; Chen & Twilley, 1998), total phosphorous was used by Chen & Twilley as an indicator to derive RNA values for their analyses. Based on their values, values of RNA are assigned to cells for model analyses reported here and used to adjust annual tree growth.

Temperature is represented as heat accumulation via annual growing degree-days (DEGD). A value of DEGD is computed within the model (Appendix A, Equation 4) using averaged January and July temperatures, and then used in model simulations to affect annual tree growth. Light is specified as the fraction of incident light intensity at the top of the forest canopy (or individual tree) based on the degree of shading by neighboring taller trees. The fraction of incident light experienced by each tree is used to adjust their growth rate.

4.3 Reproduction

At the beginning of each model year, a random number of saplings (constrained by species-specific maximum values) are added to each population. These saplings are then assigned a random continuous location on the grid and associated cell number, and the available light at their new location determines if they survive. Like other individual-based mangrove models, FORMAN does not explicitly consider seedling dispersal, instead, propagules are assumed widely distributed, and the model starts with those propagules that have successfully established and grown to achieve sapling status. Survivors are considered adults, assumed to have a dbh of 1.27 cm, and allowed to grow and experience mortality.
4.4 Growth

Tree growth is represented as the annual increase in dbh (cm), and is affected by the available light adjusted for shading, salinity and nutrient availability of the cell, and the assumed value of degree-days. A maximum growth rate is calculated for each tree based on its dbh and height. All of the environmental variables are converted (normalized) to values between zero and one. The one exception is the light effect on *L. racemosa*, which assumes a value of 1.2 at optimal light levels. The realized annual growth increment in dbh is then the product of the maximum value and the four (salinity, nutrient availability, temperature, and light) normalized factors. The salinity effect on growth uses a monotonically decreasing function from zero to one, the light (see below) and temperature effects are monotonically increasing functions, and the RNA effect has a peak around 0.9. The shapes of the functions differ among the three species.

The calculation of the available light (the x-axis of the multiplier effect) depends on the other trees on the grid. Both field studies (Wadsworth 1959; Ball 1980; Roth 1992) and greenhouse studies (McKee 1995) document differential tolerance to shading, with *L. racemosa* being the least shade-tolerant and exhibiting a competitive advantage at higher light levels (McKee 1995; Chen & Twilley 1998). The light reaching an individual tree is calculated as the fraction of incident light passing through the overlying canopy, within which the cumulative leaf area acts as a light-attenuating filter. I use a zone of influence approach (Czárán 1998) whereby each tree is located at the center of a circle defined by the length of its “sensing radius”. The sensing radius is a function of the tree’s dbh. Incident light is adjusted for the area of the circle of each tree to obtain the light available to that tree. Trees are only shaded by those trees taller
and whose sensing radii overlap with their own. I parameterized the zone of influence approach using information for a model of Caribbean mangrove species that used the related “field of neighborhood” approach (Berger et al. 2000, Piou et al. 2008).

4.5 Mortality

At the end of each model year (reproduction and growth are evaluated first), each tree is assigned a probability of death. Probability of death was determined by two factors: age and growth suppression. Trees with an annual growth increment of less than 0.01 cm for two consecutive years experience mortality due to growth suppression. If a tree did not show growth suppression, then the probability of death was from old age that increased with age dependent on the assumed maximum age for that species. A uniform random number between 0 and 1 is generated for each tree each year, and if less than the probability of death, the tree is removed from the simulation.

4.6 Initial Conditions

All simulations start from “clear-cut” conditions with one sapling of each of the three species assigned random coordinates on the grid. Each cell is assigned a value for salinity (g kg⁻¹) and RNA; a single value of DEGD is specified. The model is considered a time discrete (difference equation) model with a time step of 1 year. Processes are calculated within each year as reproduction, growth, and mortality. Model outputs for a year are the values of location, dbh, height, annual growth, and biomass at the end of that year.
5. **MODEL SIMULATIONS**

5.1 **Exercise 1: Effects of Localized Interactions**

Salinity, RNA, and shading effects were compared between the approaches of the “original” FORMAN model (uniform salinity and RNA, and lumped shading in which trees affected all trees shorter than themselves, regardless of location,) and the “new”, expanded version of FORMAN (where salinity and RNA varied as gradients across cells and shading was computed using a distributed approach using only neighboring trees). Starting from a cleared plot, the model simulated 4 ha comprised of a 20 x 20 grid of 10m x 10m cells. A buffer of 20 m (2 rows and 2 columns) was added to the 20 by 20 cells to minimize edge effects (i.e., trees near edge not affected by trees in all directions). Simulations assumed a constant climate, (30-year mean monthly temperate data for Miami, FL obtained from NOAA (a)), and a maximum sapling recruitment rate of 30 saplings per 500 m$^2$ for each of the three species.

The distributed versus lumped approaches for light effects were represented by how the sensing radius values were specified. The cumulative shading effect of neighboring trees at a given location has been implicated as a key factor in affecting tree growth and sapling recruitment (Hildenbrandt & Berger, 2000). When realistic values were used based on the dbh of each tree (Equation 18, Appendix A), then only nearby trees affected the available light to each tree (distributed). Specification of the sensing radii of all trees to be longer than the width of the 4 ha grid results in the model defaulting to the “gap version” (lumped) where all trees affect (shade if taller) all other trees in the 4 ha grid.

For the localized (gradient) soil conditions, salinity was specified as linearly increasing from 10 g kg$^{-1}$ to 100 g kg$^{-1}$ along the vertical axis (rows) of the grid, while RNA linearly
decreased from 1 to 0 along the horizontal axis (columns) of the grid plot (Figure 1). For the original gap-based version, “uniform” soil conditions, RNA and salinity were constant across all cells and set to average values of their gradient conditions (0.5 and 55 g kg\(^{-1}\), respectively). The spatial variation in salinity and RNA in mangroves is the result of the combined influence of multiple factors including tidal flooding, freshwater inputs, and local topography (Boto & Wellington 1984; McKee 1995a, Chen 1996, Chen & Twilley 1998). I used simple gradients in both salinity and RNA that encompass a wide range of conditions to emphasize how any species-specific differences would be affected by spatial variation in environmental conditions. The majority of the salinity and RNA combinations on the grid represent naturally and commonly occurring combinations of soil factors observed in mangrove forests, while two of the corners (top-left and bottom-right) represent observed but rare conditions (Figure 1). The top-left dashed area is representative of hypersaline systems such as the degraded forests of the Ciénaga Grande de Santa Marta estuary of Columbia; conditions were greatly influenced by highway construction that impeded freshwater inflow (Twilley et al. 1999). The bottom-right dashed region is representative of conditions in systems, such as the Everglades of Southern Florida, that occur due to chemical interactions with the overlying carbonate platform and freshwater sheet flow from water management activities (Chen 1996, Doyle et al. 2003).
Twenty replicate model runs starting from clear-cut conditions were performed for each of four possible treatment combinations of uniform versus gradient soil conditions and lumped versus distributed shading (Table 1). Predictions of species-specific basal area, biomass, annual productivity, and size class distributions (for the entire 4 ha grid) were compared among the four treatments at model years 35, 100, and 250. Due to temporal shifts in the competitive balance among the three species, these time intervals were selected to capture forest dynamics at early (year 35) and later stages (years 100 and 250) of forest development.
Table 1. Four simulation treatments resulting from all possible combinations of uniform and gradient soil conditions and lumped and distributed shading.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Shading</th>
<th>Soil Conditions</th>
<th>Salinity value (g kg⁻¹)</th>
<th>RNA value</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Distributed</td>
<td>Uniform</td>
<td>55</td>
<td>0.5</td>
</tr>
<tr>
<td>2</td>
<td>Distributed</td>
<td>Gradient</td>
<td>10 - 100</td>
<td>0 – 1.0</td>
</tr>
<tr>
<td>3</td>
<td>Lumped</td>
<td>Uniform</td>
<td>55</td>
<td>0.5</td>
</tr>
<tr>
<td>4</td>
<td>Lumped</td>
<td>Gradient</td>
<td>10 - 100</td>
<td>0 – 1.0</td>
</tr>
</tbody>
</table>

5.2 Exercise 2: Disturbance Scale

Disturbances of varying size, from small lightning gaps to large-scale hurricanes, are common in mangroves forests and alter the spatiotemporal availability of resources such as light, which in turn can affect forest structure and function (Lugo 1980, Lugo 2000, Tilman, 1988, Smith 1992, Smith et al. 1994). In this exercise, I investigate the effect of varying disturbance sizes (area, m²) on the simulated long-term (100 years post-disturbance) successional trajectories of the three mangrove species under various soil conditions.

As in exercise 1, the model simulated a 4 ha plot comprised of a 20 x 20 grid of 10m x 10m cells. Simulations assumed a constant climate (30-year mean monthly temperate data for Miami, FL obtained from NOAA (a)), and a maximum sapling recruitment rate of 30 saplings per 500 m² for each of the three species. RNA and salinity remained uniform across all cells within each simulation, while shading used the distributed approach to allow for neighborhood interactions among trees. Three soil conditions (treatment combinations) were simulated (Table 2). Soil Treatments 1 and 2 are representative of conditions returning to pre-alteration (benign) conditions after disturbances such as the water management and restoration efforts which occurred following anthropogenic alteration of water flow in the Ciénaga Grande de Santa Marta estuary of Columbia (Twilley et al. 1999). Soil Treatment 3 represents a more naturally and commonly co-occurring stressful salinity and RNA condition observed in
mangrove forests (or regions of forests); typically reflective of limited freshwater (and
associated nutrient) inputs.

Twenty replicates of each of the three homogeneous soil treatment conditions (Table 2)
were run under each of the five disturbance scenarios in Table 3. Each simulation started from
clear-cut conditions (one sapling per species) with the forest allowed to develop undisturbed
until model year 100, at which point a disturbance occurred in the center of grid. The
disturbance caused complete mortality to all trees within the disturbance area. Following the
disturbance, the entire forest continued to grow for another 100 years. Forest recovery in the
disturbed zones was investigated among the treatments through the outputs of species-specific
and total forest basal area and biomass 35, 75, and 100 years post-disturbance (to capture
species-specific recovery dynamics at early and later stages of development), and through the
generation of a time series of species-specific and total forest annual productivity for trees
within the disturbance zone.

Table 2. Soil treatments and corresponding salinity and RNA conditions and values.

<table>
<thead>
<tr>
<th>Soil Treatment</th>
<th>Salinity Condition</th>
<th>Salinity (g kg⁻¹)</th>
<th>RNA Condition</th>
<th>RNA</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Stress</td>
<td>60</td>
<td>Benign</td>
<td>0.7</td>
</tr>
<tr>
<td>2</td>
<td>Benign</td>
<td>30</td>
<td>Benign</td>
<td>0.7</td>
</tr>
<tr>
<td>3</td>
<td>Stress</td>
<td>60</td>
<td>Stress</td>
<td>0.4</td>
</tr>
</tbody>
</table>

Table 3. Disturbance scenarios and the area and percent of model grid affected.

<table>
<thead>
<tr>
<th>Disturbance Scenario</th>
<th>% of total simulated area</th>
<th>Area of disturbance (m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>0.0125</td>
<td>500</td>
</tr>
<tr>
<td>3</td>
<td>5</td>
<td>2000</td>
</tr>
<tr>
<td>4</td>
<td>50</td>
<td>20,000</td>
</tr>
<tr>
<td>5</td>
<td>100</td>
<td>40,000</td>
</tr>
</tbody>
</table>
5.3 Exercise 3: Model-Data Comparison (Inter-tree Distance)

Among the critical steps in the development of a meaningful and useful model is the testing of model performance against real world data. The third and final simulation exercise tested the model’s ability to predict inter-tree distances among individuals of three species. Model output was compared to field data collected in 2015 (Rivera-Monroy, unpublished data) from two sites in the Shark River Estuary located on Florida’s west coast, within Everglades National Park (ENP).

The contiguous mangrove forests of the Everglades are among the most expansive found along the Gulf Coast of the United States (Chen & Twilley 1998), with a total areal coverage estimated at 144,447 ha (Simard et al. 2006, Castañeda-Moya et al. 2013). Although mangrove forests have been present in this region for thousands of years (Scholl 1964a and b, Chen & Twilley 1998), frequent disturbances such as hurricanes, have resulted in forest stands that are fairly young and homogeneous with respect to age (Chen & Twilley 1998, Lugo & Snedaker 1974, Snedaker 1982). Environmental conditions vary along the Shark River estuary, with flooding frequency, salinity, and RNA (total phosphorus) decreasing with increased distance inland from the estuary mouth (Chen & Twilley 1998 and 1999, Castañeda-Moya et al. 2013). Approximate salinity and total phosphorus values range from 27 g kg⁻¹ and 0.2 mg cm⁻³ at an inland distance of 4.1 km to 4.6 g kg⁻¹ and 0.05 mg cm⁻³ at a distance of 18.2 km inland from the estuary mouth (Castañeda-Moya et al. 2013, Danielson et al. unpublished manuscript). Factors including site-specific disturbance histories, and the environmental gradients present along the longitudinal axis of the estuary, contribute to the variable forest structure (e.g., species composition/dominance and average tree height) observed along Shark
River, with average tree height increasing from approximately 5 m upstream to approximately 13 m near the river mouth (Castañeda-Moya et al. 2013, Danielson et al. unpublished manuscript).

For exercise 3, I utilized field data for two sites, Shark River Slough (SRS) 5 and 6, which are located 9.9 km and 4.1 km upstream from the estuary mouth (Figure 2) and are part of the Florida Coastal Everglades Long Term Ecological Research program (FCE LTER). These field sites are partitioned into two 20m x 20m plots. The datasets (provided by Rivera-Monroy, unpublished data) for each plot included the following information for all trees (with a dbh of 2.5 cm or greater) present in the plot at the time of sampling (2015): spatial data (tree distance from a specified waypoint), species, dbh, tree tag number, and status (dead or alive). For the model-data comparison, I utilized the spatial data for individual trees that had been converted from waypoint data to Cartesian coordinates (distance of each tree (m) from a single reference point; 0,0), using Mangrove Map Version 1.1 software (Pudipeddi & Rivera-Monroy 2003). A two-dimensional spatial map of trees was then generated in NetLogo for each plot, using the converted coordinate values, tree species, and dbh as inputs. Only trees whose status was denoted as “Alive” in the original dataset were included in this spatial map.

For the simulations, I used environmental conditions similar to those reported for the Shark River sites. Values used for temperature, RNA, and salinity are shown in Table 5 (Appendix A). The model simulated a 400m² plot comprised of a 2 x 2 grid of 10m x 10m cells, surrounded by a 20 m buffer around the sample plot’s perimeter. Simulations assumed a constant climate; DEGD was computed from a 54-year mean monthly temperate dataset for NOAA (b) National Climate Data Center (NCDC) Royal Palm Ranger Meteorological Station.
The model used uniform soil conditions because of the small area of the plots, and distributed shading to allow for any neighborhood effects.

Simulations started from clear cut conditions, and were run until model year 65, at which time I judged that the simulated population demographics (density and maximum dbh) were roughly similar to field data. Initial simulations utilized the site-specific sapling recruitment values published in Chen & Twilley (1998); however, these recruitment values resulted in higher tree densities compared to reported field values. In order to determine appropriate site-specific sapling recruitment rates, a sensitivity analysis, similar to that done by Chen & Twilley (1998),
was performed to determine sapling rates. During this analysis, the mean species-specific densities from 30 replicates (per recruitment scenario) were compared to field plot data in order to determine the best-fitting recruitment values for each of the two sites. Final recruitment values (maximum number of saplings added per 400 m² plot, annually) used in Exercise 3 were as follows for \textit{A. germinans}, \textit{L. racemosa}, and \textit{R. mangle}, respectively: 1,1,8 (Site SRS 5); 1,2,3, (Site SR 6) (Table 5, Appendix A).

Table 4. Size classes used to group inter-tree distances for the model-data comparisons.

<table>
<thead>
<tr>
<th>Size Class</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td>dbh (cm)</td>
<td>\leq 5</td>
<td>5 &lt; dbh \leq 10</td>
<td>10 &lt; dbh \leq 15</td>
<td>15 &lt; dbh \leq 20</td>
<td>&gt; 20</td>
</tr>
</tbody>
</table>

Inter-tree distances were calculated within the model for each of the two field data plots for sites SRS 5 and SRS 6. For the simulated plots, five replicates were run under each of the two site conditions (SRS 5 and SRS 6), and inter-tree distances were calculated at model year 65 for trees within the 400m² central sample plot (trees within the 20 m buffer zone were excluded in distance calculations). The model calculated inter-tree distances based on two attributes: size and species. For size class-based calculations, each tree in each size class calculated the distance between itself and trees in each size class (Table 4). For species-based calculations, the inter-tree distances within size classes were grouped further by species (e.g., distances between trees of a species to all other trees). To avoid duplicate pairings in analysis, the distance between each tree pair in each simulation and field plot was included only once. Probability distributions of inter-tree distances based on size alone, and based on size and species, were compared between the simulated plots at year 65 and the field plots. Cumulative distribution functions of inter-tree distances were computed per model replicate and per field plot for each of the two field sites.
6. RESULTS

6.1 Exercise 1: Effects of Localized Interactions

The largest and most consistent deviation among the simulations was predicted for the condition with gradient soil and distributed shading. This condition resulted in a size class distribution which differed greatly from the other conditions, largely due to the presence of a high number of the smallest size class trees (dbh ≤ 5 cm). During later stages of development (model years 100 and 250), the simulations with gradient soil and distributed shade resulted in much higher numbers of the smallest size class trees for all species than did the other conditions (Figure 3). As discussed below, this difference translated to differences in other predicted forest structural and functional attributes, including species-specific and total forest basal area and biomass and average annual individual tree productivity.
Figure 3. Average size class distribution under the four treatments (each combination of uniform and gradient soil factors, and lumped and distributed shading). Values represent the averages of 20 replicates. (a) R. mangle, model year 100; (b) L. racemosa, model year 100; (c) A. germinans, model year 100; (d) total forest, model year 100; (e) R. mangle, model year 250; (f) L. racemosa, model year 250; (g) A. germinans, model year 250; (h) total forest, model year 250. Changes by species (and total) are shown by comparing the left column to the right column for each row.
The more heavily left-skewed size class distribution occurring in the treatment with a soil gradient and distributed shading affected the total basal areas and biomasses of *A. germinans* and *L. racemosa* (Figures 4 and 5). Average annual individual productivity values were also lowest in this treatment, with basal area increments at model year 100 of 1.37, 3.69, and 6.04 cm² yr⁻¹ for *A. germinans*, *L. racemosa*, and total forest, respectively and 2.13, 1.68, and 4.87 cm² yr⁻¹ at model year 250. The relatively lower basal areas and biomasses of *A. germinans* and *L. racemosa* were reflected in the total forest basal area and biomass values, which were also the lowest among the four treatments (Figures 4c, 4f, 5c and 5f). The resulting low number of intermediate-sized (dbh 15-35 cm) *L. racemosa* (Figure 3b) and *A. germinans* (Figure 3c) resulted in low total basal area and biomass at year 100 (Figure 4c and 5c), while the low number of the largest size class (dbh 40+ cm) (Figure 3f and 3g) resulted in low total values in year 250 (Figure 4f).

At model year 250, the average density of the largest size class *A. germinans*, which is typically the dominant species at later stages of forest development, was low under the gradient soil and distributed shade treatment compared to the other treatments (34 trees ha⁻¹ versus 62, 77, and 90). Unlike *A. germinans* and *L. racemosa*, *R. mangle* was more successful in terms of basal area (Figures 4a and 4e) and biomass (Figures 5a and 5e) in both treatments with gradient soil than in either of the uniform soil treatments. At model year 100, *R. mangle* reached much greater sizes under the gradient soil conditions (up to 40 cm dbh), compared to the uniform soil treatments, which only resulted in *R. mangle* trees up to 20 cm (Figure 3a). With the two gradient soil treatments (with distributed or lumped shading) at model year 100, *R. mangle* reached greater biomass and basal area under the treatment with lumped shading.
conditions (Figure 4a and 5a), due to a greater number or larger size class trees (30-40 cm) in this treatment (Figure 3a).

Figure 4. Average total basal area under four treatments with varying combinations of uniform and gradient soil factors and lumped and distributed shading. Values represent the averages of 20 replicates, error bars represent minimum and maximum values for each treatment. Model year 100 (a) R. mangle (b) L. racemosa (c) A. germinans (d) total forest; Model Year 250 (e) R. mangle (f) L. racemosa (g) A. germinans (h) total forest. Changes by species (and total) are shown by comparing the left column to the right column for each row.
(Figure 4 continued)

- (c) Basal Area (m² ha⁻¹)
- (g) Basal Area (m² ha⁻¹)
- (d) Basal Area (m² ha⁻¹)
- (h) Basal Area (m² ha⁻¹)

Soil uniform, Shade distributed
Soil gradient, Shade distributed
Soil gradient, Shade lumped
Soil uniform, Shade lumped

0
10
20
30
40
50

0
20
40
60
80
Figure 5. Average total biomass under four treatments with varying combinations of uniform and gradient soil factors and lumped and distributed shading. Values represent the averages of 20 replicates, error bars represent minimum and maximum values for each treatment. Model year 100 (a) *R. mangle* (b) *L. racemosa* (c) *A. germinans* (d) total forest; Model Year 250 (e) *R. mangle* (f) *L. racemosa* (g) *A. germinans* (h) total forest. Changes by species (and total) are shown by comparing the left column to the right column for each row.
Each individual tree possesses growth multiplier values for the factors affecting tree growth (temperature, salinity, available light, and relative nutrient availability). In this exercise, the average values (among all trees in the 4 ha simulation) for the salinity growth multiplier (SSALT), available nutrient growth multiplier (NNUT), and available light growth multiplier.
(SHADE) were used to investigate the interaction between localized (gradient) soil conditions and the two shading scenarios (distributed and lumped). When comparing the average salinity (SSALT) and nutrient (NNUT) growth multiplier values among the two treatments with gradient soil conditions, the values were consistently greater for all species under the lumped shading assumption than under the distributed shading assumption. This suggests that under the lumped shade approach, a greater proportion of trees were able to thrive in areas of favorable soil conditions because the shading effect was calculated based on all trees in the entire 4 ha grid that had a lower average density than in the patches of locally high densities under distributed shading. Thus, lumped (grid-averaged) shading allowed more trees to thrive in more favorable soil areas (areas of least stress) by effectively dampening the high shade competition that would occur in high density areas under distributed shading.
Figure 6. Average nutrient (N\textsubscript{NUT}), salinity (S\textsubscript{SALT}), and available light (SHADE) growth multiplier values under treatments with gradient soil conditions. Each point represents the average value of 20 replicates, and the error bars represent the minimum and maximum average multiplier values of 20 replicates. Dashed lines connecting points are included as visual aids to make the differences resulting from the shading assumptions more clear and do not imply a linear relationship in the multiplier values from distributed to lumped shading. (a) \textit{R. mangle}, model year 100 (b) \textit{L. racemosa}, model year 100 (c) \textit{A. germinans}, model year 100 (d) \textit{R. mangle}, model year 250 (e) \textit{L. racemosa}, model year 250 (f) \textit{A. germinans}, model year 250.
The lumped shading approach therefore had the opposite effect in subregions of the grid with more stressful soil conditions, and in which tree height and growth would have already been restricted. While the lumped shading approach provided an artificial advantage in favorable areas of the grid (lower left-hand corner of Figure 7b), less populated subregions with stressful soil conditions were effectively over shaded (upper and right perimeters of Figure 7b). In unfavorable soil conditions, growth multiplier values associated with soil factors were low and acted to inhibit growth. In nature, stunted scrub mangroves in stressful soil environments are more likely to experience the greatest growth limitation due to soil factors, not light limitation. However, the lumped shading approach in this simulation disproportionally shaded these areas of high soil stress, further limiting growth in these already stressful soil zones.

Conversely, with the distributed shade assumption, more trees were able to thrive in environmentally stressful zones, as indicated by the lower average salinity and nutrient growth multipliers observed in the local soil and light condition (Figure 6), the increased number of the smallest size class trees observed in this trial (Figure 3), and the spatial distribution map (upper and right-hand perimeters of Figure 7a). Furthermore, the greatest increase in smallest size class trees for this trial were observed for A. germinans and R. mangle, the two species with the greatest potential to thrive in stressful soil conditions due to high tolerances to low nutrient availability and high salinity, respectively. While the increased number of the smallest size class trees observed with distributed shade may have been partly due to saplings establishing in localized areas of high light availability (gaps) throughout the grid, this increase was much greater in the trial with local soil conditions (Figure 3) suggesting an interaction effect between localized (gradient) soil conditions and neighborhood-based (distributed) light competition.
Figure 7. Spatial distribution map (1 replicate), model year 100. Tree icons are logarithmically proportional to individual dbh. (a) Soil gradient, shade distributed (b) Soil gradient, shade lumped.

6.2 Exercise 2: Disturbance Scale

One of the most notable effects of disturbance events was on the competitive balance between *L. racemosa* and *A. germinans*. In all simulations, *L. racemosa* was more competitive (in terms of basal area) when a disturbance event occurred than in the undisturbed condition, especially at later stages (75 and 100 years post-disturbance) of forest development (Figures 9b, 9e, 11b, 11e, 13b, 13e). The open canopy conditions resulting from the disturbance provided a competitive advantage to *L. racemosa* within the disturbance zone. In all disturbance scenarios of Soil Treatment 1, *L. racemosa* outcompeted (higher basal area and biomass), and prevented the eventual dominance of *A. germinans* that was simulated in the undisturbed condition (Figures 8 and 9).

Disturbance size had a great impact on *L. racemosa* in all soil conditions. At later recovery stages (75 and 100 years post-disturbance), there was a consistent trend of increasing
mean biomass and mean basal area (within the disturbance area) with increasing disturbance size (Figures 8-13). The greatest variability in biomass and basal area was observed at later stages of recovery for *L. racemosa* in the 500m\(^2\) disturbance trials (Figures 8e, 9e, 10b, 10e, 11b and 11e), apparently due to demographic stochasticity. *L. racemosa* has the lowest maximum age of the three species (200 years, compared to 250 years for *R. mangle* and 300 years for *A. germinans*) resulting in a greater probability of age-related mortality at later recovery stages. In a relatively small (500m\(^2\)) plot, the losses (or survival) of a few large trees can add variability to predicted basal area and biomass.

The effect of disturbance on *R. mangle* regenerating within a disturbance zone was found to be greatly affected by the soil conditions in each of the three treatments. Under the benign RNA (0.7) and stressful soil (60 g kg\(^{-1}\)) conditions of soil treatment 1, *R. mangle* was most successful regenerating in the smallest disturbance area (Figure 8a, 8d, 9a and 9d). Under the conditions of soil treatment 2 (benign salinity and benign RNA) there was no noticeable difference in mean basal area (Figures 11a and 11d) or biomass (Figures 10a and 10d) for *R. mangle* regenerating within areas impacted by various sized disturbances. Under soil treatment 3 (both stressful RNA and salinity), *R. mangle* regenerating within the disturbed area exhibited a trend of increasing basal area (Figures 13a and 13d) and biomass (Figure 12a and 12d) with increasing disturbance size; this was especially evident when comparing results for disturbance sizes of 500 m\(^2\) and 40,000 m\(^2\).

In addition to affecting forest structural attributes, productivity was also impacted by disturbance. This exercise exhibited the effects of both soil conditions and disturbance size on productivity. Annual productivity is presented here as the sum of the annual change in biomass
of individual trees (sum of annual growth). Species-specific and total forest annual biomass trajectories (Figure 14) followed productivity trends (Figure 15). The decrease in productivity (negative slope) over time observed in treatments with disturbance (Figure 15, 16, and 17) did not translate to declining biomass during the time period simulated (Figure 14). In soil treatment 3, under conditions with both stressful salinity (60 g kg⁻¹) and nutrient availability (0.4), post-disturbance productivity rates increased with increasing disturbance area, with total forest post-disturbance productivity approaching the pre-disturbance maximum (~ 5.5 t ha⁻¹ yr⁻¹) in the 20,000 m² disturbance trial (Figure 17).

The greatest total forest productivity rates (approximately 13 tons ha⁻¹ yr⁻¹ and 17 tons ha⁻¹ yr⁻¹, respectively) were observed in soil treatments 1 and 2 (least stressful soil conditions). In both of these treatments, *A. germinans* had the greatest productivity rates at the end of the simulation (model year 200) in the undisturbed condition (Figures 15 and 16), however under all disturbance scenarios, this productivity dominance shifted to *L. racemosa*, as the disturbance reverted the forest back to the open canopy conditions in which *L. racemosa* is most competitive. As in soil treatment 3, an increase in disturbance area resulted in increased productivity rates.

The portion of the forest regenerating within the disturbance zone experienced accelerated productivity rates compared to the non-disturbed condition, and the magnitude of this increased productivity was affected by soil conditions and disturbance size (Figure 18). In treatments with less stressful soil conditions and larger disturbance areas, there was greater potential to return to pre-disturbance productivity rates, and in a quicker time frame (Figure 18). The treatments with the greatest potential for accelerated post-disturbance production
were those with the least stressful soil conditions (soil treatments 1 and 2), in which the undisturbed production curves were characterized by an early peak in productivity that was relatively greater than the productivity rates observed at later developmental stages (Figure 18a, b).
Figure 8. Soil Treatment 1, total biomass within disturbance area. Error bars represent minimum and maximum values (data represents 20 replicates). Model year 75 (a) R. mangle (b) L. racemosa (c) A. germinans; model year 100 (d) R. mangle (e) L. racemosa (f) A. germinans. Changes by species are shown by comparing the left column to the right column for each row.
Figure 9. Soil Treatment 1, total basal area within disturbance area. Error bars represent minimum and maximum values (data represents 20 replicates). Model year 75 (a) R. mangle (b) L. racemosa (c) A. germinans; model year 100 (d) R. mangle (e) L. racemosa (f) A. germinans.
Figure 10. Soil Treatment 2, total biomass within disturbance area. Error bars represent minimum and maximum values (data represents 20 replicates). Model year 75 (a) R. mangle (b) L. racemosa (c) A. germinans; model year 100 (d) R. mangle (e) L. racemosa (f) A. germinans.
Figure 11. Soil Treatment 2, total basal area within disturbance area. Error bars represent minimum and maximum values (data represents 20 replicates). Model year 75 (a) *R. mangle* (b) *L. racemosa* (c) *A. germinans*; model year 100 (d) *R. mangle* (e) *L. racemosa* (f) *A. germinans*. 
Figure 12. Soil Treatment 3, total biomass within disturbance area. Error bars represent minimum and maximum values (data represents 20 replicates). Model year 75 (a) R. mangle (b) L. racemosa (c) A. germinans; model year 100 (d) R. mangle (e) L. racemosa (f) A. germinans.
Figure 13. Soil Treatment 3, total basal area within disturbance area. Error bars represent minimum and maximum values (data represents 20 replicates). Model year 75 (a) R. mangle (b) L. racemosa (c) A. germinans; model year 100 (d) R. mangle (e) L. racemosa (f) A. germinans.
Figure 14. Soil treatment 1, annual biomass within disturbance area (average of 20 replicates) under the following disturbance scenarios: (a) No disturbance (b) 500 m$^2$ (c) 40,000 m$^2$
Figure 15. Soil treatment 1, annual productivity within disturbance area (average of 20 replicates) under the following disturbance scenarios: (a) No disturbance (b) 500 m$^2$ (c) 2,000 m$^2$ (d) 20,000 m$^2$ (e) 40,000 m$^2$
Figure 16. Soil treatment 2, annual productivity within disturbance area (average of 20 replicates) under the following disturbance scenarios: (a) No disturbance (b) 500 m² (c) 2,000 m² (d) 20,000 m² (e) 40,000 m²
Figure 17. Soil treatment 3, annual productivity within disturbance area (average of 20 replicates) under the following disturbance scenarios: (a) No disturbance (b) 500 m$^2$ (c) 2,000 m$^2$ (d) 20,000 m$^2$ (e) 40,000 m$^2$
Figure 18. Total forest annual productivity within disturbance area under varying disturbance scenarios for (a) Soil Treatment 1; (b) Soil Treatment 2; (c) Soil Treatment 3. Red highlights the productivity trajectory in an undisturbed (0 m²) condition.
6.3 Exercise 3: Model-Data Comparison

There was good agreement between the model predictions and field data for the probability distributions of inter-tree distances for both sites (Figure 19). The cumulative distribution of inter-tree distances was slightly smoother for Site SRS5 than for SRS6 (Figure 19), due to a higher number of trees in field plots and simulations of SRS 5 (88 and 105 trees in field plots) in comparison to SRS 6 (55 and 66 trees in field plots).

Figure 19. Cumulative distribution function of all inter-tree distances (a) Site SRS 5 (b) Site SRS 6. Simulations used the recruitment rates determined from a sensitivity analysis.

In addition to the agreement in the probability distributions of inter-tree distances, there was also a general agreement when considering distances based on size classes (Site SRS5: Fig. 20; Site SRS 6: Fig 21, Appendix B). Mean inter-tree distances calculated from the field data (Figure 25, Appendix B) and predicted by the model remained fairly constant across all size class comparisons. The one notable exception in data-model agreement was for the distances between trees of the largest size class (between trees with dbh > 20 cm) in Site SRS 5 (Figure 20). The very low number of size class 5 trees (3 trees in both field plots, and 3-7 trees in
the field simulations) resulted in much greater variability in the observed and predicted inter-
tree distance means for this size-class pairing.

Figure 20. Inter-tree distances based on size class pairings, site SRS 5. Simulations used the sapling recruitment rated determined from a sensitivity analysis. Error bars represent minimum and maximum values. (a) class 1:1 (b) class 1:2 (c) class 1:3 (d) class 1:4 (e) class 1:5 (f) class 2:2 (g) class 2:3 (h) class 2:4 (i) class 2:5 (j) class 3:3 (k) class 3:4 (l) class 3:5 (m) class 4:4 (n) class 4:5 (o) class 5:5
(Figure 20 continued)
As in the size-class based comparisons, there was also general agreement between the model predictions and field data when species within size classes were considered (Appendix B, Figures 22u-y; 23t,y; 24j,t,y). The greatest variation was with comparisons involving the larger size classes (class 4 and 5), which were comprised of a relatively smaller number of trees in the data and in simulations. The lowest variability among the means of the model runs, and the most consistent agreement between the model predictions and field data, was for *R. mangle* (Figure 22), which was the clearly dominant species in the field plots (78 and 96 *R. mangle* compared to approximately 5 trees for each *L. racemosa* and *A. germinans*). Consideration of species in addition to size was similar to size-based only comparisons in that there were no consistent differences or trends in the inter-tree distances observed among the three species.
7. **DISCUSSION and CONCLUSIONS**

Individual-based models have been widely used to investigate dynamics in a variety of forest types, including the application to mangroves (FORMAN, Chen & Twilley 1998) used as the basis of this analysis. Most previous applications of this type of model have been on the scale of examining gap dynamics; how the forest develops in relatively small areas that, due to disturbance, become thinned or open space. The original gap-scale version of the FORMAN model assumes that a very large tree will shade all shorter trees in simulations of a few hundred square meters. In the expanded version of FORMAN presented here, the largest area of influence (shading sensing area) exerted by the largest trees is about 350 m$^2$; values by species were 352 m$^2$, 322 m$^2$ and 159 m$^2$ for the largest *A. germinans*, *R. mangle*, and *L. racemosa*, respectively. While the maximum shade sensing areas are a reasonable assumption for the areas represented in a typical gap application, the explicit consideration of the spatial nature of inter-tree competition and the ability to model spatial variability in soil conditions allowed for the simulation of spatial grids many times greater (areas up to 40,000 m$^2$) than an individual tree’s shade sensing area.

Three exercises or simulation experiments were performed to examine how accounting for localized interactions affects mangrove forest development and dynamics, how the simulated forest responds to disturbances of various sizes, and a model-data comparison using field sites in the Everglades to assess how well the model simulates an emergent property of inter-tree distances. Exercises 1 and 2 were possible because of the expansion of the model (gradient soil conditions and distributed approach to shading) to allow for simulation of larger spatial grids than those used for gap analyses.
7.1 **Effects of Localized Interactions**

The results of this study found the structure and productivity of simulated mangrove forests to be sensitive to complex interactions between localized soil conditions and neighborhood-based (distributed) light competition among trees. The importance of the explicit consideration of localized light competition was most evident in comparisons of forests simulated under the same spatially-varied soil conditions (a continuum of benign to extremely stressful salinity and RNA values), but under two different light competition assumptions: original gap (lumped, grid-averaged) and new (distributed, neighborhood-based) shading. The grid-wide variability of soil stress resulted in species-specific growth potentials that were spatially non-homogeneous. This caused the lumped shading assumption to become unrealistic, as grid-averaged light competition overestimated shading in the already growth-limited, high stress areas of the grid, while it underestimated the shade intensity in favorable soil zones with high growth potential. Conversely, consideration of neighborhood light competition with gradient soil conditions acted to limit tree growth in favorable soil zones, and allowed for the establishment of trees in less optimal habitats. Under gradient soil conditions, the two shading approaches yielded forests that varied significantly in their species-specific size class distributions, basal area, biomass, and annual productivity. The effects of neighborhood shade competition varied temporally and among species, most notably resulting in a relative decline in the basal area and biomass of *A. germinans* and *L. racemosa* at later developmental stages, which in turn significantly affected total forest structural attributes. The great deviation (decrease in basal area and biomass) in forest structure and function observed under gradient soil and distributed shade highlights the importance of including spatial soil details in
simulations in which localized shade competition is considered. This is likely an increasingly important consideration in simulations in which spatial soil variables (salinity and nutrient availability) vary greatly.

The differences arising in forest structure and function under the lumped and distributed shading approaches highlight the importance of the expanded model’s spatially-explicit consideration of localized light competition. The limitation of excessive density and tree growth observed under the distributed light assumption is consistent with theoretical ecology concepts such as self-thinning (density-dependent mortality) (Lin et al. 2013). Differences in self-thinning trajectories due to various modes of competition (aboveground, asymmetric vs. belowground, relatively “symmetric” competition) are an area of particular interest in mangrove ecology (Lin et al. 2013). Future applications of the model could be used to investigate self-thinning trajectories and mass-density relationships in mangrove forests.

7.2 Effects of Disturbance Scale

The presence of forest gaps has been identified as an important factor in forest recovery following disturbance (Smith et al. 1994). Studies by Smith et al. (1994) and Brokaw & Grear (1991) found that trees (often young saplings) growing within forest gaps prior to hurricane disturbance, experienced significantly lower mortality rates than did trees in the surrounding forest. Field studies have shown that relatively young and small trees (less than 1 m tall) of the three mangrove species simulated in the FORMAN model used here are able to produce viable propagules, highlighting the importance of these small surviving saplings to recruitment and forest recovery following disturbance (Smith et al. 1994). Propagules are often observed in great abundance on the floor of mangrove forests (Victor Rivera-Monroy, pers. comm.),
therefore canopy gaps created by disturbance act as “moving windows of opportunity”,
creating more optimal light conditions that favor propagule establishment and the subsequent
growth of seedlings and saplings (Berger et al. 2008, Victor Rivera-Monroy, pers. comm.).

Light availability is highly sensitive to disturbances that alter forest canopy structure,
and is a key resource governing species composition due to differential shade tolerance
exhibited by mangrove species. As the most shade-intolerant species, _L. racemosa_ experienced
the greatest increase in productivity and competitive ability following disturbance, especially at
later stages of development during which there was a consistent trend of increasing mean
biomass and basal area with increasing disturbance size (Figures 8-13). This finding is consistent
with suggestions that smaller gap size may limit the regeneration of certain species, such as the
shade-intolerant _L. racemosa_ (Baldwin et al. 2001; Feller et al. 2009). In conditions of salinity
stress and benign RNA, this post-disturbance competitive advantage resulted in a shift in
species dominance (relative to the undisturbed condition) from _A. germinans_ to _L. racemosa_.
(Figures 8 and 9).

The effect of disturbance size on _R. mangle_ was found to be sensitive to soil conditions.
Under the benign RNA and stressful salinity conditions of soil treatment 1, _R. mangle_ was most
competitive in the smallest disturbance treatment (Figures 8 and 9). However, this trend was
not consistent. Under the benign soil conditions of soil treatment 2, there was no clear
difference in the competitive ability of _R. mangle_ among disturbance treatments (Figures 10
and 11), while under the stressful soil conditions of Soil Treatment 3, _R. mangle_ exhibited
increased biomass and basal area with increasing disturbance size (Figures 12 and 13). While _R.
mangle_ is widely regarded as a shade-tolerant species (McKee 1995, Chen & Twilley 1998), field
studies, such as that by López-Hoffman et al. (2007), have suggested *R. mangle* to be gap-dependent, exhibiting a competitive advantage in gaps with high light availability. The present study suggests the effect of disturbance on *R. mangle* to be complex and dependent on not only gap size, but also on soil conditions.

The portion of the forest regenerating within the disturbance zone experienced accelerated productivity rates compared to the non-disturbed condition, and the magnitude of this increased productivity was affected by soil conditions and disturbance size (Figure 18). There was an inverse relationship between post-disturbance production rates and soil stress, as treatments with less stressful soil conditions (and larger disturbance areas) experienced faster recovery rates and increased potential to return to pre-disturbance production rates (Figure 18). The observed post-disturbance productivity trends have important implications for activities such as the management and restoration of hydrologic regimes in degraded forests (Twilley et al. 1999). Soil stresses (e.g., hyper-salinity, oligotrophy, toxic soil compounds) are factors of particular concern to restoration managers, and have been identified as key determinants affecting restoration trajectories and recovery times following disturbance (Twilley et al. 1999). How the dynamics of the affected area affect the total forest of interest depends on the proportion of the forest area affected by the disturbance. I focused on the dynamics of the affected area in my analysis.

In nature, mangrove forest structure and function are altered by disturbances of varying frequency, scale, and intensity (Chen & Twilley 1998). Disturbances range from small scale (m²) events such as a tree fall to large scale (ha) events such as hurricanes (Smith et al. 1994, Chen & Twilley 1999). At the regional and landscape level, a mangrove forest is a structurally complex
patchwork of smaller components in different equilibrium states, resulting from localized disturbance histories (Twilley et al. 1998). In this exercise, trees in the disturbance area experienced complete and immediate mortality; however in nature, mortality can be delayed (Smith et al. 1994) and a variety of factors (species, tree size) contribute to disturbance-related mortality (Smith et al. 1994). The rate and trajectory of recovery following disturbances are highly affected by the initial conditions in the area, including the size and species composition of surviving trees, which directly affects the intensity of competition for resources such as light (Shugart 1984, Botkin 1993, Twilley et. al 1998). In the simulations performed here, environmental conditions remained temporally and spatially constant; however, physical conditions, including humidity and soil temperature, are often much different in a disturbed region than in surrounding forest (Smith et al. 1994). Soil factors such as salinity and nutrient availability can vary during and following disturbances, as with flooding from hurricane events (Smith et al. 1994). Another assumption in the analysis reported here is that sapling recruitment remained constant for all disturbances. There may be a relationship between disturbance area and sapling recruitment rates, as a small disturbed zone may receive more recruits per unit area from the surrounding, undisturbed forest (Turner et al. 1998).

Present mangrove IBMs do not explicitly model propagule dispersal, and instead begin with either the seedling (MANGRO - Dolye 1997) or sapling stage (FORMAN - Chen & Twilley 1998, KIWI - Berger et al. 2000). In FORMAN, the assumption that propagules are widely distributed (and are therefore are not limiting), is achieved by setting the annual sapling recruitment rate high, with light availability determining which propagules become sapling recruits.
7.3 Model Testing with Field Data

In a test of the model’s ability to predict spatial relationships, this study found good agreement between model predictions and field data for the probability distributions of inter-tree distances (Figure 19). This same good agreement occurred when the distribution of inter-tree distances were examined by size-class (Site SRS5: Figure 20; Site SRS 6: Fig 21, Appendix B) and by each species within sizes classes (Appendix B, Figures 22u-y, 23t, 23y, 24j 24t, 24y). Both the model and data showed no consistent differences or trends in the probability distributions of inter-tree distances across size-classes or for species within size-classes. It is possible that differences in inter-tree distances may occur for size-classes or among species (or for other covariates) at a regional or landscape scale (with increased sample size especially for the far less dominant species, A. germinans and L. racemosa), or when soil conditions vary greatly and contribute to species and structural zonation. Given the generally good data-model agreement demonstrated in this study, suggested future applications of the model should include investigations of spatial relationships under varying soil conditions and at a larger spatial scale than the 20 m x 20 m field plots analyzed here.

Initial simulations for the model-data comparison utilized the site-specific sapling recruitment values reported by Chen & Twilley (1998). However, these recruitment values could not generate plots with both species-specific densities and size classes consistent with the field data. This may be due to the fact that the simulated plots started from a clear-cut condition as opposed to starting from a recreated, known initial condition observed at some point in the plots’ past. Site- and species-specific sapling recruitment rates are not well documented and have therefore been determined in previous modeling efforts through
sensitivity analysis (e.g., Chen & Twilley 1998). The initial establishment of saplings in the FORMAN model is based solely on available light. The different approaches used to calculate available light in the original (gap, Chen & Twilley 1998) and expanded (local light competition) versions of the FORMAN model may also contribute to the need for additional adjustment of the species-specific sapling recruitment rates under the new assumptions of the local shading approach. Data for species- and site-specific recruitment rates may add confidence to the modeled recruitment process that can influence simulated forest dynamics and its response to disturbances. Given the model’s sensitivity to sapling recruitment, as exhibited by the need to adjust recruitment rates to fit field data in the inter-tree distance exercise, it is possible that the results obtained in Exercises 1 & 2 under the assumption of high sapling recruitment (30 saplings per 500m² per species), may have been drastically different under lower recruitment scenarios. Future studies may reexamine these questions under different recruitment rates.

7.4 Implications for Climate Change

Despite the assumptions of the simplified disturbance experiment in this study, the results demonstrate the potential for accelerated forest production following disturbance, and that these production values are dependent on environmental conditions as well as disturbance size. Understanding how disturbances affect forest productivity has been of great interest, as the accelerated production rates observed during recovery may have serious implications on CO₂ uptake and the global carbon cycle (Houghton 1995; Robert Twilley pers. comm.) Balancing the global carbon budget is a major effort, and there is an unaccounted for “missing sink” responsible for an annual uptake of approximately 1.6 PgC yr⁻¹; it has been suggested that this missing sink is terrestrial (Houghton 1995). Houghton (1995) suggests that while human-related
(deliberate) land-use change has been identified and quantified as a net source of carbon, “inadvertent” changes in terrestrial systems due to natural disturbance are less well documented and may be a key factor in the missing carbon sink. For example, growing forests function as carbon sinks although only the regrowth of forests following anthropogenic activities such as logging have been included in the calculation of carbon fluxes due to land-use change (Houghton 1995). A greater understanding of the mechanisms associated with carbon fluxes due to natural changes in terrestrial ecosystems, including that gained through modeling of mangrove responses to disturbances, may provide insight to the missing carbon sink.

Rovai et al. (2015) highlight the problem of “geographical sampling bias.” They state that, due to extrapolation errors associated with traditional methods of scaling biomass estimates based on site-level data to continental scale, mangrove above-ground biomass in the Neotropics is likely overestimated by 25 to 50%. Great variation in biomass exists among and even within the world’s mangrove forests resulting from a suite of climatic, environmental, and geomorphological variables (Twilley & Rivera-Monroy 2009) that have typically not been accounted for in traditional methods of estimating continental-scale mangrove biomass (Hutchinson et al. 2014, Rovai et al. 2015). Mangrove systems have been prominent in the climate change discussion due to their great ability to store and sequester carbon and their associated potential role and value in global carbon exchanges (Bouillon et al. 2008, Costanza et al. 2014, Rovai et al 2015). However, in order to understand the role that these forests play in the global carbon cycle, there must be accurate methods of estimating biomass at large spatial scales (Rovai et al. 2015).
7.5 A Role for IBMs in an Age of Remote-Sensing

Shugart et al. (2015) suggest that a combination of new remote sensing technologies and IBMs may provide the answer for narrowing the gap in accuracy between site- and continental-scale predictions of forest structure and function. A limitation of the current process-based models used to predict global-scale forest structure is an inability to consistently and accurately track the fine-scale movement of carbon through the ecosystem due to assumptions regarding its allocation to different processes and structural elements, which can vary greatly among forests of different structural types (Shugart et al. 2015). It has been suggested that the individual-based approach of IBMs may provide insight and improve upon these inaccuracies (Purves & Pacala 2008, Shugart et al. 2015); however, continental-scale datasets would be needed to test such IBM predictions. LiDAR and radar technologies are now capable of generating 3D maps of large-scale forest structural elements, and can be used to investigate changes in forest structure over time (Shugart et al. 2015). IBMs can generate outputs for the same types of variables that are observed by remote sensing technologies (tree height, basal area, biomass, leaf area). Therefore, these remotely collected large-scale data sets can be used to test IBM predictions of forest structure at the landscape level and thus improving the predictive capability of these models and address the issue of scaling up of local scale predictions and observations (Shugart et al. 2015). The expanded model used here provides a demonstration of how IBMs can be expanded to permit simulations across spatial scales, which while still limited to the km scale in scope, are a very first step in moving beyond the gap scale.
REFERENCES


Pudipedi, K. and V.H. Rivera-Monroy. 2003. MANGROVE MAP VERSION 1.1. Ecology Center, Department of Biology University of Louisiana at Lafayette.


APPENDIX A

A.1 Overview

The version of the FORMAN model used here is from Chen & Twilley (1998) for mangrove forests, modified to allow for localized soil and shading effects. The model simulates mangrove forest succession through the yearly reproduction, growth, and mortality of individual trees of three species, *Avicennia germinans*, *Laguncularia racemosa*, and *Rhizophora mangle*. The environmental variables and biological processes in Chen & Twilley that depended on grid size were adjusted for the grid size used in simulations presented here. Table 5 lists the model inputs and the values used in simulations.

Table 5. Species-specific and exercise-specific parameters and environmental inputs used in simulations in this research. Values without any denotation, or which are denoted ¹, are from Chen & Twilley (1998); ²Piou et al. (2008); ³NOAA (a); ⁴NOAA (b). Denotations *³, *¹, *² indicate values used in model exercises 1, 2, and 3, respectively.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th><em>Avicennia germinans</em></th>
<th><em>Laguncularia racemosa</em></th>
<th><em>Rhizophora mangle</em></th>
</tr>
</thead>
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<td>$G$</td>
<td>Growth constant</td>
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<td>243</td>
<td>267</td>
</tr>
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<td>$D_{\text{max}}$</td>
<td>Maximum dbh (cm)</td>
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<td>80</td>
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<td>$AGE_{\text{max}}$</td>
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<td>250</td>
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<td>71.58</td>
<td>77.26</td>
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<td>$b_3$</td>
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<td>38.90</td>
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<td>7636</td>
<td>7636</td>
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<td>$U_i$</td>
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<td>65.0</td>
<td>58.0</td>
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<th>Parameter</th>
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<th>Laguncularia racemosa</th>
<th>Rhizophora mangle</th>
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<td>$S_{max}$</td>
<td>Maximum number of annual sapling recruits *per 500m$^2$; †per 400m$^2$</td>
<td>30***, 1 (SRS5) ‡, 1 (SRS6) †, 2 (SRS6) †</td>
<td>30***; 8 (SRS5) †, 3 (SRS6) †</td>
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<td>RNA</td>
<td>Relative nutrient availability</td>
<td>0-1.0*; 0.2-0.7†; 0.54 (SRS5) †, 0.7 (SRS6) †</td>
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<tr>
<td>Salinity</td>
<td>Salinity (g kg$^{-1}$)</td>
<td>0-100*; 30-100†; 14.3 (SRS5) †, 17.3 (SRS6) †</td>
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<td>TJan</td>
<td>Average monthly temperature of January ($°C$)</td>
<td>19.2*†; 19.14565†4</td>
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<td>TJuly</td>
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<td>28.2*†; 28.01628†4</td>
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### A.2 Grid Configuration and Environmental Variables

The model uses a two-dimensional grid of square cells. Each cell is assigned a value for salinity and RNA. Values of salinity (g kg$^{-1}$) are directly assigned to each cell. RNA values are between zero and one and assigned to cells. Given the assumption that nutrient limitation is driven by total phosphorus, RNA was specified by Chen & Twilley (1998) using a revised version of the Monod (1942) function by Bridgham et al. (1995):

$$ PR = \frac{(R_{ac} - R_{min})PR_{max}}{R_{ac} - R_{min} + \alpha} $$ (1)
where $PR_{\text{max}}$ is the maximum production, $R_{ac}$ is the amount of resource acquired, $R_{\text{min}}$ is nutrient availability at zero production, and $\alpha$ is half saturation constant with respect to $R_{ac}$.

Chen & Twilley (1998) used available information and computed RNA as $PR/PR_{\text{max}}$. Chen & Twilley (1998) used salinity values of 17.3 g kg$^{-1}$ and 14.3 g kg$^{-1}$ for Sites S3 and S4 (now designated “SRS6” and “SRS5”, respectively, by the Florida Coastal Everglades (FCE) Long Term Ecological Research (LTER) Network) and RNA values of 0.70 and 0.54 for Sites S3 and S4 for their simulation of sites in the Shark River estuary. We used their values for Shark River-like simulations, and also like Chen & Twilley, we additionally did simulations that varied salinity and RNA in gradient patterns over a wide range of possible values to explore general model responses to environmental variation.

Temperature was represented as $DEGD$ and was computed from an assumed average January and average July temperatures.

\[
T_1 = (T_{\text{July}} \times 1.8 + 32) + (T_{\text{Jan}} \times 1.8 + 32) + (dT \times y) \quad (2)
\]
\[
T_2 = (T_{\text{July}} \times 1.8 + 32) - (T_{\text{Jan}} \times 1.8 + 32) + (dT \times y) \quad (3)
\]
\[
DEGD = T_2 \left( \frac{365}{2\pi} \right) - 182.5 \left( 47.0 - \left( \frac{T_1}{2} \right) \right) + \left( \frac{365}{T_2 \pi} \right) \left( 47.0 - \left( \frac{T_1}{2} \right) \right)^2 \quad (4)
\]

where $T_{\text{July}}$ is the average temperature of July ($^\circ$C), $T_{\text{Jan}}$ is the average temperature of January ($^\circ$C), $dT$ is the annual change in temperature ($^\circ$C yr$^{-1}$), and $y$ is the model year. The “$dT$” term was reported in Chen & Twilley (1998) to allow for simulation of an increasing temperature scenario; $dT$ was set to zero in all simulations presented here. $DEGD$ was assumed uniform across the grid and the same year to year.
Available light to a tree is specified in Chen & Twilley as part of a single equation that included the incident light at the top of canopy, effects of shading, and light extinction. We use their equation adapted to other sized grids and to allow for local shading from neighboring trees.

A.3 Reproduction

At the beginning of the model year, a realized number of saplings are added to each population and placed randomly on the grid where light is then used to determine if they survive to become adults. First, the maximum number of saplings \(S_{\text{max}}\) that can be added to each population assuming optimal light conditions is specified for each species. We used the values reported in Chen & Twilley, adjusted proportionately for the area of our grid relative to their 500 m\(^2\) grid. The realized number of saplings for each species each year is then the \(S_{\text{max}}\) times a uniform random number. The adjustment of the realized number of saplings for sub-optimal light conditions (survival) used the available light computed as with adult trees based on the location and assumed dbh value of each sapling (see Equation 18 for \(A_L\)). Because of the assumed small size of the saplings, all adult trees within the assumed neighborhood of influence contribute to the shading of saplings. Slightly different equations for survival are used for \(A.\ germinans\) and \(R.\ mangle\) (Equation 5) versus the less shade-tolerant \(L.\ racemosa\) (Equation 6):

\[
\text{If } k > A_L^2 \text{ the sapling dies} \quad (5)
\]

\[
\text{If } k > A_L^{2.5} \text{ the sapling dies} \quad (6)
\]

where \(k\) is a uniform random number. Dead saplings are removed from the population; surviving saplings are treated as adults and continue to the growth portion of the model.
A.4 Growth

Tree growth is represented by annual increases in dbh (cm) and is affected by the environmental factors of salinity and nutrients (cell-specific), temperature (grid-wide), and light (depends on shading by neighbors). Height ($H$, cm) is then determined from dbh using the following equation (Botkin 1993; Chen & Twilley 1998):

$$H = 137 + b_2D - b_3D^2$$

(7)

Tree growth under optimal conditions ($G_{max}$) is calculated as (Botkin 1993, Chen & Twilley 1998):

$$G_{max} = \frac{\Delta D}{\Delta t} = \frac{GD(1-D+H)}{D_{max}^2 H_{max}^2}$$

(8)

where $G$ is a species-specific growth constant, $D$ is tree diameter (dbh), $D_{max}$ and $H_{max}$ are species-specific constants for maximum dbh (cm) and maximum tree height (cm), respectively; $b_2$ and $b_3$ are species-specific constants in the height to dbh relationship; and $H$ is tree height (cm). Realized growth is then computed from $G_{max}$ and the normalized effects of salinity, nutrient availability, temperature, and available light.

$$\Delta D = G_{max} \times SSalt \times NNut \times Temp \times Shade$$

(9)

where $\Delta D$ is the realized annual growth in dbh (cm). Individual tree biomass (grams) is calculated as:

$$\text{Biomass} = t \times \left( \frac{D^2 H}{100} \right)^w$$

(10)

where $t$ and $w$ are constants in the dbh to biomass relationship, $D$ is tree diameter (dbh, cm), and $H$ is tree height (cm).
The SSalt multiplier limits growth due to salinity stress, which has long been implicated as a key defining variable in mangrove forest structure, zonation, and productivity (Macnae 1968; Clarke & Hannon 1970; Lugo & Sneadaker 1974; Cintrón et al. 1978; Chen & Twilley 1998). Greenhouse studies have found many mangrove species, including A. germinans, L. racemosa, and R. mangle, to be facultative halophytes that exhibit differential salt tolerance, the former being the most salt tolerant of the three species (Chapman 1976; Scholander et al. 1962; Ball 1988, McKee 1993; Chen & Twilley 1998). SSalt is calculated using the following equation by Rastetter (1990):

$$ SSalt = \frac{1}{1 + e^{d(Ui - U)}} $$

where $U$ is salinity (g kg$^{-1}$); $Ui$ is a species-specific constant for the effect of salinity on growth (g kg$^{-1}$), the value of $U$ which results in an SSalt value of 0.5; $d$ is a species-specific constant for the effect of salinity on growth (Rastetter 1990; Chen & Twilley 1998).

NNut imposes growth limitation due to relative nutrient availability (RNA) and is calculated as from the assigned RNA values (Weinstein et al. 1982):

$$ NNut = c_1 + c_2 RNA + c_3 RNA^2 $$

where $c_1$, $c_2$, and $c_3$ are constants for the effect of nutrient availability on growth.

The temperature effects multiplier (Temp) is calculated from the specified value of DEGD.

$$ Temp = 1 - \left( \frac{DEGD_{min}}{DEGD} \right)^2 $$

where $DEGD_{min}$ is the minimum value of DEGD within the geographic range of each species distribution.
Growth inhibition due to shading has been described by Botkin et al. (1972) for shade-tolerant \((Equation 13)\) and shade-intolerant \((Equation 14)\) species:

\[
\begin{align*}
    r_N(AL) &= 1 - e^{-4.64(AL-0.05)} \\ \\
    r_I(AL) &= 2.24(1 - e^{-1.136(AL-0.08)})
\end{align*}
\]

where \(AL\) is the light reaching an individual tree (see below). The value of \(Shade\) for \(A. germinans\) and \(R. mangle\) is directly the value of \(r_N(AL)\); \(Shade\) for \(L. racemosa\) is calculated from both \(r(AL)\) values as:

\[
Shade = \frac{r_N(AL) + r_I(AL)}{2}
\]

The light available to each tree \((AL)\) depends on the incident light available to the tree and the adjustment of this incident light for shading by the cumulative leaf area \((TLA, m^2)\) of neighboring trees that are taller. The distributed approach used here is based on the “zone of Influence” \((ZOI)\) concept developed by Czárán (1998), with parametrization for Caribbean mangrove species developed using a similar approach \(field of neighborhood)\) by Berger et al. \((2000)\) and Piou et al. \((2008)\). We first determine the leaf area of each tree in order to eventually compute the total leaf area of the neighboring trees that influence each tree. Leaf area \((LA, m^2)\) is computed from \(dbh\) as:

\[
LA = a(dh)^b
\]

where \(a\) and \(b\) are species-specific constants \((Cintrón & Schaeffer-Novelli 1984)\). [note: In Chen & Twilley \((1998)\), this calculation was done in two steps. They first computed leaf mass \((LW)\) from \(LW = aD^b\), and then a second equation was used to convert leaf mass to leaf area \((LA)\): \([LA = cLW]\), where “\(c\)”, a species-specific ratio of leaf area \((m^2)\) to leaf mass \((g)\).]
Knowing the leaf area and the location and height of each tree, we next determine which trees influence an individual tree via shading (i.e., neighborhood effect) and contribute to the total leaf area (TLA) determining shading. The length of a tree’s shade sensing radius is calculated as a function of the tree’s dbh:

$$R = g \times rbh^y$$  \hspace{1cm} (18)

where $R$ is the shade sensing radius (m), $rbh$ is half the dbh, and $g$ and $y$ are species-specific scaling parameters (Piou et al. 2008). A circle is calculated for each tree based on its sensing radius $R$. To determine the leaf area affecting an individual tree, we consider all trees whose circles overlap with the circle of the tree of interest. We adjust for partial overlap by computing the fraction of the area of the neighboring tree’s circle that lies within the circle of the tree of interest. We sum the leaf area of the neighboring trees that are taller, adjusting by the product of the shading tree’s total leaf area and the fraction of overlapping area, to obtain the value of total leaf area contributing to shading (TLA). This method assumes that leaf area within a tree’s canopy is evenly distributed.

Finally, we use the TLA and the same aggregate equation used by Chen & Twilley to determine the value of AL for equations (14) and (15). Incident light was specified by Chen & Twilley as a single equation that included the incident light estimated from an equation based on latitude, attenuation, and a 500 m$^2$ area. The light available to each tree in the new version of the model uses the same aggregate equation, adjusted for the light available to any sized grid (proportional adjustment from the 500 m$^2$ used in Chen & Twilley) and with the leaf area determined via the zone of influence approach (rather than for every tree affecting every other tree).
$AL = e^{\left(-\frac{TLA_{500}}{179856\pi(R^2)}\right)}$ (19)

[Note: The light calculation adjustments were based on the C++ code of the Chen & Twilley model that included this aggregated equation. We performed a series of model simulations with the new version of the model to mimic the Chen & Twilley version and generated results that agreed for their 500 m$^2$ grid. We then performed simulations with shading effects that were grid-wide or local and the results were consistent (total number, basal area, and dbh size frequencies by species and for all trees over 300 year simulations) for smaller and larger grids that used our adjustments to the AL equation. For example, simulations with the version of the new model that mimicked Chen & Twilley, but with grid sizes of 250, 3,000, 7,000 and 10,000 m$^2$, as opposed to their original 500 m$^2$ grid, generated forests with similar species compositions and with similar values of basal area and other measures when expressed as per m$^2$. The same simulations repeated with shading being determined by increasing value of the sensing radius also produced the expected results of output measures progressively approaching the case of the Chen & Twilley that assumed all trees affect each other. Results are available from the author.]

A.5 Mortality

At the end of each model year, each tree is assigned a probability of death representing mortality from growth suppression or from old age. If a tree’s annual growth increment ($\Delta D$) is less than 0.01 cm for two consecutive years, the probability of death due to growth suppression is 0.368 (Solomon 1986; Pastor & Post 1986). If a tree did not suffer growth suppression, then its probability of death is calculated as:
probability of death = \left( \frac{4.0}{Age_{max}} \right) 

where $Age_{max}$ is a species-specific parameter for maximum tree age (Botkin et al. 1972; Shugart 1984; Chen & Twilley 1998). If a random uniform number was less than the probability of death, the tree died and was removed from the model.
Figure 21. Inter-tree distances based on size class pairings, site SRS 6. Error bars represent minimum and maximum values. (a) class 1:1 (b) class 1:2 (c) class 1:3 (d) class 1:4 (e) class 1:5 (f) class 2:2 (g) class 2:3 (h) class 2:4 (i) class 2:5 (j) class 3:2 (k) class 3:3 (l) class 3:4 (m) class 3:5 (n) class 4:4 (o) class 5:5
(Figure 21 continued)
(Figure 21 continued)
Figure 22. Inter-tree distances based on size class pairings, *R. mangle*, site SRS 5. Error bars represent minimum and maximum values. (a) class 1:1 (b) class 1:2 (c) class 1:3 (d) class 1:4 (e) class 1:5 (f) class 2:1 (g) class 2:2 (h) class 2:3 (i) class 2:4 (j) class 2:5 (k) class 3:1 (l) class 3:2 (m) class 3:3 (n) class 3:4 (o) class 3:5 (p) class 4:1 (q) class 4:2 (r) class 4:3 (s) class 4:4 (t) class 4:5 (u) class 5:1 (v) class 5:2 (w) class 5:3 (x) class 5:4 (y) class 5:5.
(Figure 22 continued)
(Figure 22 continued)
Figure 22 continued

(Figure 22 continued)
Figure 23. Inter-tree distances based on size class pairings, *L. racemosa*, site SRS 5. Error bars represent minimum and maximum values. (a) class 1:1 (b) class 1:2 (c) class 1:3 (d) class 1:4 (e) class 1:5 (f) class 2:1 (g) class 2:2 (h) class 2:3 (i) class 2:4 (j) class 2:5 (k) class 3:1 (l) class 3:2 (m) class 3:3 (n) class 3:4 (o) class 3:5 (p) class 4:1 (q) class 4:2 (r) class 4:3 (s) class 4:4 (t) class 4:5 (u) class 5:1 (v) class 5:2 (w) class 5:3 (x) class 5:4 (y) class 5:5.
(Figure 23 continued)
(Figure 23 continued)
(Figure 23 continued)

(Figure w)

(Figure x)

(Figure y)
Figure 24. Inter-tree distances based on size class pairings, *A. germinans*, site SRS 5. Error bars represent minimum and maximum values. (a) class 1:1 (b) class 1:2 (c) class 1:3 (d) class 1:4 (e) class 1:5 (f) class 2:1 (g) class 2:2 (h) class 2:3 (i) class 2:4 (j) class 2:5 (k) class 3:1 (l) class 3:2 (m) class 3:3 (n) class 3:4 (o) class 3:5 (p) class 4:1 (q) class 4:2 (r) class 4:3 (s) class 4:4 (t) class 4:5 (u) class 5:1 (v) class 5:2 (w) class 5:3 (x) class 5:4 (y) class 5:5.
(Figure 24 continued)
(Figure 24 continued)
(Figure 24 continued)
Figure 25. Inter-tree distances based on size class pairings (x-axis), calculated from field data for Site SRS 5. Error bars represent minimum and maximum values. Plot 1 (a) R. mangle (b) L. racemosa (c) A. germinans; Plot 2 (d) R. mangle (e) L. racemosa (f) A. germinans.
(Figure 25 continued)
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