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## Swamp ecology in a dynamic coastal landscape: an investigation through field study and simulation modeling

Susanne Sigrid Hoepfner

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**SWAMP ECOLOGY IN A DYNAMIC COASTAL LANDSCAPE: AN INVESTIGATION  
THROUGH FIELD STUDY AND SIMULATION MODELING**

A Dissertation

Submitted to the Graduate Faculty of the  
Louisiana State University and  
Agricultural and Mechanical College  
in partial fulfillment of the  
requirements for the degree of  
Doctor of Philosophy

in

The Department of Oceanography and Coastal Sciences

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## ABSTRACT

Increased flooding, nutrient and sediment deprivation, and saltwater intrusion have been implicated as probable causes of coastal swamp deterioration in the Mississippi Delta. An understanding of the interactive effects of these factors is required to enable successful planning of wetland restoration activities. I used field data collected from 2000 till 2005 at forty study sites to characterize the baseline conditions of the Maurepas swamp. I used a cluster analysis to identify four swamp habitat clusters, and characterized the clusters on the basis of soil properties, salinity, basal area, stem density, and other tree-related variables. ANOVA and related statistical techniques showed that three of the four habitat clusters exhibited tree biomass and densities indicative of flooding stress, and one cluster showed high tree mortality in response to salt-water intrusion. I then developed a two-species individual-based forest succession model (IBM) of a coastal swamp. The IBM followed the weekly growth, mortality, and reproduction of individuals of *Taxodium distichum* and *Nyssa aquatica* trees in a 1-km<sup>2</sup> spatial grid, using historical time-series of stage and salinity data as inputs. IBM simulations predicted that increased flooding leads to swamps with reduced basal areas and stem densities, while increased salinity (~1-3 psu) resulted in lower basal areas. The IBM showed a tendency to overestimate wood production and the dominance of *T. distichum* in comparison to field data. Lastly, I compared the predictions of the IBM and a widely-used landscape model. I used salinity and flooding conditions simulated by the landscape model in eight of its 1-km<sup>2</sup> cells as input to the IBM, and compared both models' predictions of habitat change over 100 years. The models showed good agreement in their predictions of marsh persistence and swamp to marsh conversion. The IBM, however, showed higher sensitivity to changes in both



salinity and flooding than the landscape model, and never predicted swamp persistence. The next generation of models for forecasting coastal habitat change in the Mississippi Delta will likely be a combination of the individual-based and landscape models used in this dissertation.

## **CHAPTER 1: GENERAL INTRODUCTION**

### **1.1 Introduction**

The loss of coastal wetlands has become a topic of international concern because of their immense ecological and economic value worldwide (UNESCO, 1971). Coastal wetlands are highly productive ecosystems that play a vital role in shoreline protection, floodwater retention, nutrient and sediment removal from surface water, biomass export to serve as the basis for coastal aquatic foodchains, nutrient cycling, and carbon storage (Mitsch and Gosselink, 2000). The causes of worldwide wetland loss are manifold and complex and include many human impacts. Human impacts include wetland drainage, stream channelization, construction of flood control structures, pollution, peat mining, groundwater withdrawal, land subsidence following resource extraction, and filling for waste disposal or construction (Mitsch and Gosselink, 2000). The major causes of natural wetland loss include subsidence, sea-level rise, hurricanes and storms, erosion, and droughts. Increases in the frequency and magnitude of severe weather events predicted by General Circulation Modeling (Trenberth, 1999), and the anticipated acceleration in eustatic sea-level rise in the 21<sup>st</sup> century, are predicted to lead to increasing rates of loss of coastal wetlands (Nicholls, 2004).

Deltaic wetlands are particularly vulnerable to increasing rates of eustatic sea-level rise because they experience high rates of regional subsidence in addition to eustatic sea-level rise. The combination of eustatic sea-level rise and regional subsidence, which is mostly the result of sediment de-watering, compaction, tectonic subsidence, and the withdrawal of oil, gas or groundwater deposits from coastal reservoirs (Morton et al., 2002), is generally referred to as relative sea-level rise

(RSLR). RSLR has been reported as high as 5 mm yr<sup>-1</sup> in the Nile Delta (Stanley, 1988), roughly 2.4 mm yr<sup>-1</sup> in Venice Lagoon (Ferla et al., 2007), and 2.1 mm yr<sup>-1</sup> in the Rhône delta (Suanez et al., 1997; Pont et al., 2002). In the Mississippi River delta, RSLR is in excess of 10 mm yr<sup>-1</sup> (Penland and Ramsey, 1990).

Due to their high rates of subsidence, deltaic wetlands provide a unique opportunity to study the patterns and processes of wetland loss, and to explore strategies for wetland restoration and conservation. The Mississippi River deltaic plain is worthy of particular attention, because RSLR in this delta complex is among the highest in the world. As a result of the changes in the natural processes of deltaic development, coastal Louisiana currently experiences approximately 90% of the nation's coastal wetland loss at rates totaling roughly 62 km<sup>2</sup> of wetland loss per year (Barras et al., 2003). To offset RSLR, coastal wetlands must be able to accrete at rates equal to or greater than the rising water levels (Baumann et al., 1984; Cahoon, 1994). Field and modeling studies (DeLaune et al., 1983; Reyes et al., 2000; Rybczyk and Cahoon, 2002) show that many coastal marshes in the Mississippi Delta are currently not keeping up with RSLR, and are thus likely to be lost to open water if present accretion deficits are not overcome. Possible solutions to this problem include increasing the sediment supply to wetlands that show accretion deficits to increase sedimentation rates directly and to improve soil conditions, and increasing freshwater and nutrient flows into subsiding systems to stimulate increased organic matter production (Rybczyk et al., 2002; Mendelssohn and Kuhn, 2003; Day et al., 2007).

Coastal swamps are among the rapidly vanishing wetland habitats in Louisiana that are impacted by the interactive effects of increased flooding, nutrient and sediment deprivation, and saltwater intrusion. The loss of coastal wetland forests in the

Mississippi River Deltaic Plain has not been addressed until recently, due to the fact that the transition of swamp to marsh or open water in response to excessive flooding often takes decades to complete (Conner and Day, 1988; Barras et al., 1994; Chambers et al., 2005), and thus is not as noticeable and easy to monitor as marsh conversion to open water (Chambers et al., 2005). Long-term monitoring data and simulation models are needed to predict long-term changes in swamp habitat (Conner and Brody, 1989). In this dissertation, I focus on using field data and individual-based modeling to characterize the current conditions of the Maurepas swamps located in the Pontchartrain Basin in Louisiana, USA, and to better understand the effects of flooding and salinity on the forest dynamics.

The Maurepas wetlands include approximately 563 km<sup>2</sup> of second-growth *Taxodium distichum* – *Nyssa aquatica* dominated swamps, interspersed with 150 km<sup>2</sup> of fresh and intermediate marshes. The swamps in the Maurepas basin were logged in the early 1900s, and large areas on the eastern part of the basin have not re-grown since then. The Maurepas wetlands are impacted by saltwater intrusion and by elevated levels of subsidence (Pezeshki et al., 1987), and are experiencing increases in flooding (Thomson et al., 2002). Extensive monitoring and experimental studies have been undertaken from 2000 till the present to evaluate the restoration needs and potential of these wetlands (Beville, 2002; Parsons, 2002; Lane et al., 2003; Shaffer et al., 2003; Day et al., 2004; Effler et al., 2006; Shaffer et al., 2007). Based on the findings of these monitoring studies, a Mississippi River diversion into the swamp has been approved as a restoration project for the Maurepas wetlands under the Coastal Wetlands, Protection, Planning and Restoration Act (CWPPRA, Public Law 101-646, 1990), and is currently in Phase 1 (engineering) of its implementation.

## 1.2 Dissertation Overview

In chapter 2, I use field data to characterize the baseline conditions of the Maurepas swamp and to associate swamp conditions with possible environmental causal factors. Field data were collected from 2000 till 2005 at forty study sites throughout the Maurepas basin. The data collected included annual measurements of tree diameters, the annual collection of litterfall, a one-time collection of soil samples, and periodic measurements of soil salinity. I use a cluster analysis to identify four swamp habitat clusters within the Maurepas Basin. I then characterize the habitat clusters on the basis of soil strength (i.e., soil bulk density), mean annual salinity, basal area, stem density, standing wood biomass, and species composition using ANOVA.

In a second set of analyses in Chapter 2, I use stage data collected at Pass Manchac, annual precipitation data, and soil salinity values as environmental covariates in ANCOVA and logistic regression models to help explain the observed variation in annual aboveground biomass production, biomass allocation (i.e., leaf litter versus wood), and cumulative percent tree mortality among the habitat clusters and through time, and to infer the effect of flooding and salt-water intrusion on swamp forest dynamics.

In Chapter 3, I use the data collected and analyzed in Chapter 2 to help develop a two-species individual-based forest succession model for the Maurepas swamp. The model follows the growth, mortality, and reproduction of individuals of baldcypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*) trees from birth to death on a weekly time step in a 1 km<sup>2</sup> spatial grid of 10m x 10m cells. The model accommodates differential flooding on the scale of 10's of meters (i.e., cells), and allows for species-specific responses to flooding and to changes in salinity. I use repeating sequences of

historical time-series of stage (water levels) and salinity collected within the Maurepas Basin as input for the swamp IBM. I calibrate the model to stem densities, basal areas, and wood production rates reported in the literature (baseline conditions), and corroborate the model by using the calibrated model to roughly simulate conditions in the swamp habitats in the Maurepas Basin, as identified in the cluster analysis of Chapter 2, and compare predicted and observed stem density, basal area, and wood production across the habitat types. I then change the mean elevation of the cells, variability in elevation of the cells, and salinity, and compare model predicted responses of basal area, stem density, wood production, and species composition over 500 years between the altered conditions and baseline conditions.

In Chapter 4, I compare the predictions of a landscape model (Reyes et al., 2000) of the Mississippi Delta Model that was adapted to the Maurepas basin with the predictions of the detailed swamp forest IBM developed in Chapter 3. I use the environmental conditions (salinity and flooding) simulated by the landscape model as input to the IBM, and then compare the landscape and IBM predictions of swamp forest change over 100 years. Based on the results using identical environmental conditions, I then repeat the IBM simulations using modified salinity and flooding to better understand the similarities and differences between the two models.

In the final chapter (Chapter 5), I summarize the major results of the Maurepas field study (Chapter 2), the individual-based modeling results (Chapter 3), and the comparison of the individual-based model to the landscape model (Chapter 4). I identify major environmental stressors that impact tree growth and survival in the Maurepas swamps. I then discuss the implications of my IBM results, pointing out caveats about which results should be interpreted with caution, and indicate how the model could be

improved to increase the realism and robustness of my modeling results. Lastly, I discuss the comparison of the IBM and the landscape model, and show how the models can be used to inform each other to improve our forecasting ability for how swamp forests respond to changes in environmental conditions in coastal landscapes.

Habitat change in coastal swamps in response to increasing flooding and gradual, low-concentration saltwater intrusion is a slow process that is not easily detected with field monitoring data alone. Once swamp degradation becomes obvious in the form of conversion to marsh or open water, expensive large-scale restoration efforts are needed to improve environmental conditions sufficiently to allow for re-forestation, and re-forested wetlands may take decades to develop back into a functioning swamp. A combination of field studies and simulation modeling approaches are needed to forecast swamp forests responses to changes in environmental conditions in coastal landscapes, so that restoration needs are identified early and so that the possible benefits of alternative restoration actions can be evaluated.

Considering the ecological, economic, cultural, and aesthetic importance of forested wetlands worldwide, an improved understanding of the processes of forested wetland loss and the potential for wetland preservation and restoration is required to ensure the future of these valuable ecosystems.

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## **CHAPTER 2: THROUGH DROUGHTS AND HURRICANES: TREE MORTALITY, FOREST STRUCTURE, AND BIOMASS PRODUCTION IN A COASTAL SWAMP TARGETED FOR RESTORATION IN THE MISSISSIPPI RIVER DELTAIC PLAIN**

### **2.1. Introduction**

Recognizing the immense ecological and economic value of coastal wetlands worldwide, the current loss and anticipated increasing rate of loss of these valuable habitats due to accelerated eustatic sea-level rise (Nicholls, 2004) has become a topic of international concern (UNESCO, 1971). Coastal wetlands play a vital role in shoreline protection, floodwater retention, nutrient and sediment removal from surface water, biomass export to serve as the basis for coastal aquatic food chains, nutrient cycling, carbon storage, and the cultural heritage of people (Mitsch and Gosselink, 2000). Despite the plethora of ecosystem services they provide, roughly 1% of the identified coastal wetlands worldwide were lost annually in the later part of the 20<sup>th</sup> century, and most of these were lost through direct human reclamation (Hoozemans et al., 1993).

In the case of the vast wetlands associated with the Mississippi River deltaic plain, wetland loss through deltaic deterioration and subsidence has accelerated considerably over the last 150 years, primarily through human intervention in natural deltaic processes (Coleman et al., 1998; Day et al., 2000; Day et al., 2007). Current estimates indicate that wetland habitat is currently declining at roughly 62 km<sup>2</sup> per year (Barras et al., 2003) in the Mississippi River Delta complex, accounting for 90% of the United States' coastal wetland loss in an area that contains roughly 30% of the coastal wetlands of the contiguous United States (Dahl, 2000). The high rates of wetland loss in the Mississippi River Delta Complex have been recognized by federal and state agencies as a problem of national concern, and have led to the passing of the Coastal

Wetlands Planning, Protection and Restoration Act (CWPPRA, Public Law 101-646, 1990), which provides funding to support remediation and restoration projects intended to slow or reverse coastal wetland loss. One of the most promising restoration techniques investigated appears to be the construction of controlled and uncontrolled Mississippi River diversions (Day et al., 2000; Mitsch et al., 2001; Day et al., 2007), a technique that restores the natural flow of sediments, nutrients, and freshwater into degrading marshes and swamps in order to slow, halt, or reverse the process of deterioration (Coleman et al., 1998).

Among the rapidly disappearing coastal wetland types is coastal swamp, a highly productive, species-rich habitat. Coastal swamps have a high capacity for floodwater retention, they reduce wind shear during storms, and they have a high resistance to direct hurricane wind damage (Touliatos and Roth, 1971; Doyle et al., 1995). Since the passage of hurricanes Katrina and Rita through the Louisiana coastal zone in August and September 2005, there has been an increasing awareness and appreciation of the role coastal wetlands play in storm abatement and floodwater retention. Unfortunately, many coastal swamps in the Mississippi River Delta Complex show little to no regeneration (Conner et al., 1986; Myers et al., 1995; Visser and Sasser, 1995), and are converting to marshes or open water (Barras et al., 1994) due to multiple hydrologic alterations (i.e., altered flow or impounding due to levees, raised railroad tracks, logging pull-boat scars, and canals), separation from riverine inputs, saltwater intrusion, sea-level rise, and subsidence. Few, if any, of the remaining forested wetlands (e.g., swamps, bottomland hardwood forests) in the Mississippi River Deltaic Plain are virgin stands. The cypress lumber industry thrived in Louisiana between 1880 and 1925, and most of the vast expanses of virgin stands of *Taxodium distichum* from north Louisiana

to the Gulf of Mexico were logged (Conner and Day, 1976). Common logging practices of that time period resulted in several major alterations to the natural hydrology of swamps through the construction of canals and raised railroad tracks for access to the swamp and through the construction of levees to flood areas of the forest to float out logs (Conner, 1994a). In addition, the completion of the Mississippi River flood-control levees in the 1930s disconnected large portions of the deltaic wetlands from their riverine sources (Shaffer et al., 2005).

One of the areas proposed for restoration through a Mississippi River restoration diversion under CWPPRA funding is the Lake Maurepas wetland complex in the upper Lake Pontchartrain Basin. Extensive monitoring, experimental, and modeling studies were undertaken to assess the restoration need of these forested wetlands and to evaluate likely swamp responses to the implementation of a restoration diversion from the Mississippi River (Beville, 2002; Parsons, 2002; Lane et al., 2003; Shaffer et al., 2003; Day et al., 2004; Effler et al., 2006; Shaffer et al., 2007). The objectives of this chapter are to determine the baseline swamp conditions throughout the Maurepas swamp and to associate swamp conditions with causal factors.

## **2.2. Methods**

### **2.2.1. Study Area**

The study area is located south of Lake Maurepas in the Lake Pontchartrain Basin, a marginal deltaic basin of the Mississippi River delta complex in the southeastern United States. Lake Maurepas is an oligohaline coastal lake with an average depth of approximately 2 meters. Three rivers along the north and west of the lake discharge roughly  $144 \text{ m}^3 \text{ sec}^{-1}$  of freshwater into the lake (Flowers and Isphording, 1990), which then drain through Pass Manchac into Lake Pontchartrain to the east

(Figure 2.1). Regional estimates place relative sea level rise (RSLR) between 3.6 and 4.5 mm yr<sup>-1</sup> in this basin (Penland and Ramsey, 1990). The climate in this region is subtropical and it is strongly influenced by the Gulf of Mexico, with an annual average temperature of 20°C and an average annual rainfall of 1,630 mm. Periods of freezing are generally short (< 24 hours) and infrequent, and the growing season can be as long as 300 days (National Climactic Data Center, Asheville, NC). The wetlands south and west of Lake Maurepas, which are targeted for restoration, consist of roughly 550 km<sup>2</sup> of *Taxodium distichum* – *Nyssa aquatica* dominated swamps, interspersed with 150 km<sup>2</sup> of fresh and intermediate marshes. Wetland elevations generally range from 0.30 to 0.55 m (NAVD88)(Day et al., 2004), with the notable exception of relict man-made structures such as canal spoil banks and abandoned railroad tracks. The swamps in this region are impacted by saltwater intrusion and elevated levels of subsidence (Pezeshki et al., 1987) and experience a lack of sediment and nutrient input (Shaffer et al., 2001; Lane et al., 2003; Effler et al., 2006). In addition, tree recruitment is limited severely by the mammalian seedling predator nutria (*Myocastor coypus*) (Myers et al., 1995; Beville, 2002), and in many areas of the swamp *T. distichum* and *N. aquatica* are defoliated annually by outbreaks of baldcypress leafrollers (*Archips goyerana*) and forest tent caterpillars (*Malacosoma disstria*) (Effler et al., 2006; Fox, 2006).

My 5-year study period encompassed extreme climactic conditions ranging from a severe drought to greatly extended periods of storm related flooding. I determined mean annual precipitation and an estimate of annual flooding for each year of the study as a measure of annual variation (Figure 2.2). I acquired stage data for Pass Manchac (Gage ID# 85420) for the period from January 2000 to December 2004 from the United States Army Corps of Engineers, New Orleans District. Daily 0800 stage data were

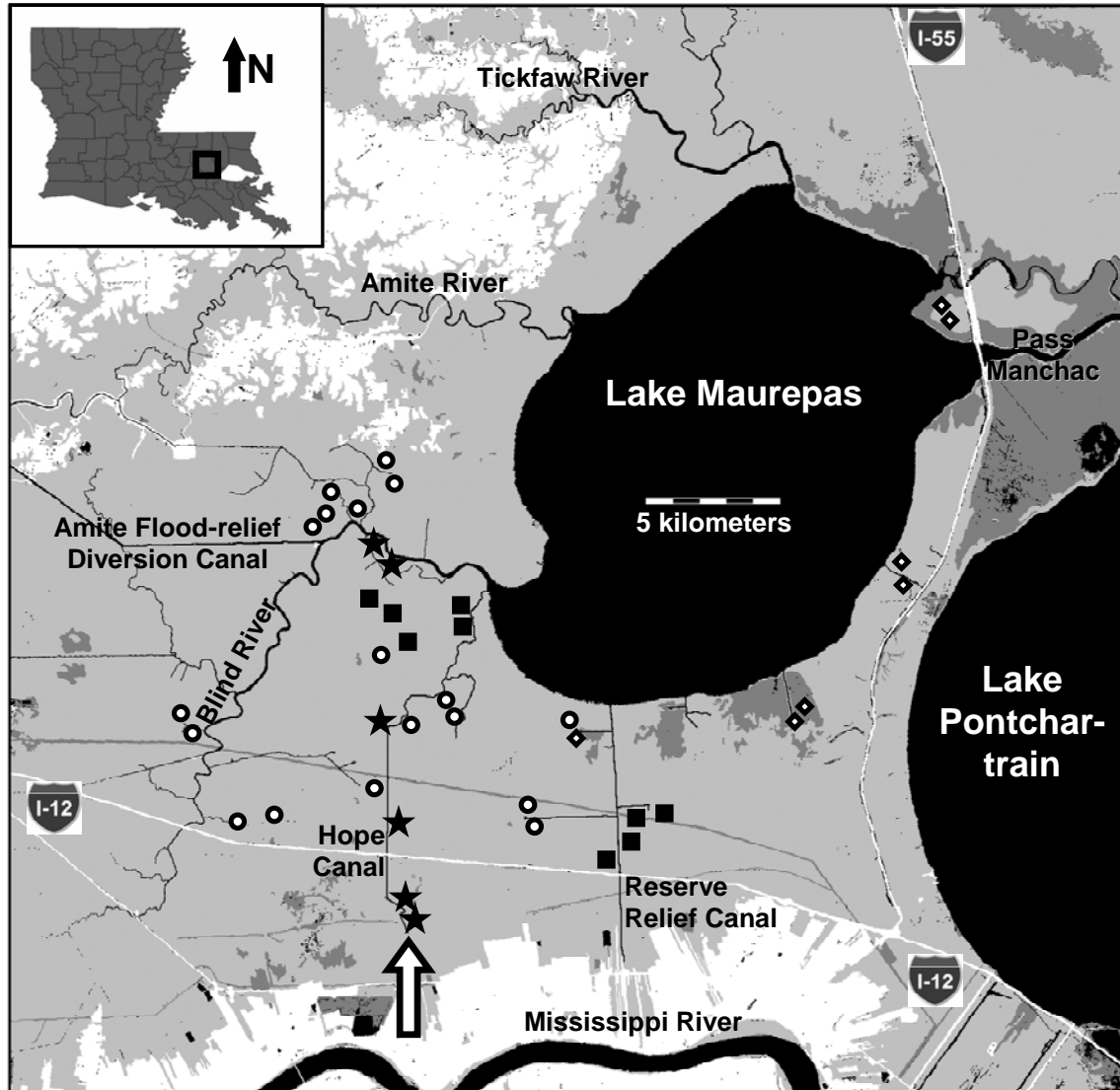


Figure 2.1 - Plot locations in the swamps on the southern shore of Lake Maurepas, Pontchartrain Basin, Louisiana, USA. Hope Canal plots are marked as solid stars, Interior-West plots as empty circles, Interior-East Plots as solid squares, and Lake plots as empty diamonds. The location of the planned Diversion Canal from the Mississippi River is indicated by a white arrow. Upland areas are shown in white, swamps in light gray, marshes in dark gray, and open water in black. Pass Manchac is the major waterway connecting Lake Maurepas to Lake Pontchartrain and ultimately to the Gulf of Mexico.

converted to proportional annual flooding indices by calculating the proportion of days within the growing season (April 1<sup>st</sup> – October 31<sup>st</sup>) during which the stage at Pass Manchac exceeded 35.1 cm, which represents the average elevation of the Maurepas swamps (Day et al., 2004). In 2000, coastal Louisiana experienced the driest May-

October period on record, leading to severe drought conditions (National Environmental Satellite, Data, and Information Service (NESDIS)). Unusually long periods of storm-related flooding occurred in 2002 with the successive passages of tropical storm Hanna (September 14, 2002), Hurricane Isidore (September 26, 2002), and Hurricane Lili (October 3, 2003) just south of the study area. This wide range of climactic conditions enabled me to sample the swamps under a wide range of environmental conditions.

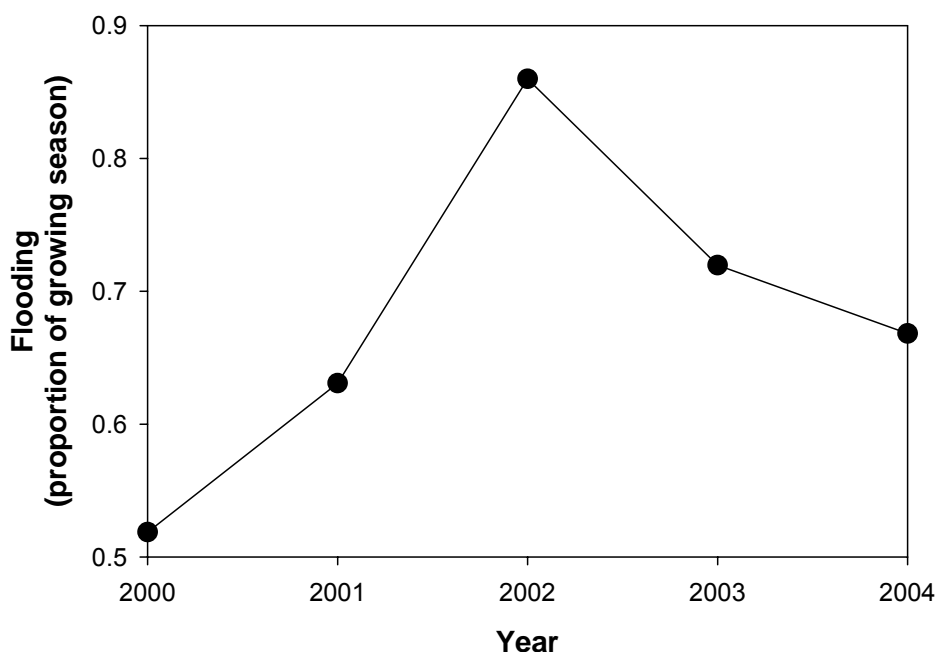


Figure 2.2 - Annual flooding during the study period, expressed as the proportion of the growing season during which Pass Manchac stage exceeded average swamp elevation in the Maurepas swamp. Severe drought conditions occurred in 2000, and the passage of two hurricanes and one tropical storm impacted local water levels in 2002.

In early spring 2000, forty 25m x 25m study plots were established within the swamps along the southern part of Lake Maurepas (Figure 2.1). Study plots were selected throughout the swamp in an effort to capture all observed environmental gradients and to achieve a maximum spatial coverage in the projected impact zone of the planned restoration diversion. Taken together, all study plots characterize an area roughly 250-km<sup>2</sup> in size. The first two years of data (2000 and 2001) were collected and

analyzed previously during my Master's research at Southeastern Louisiana University (Hoepfner, 2002); the subsequent three years of data were collected by Dr. Gary Shaffer and colleagues at Southeastern Louisiana University, and the statistical analysis of all five years of data taken together were done as part of this dissertation.

### 2.2.2. Data Collection

Plot-specific environmental data measured throughout the study area included a one-time collection of soil bulk density samples and the collection of salinity data each year. Soil cores for bulk density analysis were collected to a depth of 10 cm during spring/summer of 2003. To minimize the influence of soil micro-scale heterogeneity, five replicate soil cores were taken at each plot, and each sample was handled separately during processing. Each sample was dried to constant mass at 65°C in a ventilated oven, before soil core weights were measured. Replicate core weights were averaged to yield a plot average for the final analysis. Salinity data was collected from two capped, 0.75 m deep PVC wells at each sampling plot. All wells were evacuated during plot visits and allowed to refill prior to taking salinity readings. I measured soil salinity in each well during six to ten plot visits annually from 2000 till 2004, and averaged all observations to yield a measure of annual mean soil salinity at each plot.

I estimated forest structure, species importance, annual wood production, and tree mortality data from annually collected tree diameter data and an annual evaluation of whether each tree was alive or dead. Three forest structure variables were analyzed: basal area, stem density, and standing wood biomass. At each plot, all trees with diameters greater than 5 cm were tagged at breast height during February and March 2000 (*N. aquatica* and *T. distichum* were tagged above fluted bases or buttress swells). Shrubby species, such as *Morella cerifera* and *Cephalanthus occidentalis*, were tagged



on main branches roughly 1.5 m from the base. Diameters of all tagged individuals were re-measured during October and November each year during the study. Saplings or shrubs whose diameters reached 5 cm during the year were tagged and added to the database. By November 2004, my tree database encompassed a total of 2,219 trees.

Prior to analysis, the diameter data was harmonized following the guidelines of Sheil (1995) by comparing each tree diameter to previous and successive evaluations in the record. Individual tree data was checked and corrected on the basis of logical consistency, such that stems cannot change species, cannot be dead if they are alive in a successive year, and cannot grow outside 'common sense' possibility. The guidelines for 'acceptable' diameter change were based on each tree's previous growth record. Diameter changes of  $-0.2 \text{ cm year}^{-1}$  and  $+0.7 \text{ cm year}^{-1}$  were operational limits used to identify records for verification.

To examine the structural role and mortality of the dominant tree species, basal areas, stem densities, standing wood biomass, an importance value index (IVI) as an integrator of both species frequency and relative size, and cumulative percent mortality were calculated from the available diameter data and associated tree characteristics (i.e., species and alive/dead status). The IVI was calculated for each plot using the relative density, relative dominance in basal area, and relative frequency of each tree species identified in the swamp based on the formulae of Kershaw and Looney (1985). Standing tree biomass was calculated for each year based on measured diameters using wood biomass regression formulae found in the literature (Clark et al., 1985; Scott et al., 1985; Muzika et al., 1987). Size-class distributions by species were not analyzed statistically, but are included graphically to aid in the interpretation of other structural variables. Cumulative mortality was calculated as the sum of all trees (regardless of

species) dying per plot during the 5-year study period, and was expressed as a percent of the total number of trees tagged at a plot during all five years (i.e., baseline stem density plus recruits).

Tree aboveground primary productivity was measured through annual changes in wood biomass and the amount of leaf litter produced. Leaf litter was collected in five 0.25-m<sup>2</sup> litter traps installed haphazardly at roughly even spacing throughout the 25m x 25m study plots. The litter traps were constructed with 1 mm mesh screen to collect litter approximately 1 meter above the ground to prevent loss from flooding events. Collected leaf litter was dried to constant mass at 65 °C., sorted into *T. distichum*, *N. aquatica* and 'other' litter, and weighed. Annual wood production was calculated as the difference in each tree's calculated biomass (see above) from year to year, summed by species by plot. Aboveground biomass allocation to leaf litter (i.e., the proportion of aboveground biomass production that is leaf litter) was calculated by dividing each plot's annual litter production by its total annual aboveground biomass production.

### 2.2.3. Data Analysis

To classify the forty swamp sites into swamp habitat types, cluster analysis was conducted. The variables used as the basis for clustering the plots were environmental conditions (i.e., annual mean soil salinity in years 2000 through 2004 and bulk density), forest structure (i.e., basal area and stem density), and species composition (i.e., IVIs of *T. distichum*, *N. aquatica*, and *A. rubrum* var. *drummondii*). Variables were standardized to z-scores prior to clustering to give all variables equal weighting. The plot clustering analysis was performed using the squared Euclidean distance metric and Ward's minimum variance algorithm (Ward, 1963). I used the inverse scree test (Lathrop and Williams, 1987) and the pseudo F test (Calinski and Harabasz, 1974) to

delimit the range of cluster solutions. I then inspected the dendrogram and cluster profiles to select the most parsimonious and interpretable cluster solution based on these indices. In all subsequent analyses, data were analyzed and presented at the level of the classified swamp habitat clusters rather than at the level of the individual plot, and I termed each cluster as a swamp habitat type.

Environmental conditions and forest structure variables were analyzed using ANOVA and logistic regression to quantify habitat differences and temporal effects. Soil bulk density data was analyzed in a one-way analysis of variance (ANOVA) design to test for habitat cluster differences. Soil salinity data was analyzed in a repeated measures ANOVA design with swamp habitat cluster and year as predictors. Forest structural variables (i.e., stem density, basal area, and standing wood biomass) were analyzed in a MANOVA design to test for significant habitat and time effects and for habitat-time interactions. Subsequently, I used univariate repeated measures ANOVAs to test habitat and time effects and interactions for each structural variable, fitting time as linear trends in each model. Mean size-class distributions were presented graphically by habitat cluster. Total cumulative percent tree mortality was analyzed in a one-way ANOVA design to determine habitat cluster differences.

Total aboveground tree primary production (i.e., wood production plus leaf litter) and biomass allocation (i.e., the proportion of aboveground biomass production that is litter) were analyzed separately for *T. distichum*, *N. aquatica*, and 'Other' (all remaining species combined) using repeated measures analysis of covariance (ANCOVA) models. The main effect in each ANCOVA model was habitat type, and all models included annual estimates of the proportion of the growing season that was flooded as a covariable. Due to the rare appearance of *N. aquatica* in one habitat cluster, the

aboveground biomass production and biomass allocation models for *N. aquatica* excluded this habitat cluster from the analysis. Similarly, the same habitat cluster was excluded from the biomass allocation models for 'Other' tree species, because the midstory woody species found in this habitat cluster were generally different from those found at the remaining swamp interior.

I generated all data analyses using SAS software, Version 9.1.2, of the SAS System for Windows (SAS Institute Inc., 2000-2004). Model assumptions for ANOVA and ANCOVA models were tested, and where appropriate, transformations were used to better meet model assumptions. All post-hoc pairwise differences reported were significant at a protected  $\alpha=0.05$  level by using Tukey-Kramer-adjusted LSD's to determine differences between habitat clusters and years.

## **2.3. Results**

### **2.3.1. Swamp Habitat Characterization**

Four distinct swamp habitat clusters were identified (Figure 2.3) and used as the basis for subsequent analyses of environmental variables, forest structure, aboveground production, aboveground biomass allocation, and mortality (Figure 2.1). The first cluster of sampling plots included four plots near Hope Canal and two plots impacted by the Amite Flood-relief Diversion Canal (stars in Figure 2.1). The plots in this cluster represent the most intact swamp sampled, and are hereafter collectively referred to as the "Hope Canal" habitat cluster. The second cluster of plots consisted of eighteen plots throughout the western side of the swamp interior (circles in Figure 2.1), hereafter referred to as the "Interior-West" habitat cluster. Most of the Interior-West plots are hydrologically isolated from Lake Maurepas. The third cluster of plots consisted of nine plots located throughout the eastern side of the swamp interior

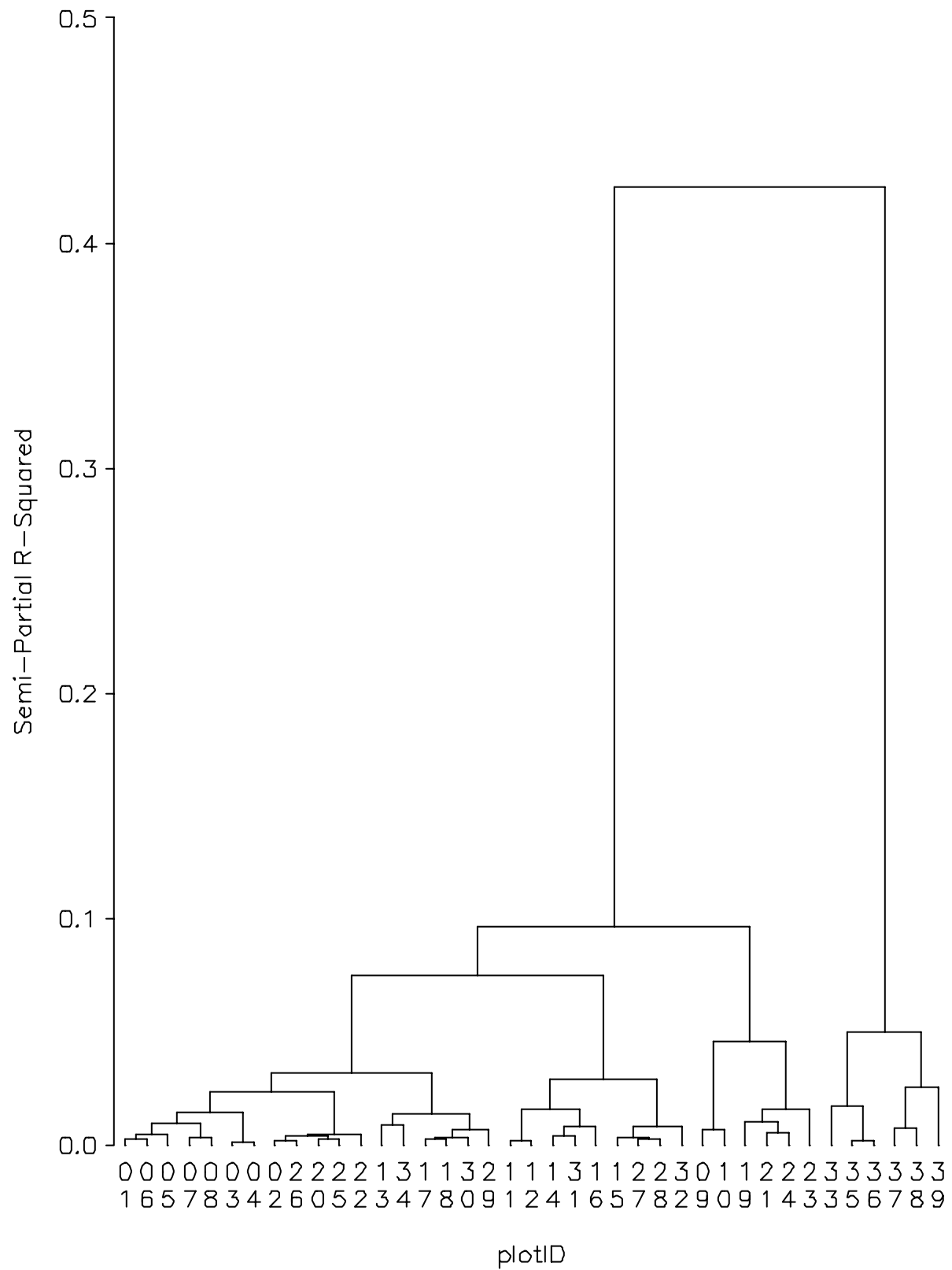


Figure 2.3 - Cluster dendrogram of field plots sampled in the Maurepas swamp.

(squares in Figure 2.1). Hereafter referred to as the “Interior-East” habitat cluster, the plots in this cluster are in close proximity to larger bayous or canals and experience frequent water exchange with the lake. The fourth and most distinct cluster consisted of seven plots located around the eastern and southeastern margin of Lake Maurepas (diamonds in Figure 2.1), hereafter referred to as the “Lake” habitat cluster. The Lake plots are located in the vicinity of Pass Manchac, which is the main waterway between Lake Maurepas and Lake Pontchartrain, and thus these plots have the highest potential for water exchange with the lake and are most likely to experience saltwater intrusion events. Overall, the Interior-East and Interior-West clusters represent the majority of the swamp area on the southwestern shore of Lake Maurepas.

Swamp habitat clusters differed significantly in their environmental conditions, and mean salinity levels in each habitat cluster changed over time. Bulk densities differed among habitat clusters ( $F_{3,12.7} = 6.32$ ,  $p = 0.0073$ ), with Lake habitat plots having lower bulk densities than any other habitat cluster (Table 2.1). The analysis of the soil salinity data revealed that salinity differed significantly between habitat clusters ( $F_{3,48.9} = 48.91$ ,  $p < 0.0001$ ) and between years ( $F_{4,74.5} = 126.60$ ,  $p < 0.0001$ ). Soil salinity was highest at the Lake habitat plots ( $LSMean_{\text{habitat}} = 2.16 \pm 0.09$  psu), and lowest at the Hope Canal habitat plots ( $LSMean_{\text{habitat}} = 0.81 \pm 0.10$  psu). Both of the Interior habitat clusters had significantly lower salinity levels than the Lake plots, and salinity levels at the Interior-West plots ( $LSMean_{\text{habitat}} = 0.98 \pm 0.06$  psu) also were not significantly different from salinity levels at the Hope Canal habitat plots. Salinity decreased significantly every year from maximum observed salinities during the drought in 2000 until 2003, then slightly increased in 2004 (Figure 2.4). A significant interaction between habitat cluster and years ( $F_{12,98.6} = 4.89$ ,  $p = 0.0001$ ) indicated that habitat type

differences in soil salinity were greatest during the drought in 2000 and diminished in subsequent years (Figure 2.4).

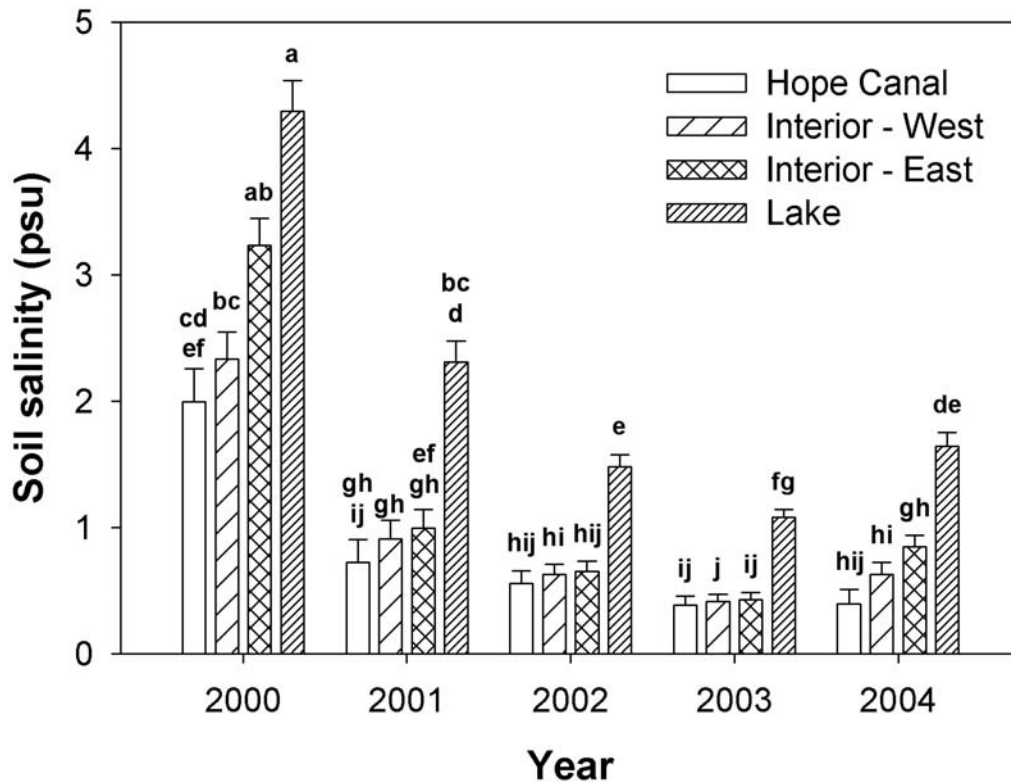


Figure 2.4 - Annual mean soil salinity ( $\pm$  SE) in the four identified swamp habitat clusters from 2000-2004. A significant interaction between habitat clusters and years indicates that habitat differences in salinity were greatest during the drought in 2000 and have diminished since then. Shared letters indicate that means are not significantly different based on post-hoc pairwise comparisons.

### 2.3.2. Community Structure and Composition

Forest structure (stem density, basal area, and wood biomass) differed greatly between swamp habitat clusters and changed significantly over the 5-year study period, particularly at the Hope Canal plots. The MANOVA of stem density, basal area, and standing wood biomass indicated a significant swamp habitat effect (Wilk's Lambda

Table 2.1- Least Square Means ( $\pm$  SE) of the structural swamp characteristics and bulk densities of the four identified Maurepas swamp habitat clusters. Shared letters in a column indicate that habitat means are not significantly different based on post-hoc pairwise comparisons.

Swamp Habitat Cluster	Basal Area (m <sup>2</sup> ha <sup>-1</sup> )	Stem Density (trees ha <sup>-1</sup> )	Standing Wood Biomass (kg m <sup>-2</sup> )	Bulk Density (g cm <sup>-3</sup> )
Hope Canal	57.12 ( $\pm$ 3.75) a	1058 ( $\pm$ 83) a	27.68 ( $\pm$ 1.75) a	0.207 ( $\pm$ 0.031) a
Interior-West	31.72 ( $\pm$ 1.98) b	762 ( $\pm$ 48) b	13.56 ( $\pm$ 0.92) b	0.136 ( $\pm$ 0.008) a
Interior-East	23.19 ( $\pm$ 2.80) b	731 ( $\pm$ 68) b	10.15 ( $\pm$ 1.30) b	0.137 ( $\pm$ 0.008) a
Lake	7.96 ( $\pm$ 3.17) c	376 ( $\pm$ 77) c	3.12 ( $\pm$ 1.48) c	0.106 ( $\pm$ 0.006) b

Table 2.2 - Baseline (1999) importance value indices ( $\pm$  SD) of woody species found in the four identified Maurepas swamp habitat clusters.

Species	Hope Canal	Interior West	Interior East	Lake
<i>Taxodium distichum</i>	0.346 ( $\pm$ 0.098)	0.213 ( $\pm$ 0.104)	0.324 ( $\pm$ 0.062)	0.619 ( $\pm$ 0.313)
<i>Nyssa aquatica</i>	0.272 ( $\pm$ 0.126)	0.611 ( $\pm$ 0.102)	0.304 ( $\pm$ 0.114)	0.051 ( $\pm$ 0.073)
<i>Acer rubrum</i> var. <i>drummondii</i>	0.205 ( $\pm$ 0.082)	0.096 ( $\pm$ 0.053)	0.216 ( $\pm$ 0.108)	0.182 ( $\pm$ 0.183)
<i>Fraxinus</i> spp.	0.130 ( $\pm$ 0.109)	0.043 ( $\pm$ 0.050)	0.025 ( $\pm$ 0.029)	0.027 ( $\pm$ 0.035)
<i>Nyssa sylvatica</i> var. <i>biflora</i>	0.035 ( $\pm$ 0.071)	0.032 ( $\pm$ 0.045)	0.102 ( $\pm$ 0.109)	0.023 ( $\pm$ 0.040)
<i>Quercus</i> spp.	0.012 ( $\pm$ 0.026)	0.001 ( $\pm$ 0.004)	0.002 ( $\pm$ 0.006)	
<i>Salix nigra</i>		0.002 ( $\pm$ 0.009)		0.016 ( $\pm$ 0.023)
<i>Morella cerifera</i>		0.002 ( $\pm$ 0.004)	0.025 ( $\pm$ 0.033)	0.063 ( $\pm$ 0.071)
<i>Cephalanthus occidentalis</i>			0.003 ( $\pm$ 0.005)	
<i>Persea borbonia</i>				0.002 ( $\pm$ 0.005)
<i>Magnolia virginiana</i>				0.002 ( $\pm$ 0.005)
<i>Triadica sebiferum</i>				0.015 ( $\pm$ 0.026)



= 0.46,  $p < 0.0001$ ), a significant effect of time (Wilk's Lambda = 0.97,  $p = 0.0433$ ), and a significant interaction of habitat and time (Wilk's Lambda = 0.92,  $p = 0.0327$ ). Swamp habitat clusters differed significantly in stem density ( $F_{3,46.6} = 4.73$ ,  $p = 0.0058$ ), basal area ( $F_{3,35.8} = 32.38$ ,  $p < 0.0001$ ), and standing wood biomass ( $F_{3,35.7} = 36.66$ ,  $p < 0.0001$ ). Hope Canal plots had significantly higher stem densities, greater basal areas, and greater standing wood biomass than any other habitat cluster. Interior-West and Interior-East plots did not differ significantly from one another in any of the three forest structural variables, but both had significantly greater basal area, stem density, and wood biomass than the Lake plots (Table 2.1). A graph of the significant time-by-habitat cluster interaction ( $F_{3,225} = 14.08$ ,  $p < 0.0001$ ) showed that stem densities decreased significantly at the Lake plots over the 5-year study period, while all other habitat clusters exhibited slight increases in stem density (Figure 2.5). A similar time-by-habitat cluster interaction for basal areas ( $F_{3,194} = 5.70$ ,  $p = 0.0009$ ) and standing wood biomass ( $F_{3,194} = 6.85$ ,  $p = 0.0002$ ) indicated that basal areas and standing wood biomass increased slightly at the Hope Canal plots, while all other habitat clusters remained relatively stable (not shown).

Overall, the Maurepas swamp is dominated by *T. distichum* and *N. aquatica* in the canopy and by *A. rubrum* var. *drummondii* and *F. pennsylvanica* in the midstory, but these relationships vary among the four habitat clusters (Table 2.2). The Hope Canal habitat plots exhibited the greatest structural complexity (i.e., largest basal areas, highest stem densities, greatest biomass). At the Hope Canal plots, *T. distichum* achieved slightly higher IVIs than its canopy competitor *N. aquatica*. While *A. rubrum* var. *drummondii* remained confined to the midstory, it reached almost the same IVI as *N. aquatica* at the Hope Canal plots, and even *F. pennsylvanica* were present in high

numbers. Despite a significantly reduced structure, a similar species composition pattern also was observed at the Interior-East habitat plots. By contrast, the canopy dominance was shifted decisively towards *N. aquatica* over *T. distichum* at the Interior-West plots, where *A. rubrum* and *F. pennsylvanica* played only minor roles. *Nyssa aquatica* was almost completely absent from the Lake plots, such that *T. distichum* reached complete canopy dominance at most Lake plots. Scrubby species, such as *Salix nigra*, *M. cerifera*, and *C. occidentalis* made sporadic appearances at the structurally less dense Interior-West, Interior-East, and Lake plots, and even the invasive species *Triadica sebiferum* had managed to take a foothold at some of the Lake plots (Table 2.2).

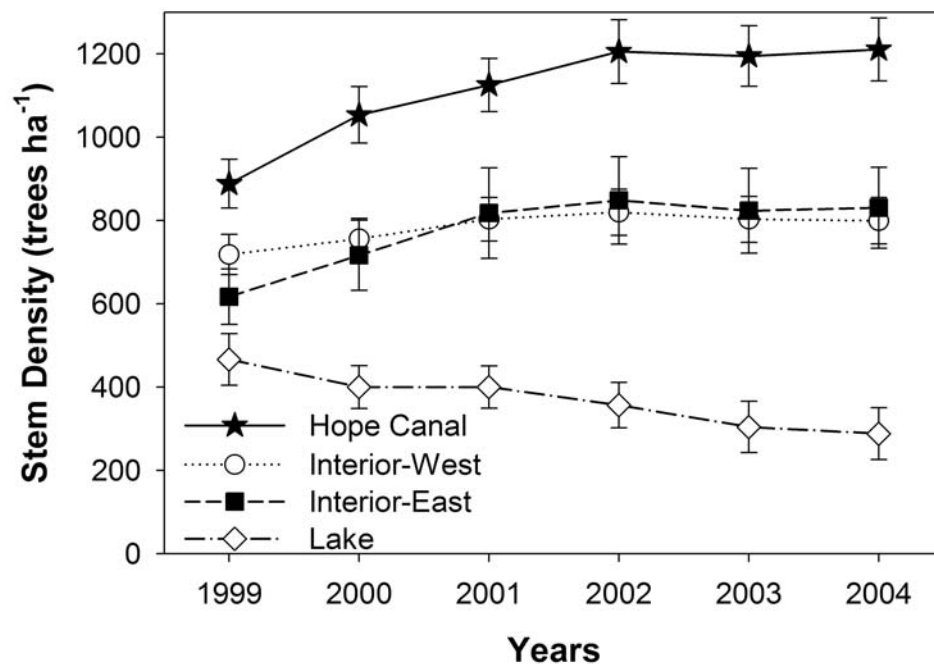


Figure 2.5 - Mean stem density ( $\pm$  SE) in each habitat cluster over time. Stem density has steadily decreased over time at the Lake plots, while all other habitat clusters experienced slight increases in stem density.

Taking a closer look at the size-class distributions by species (i.e., *T. distichum*, *N. aquatica*, and all others species combined into 'other') in each of the habitat clusters,

it became apparent that the high IVI values of *A. rubrum* and *F. pennsylvanica* were driven by their numerical dominance in the smallest size-classes (i.e., 5-10 cm and 10-20 cm DBH; Figure 2.6). By contrast, the canopy species *N. aquatica* was almost entirely absent from the smallest size-class. Low numbers of larger trees (i.e., 50-60 cm and >60 cm DBH) of all species at Interior-West, Interior-East, and particularly at the Lake plots, indicated that these plots are lacking the mature canopy structure that is present at the Hope Canal plots.

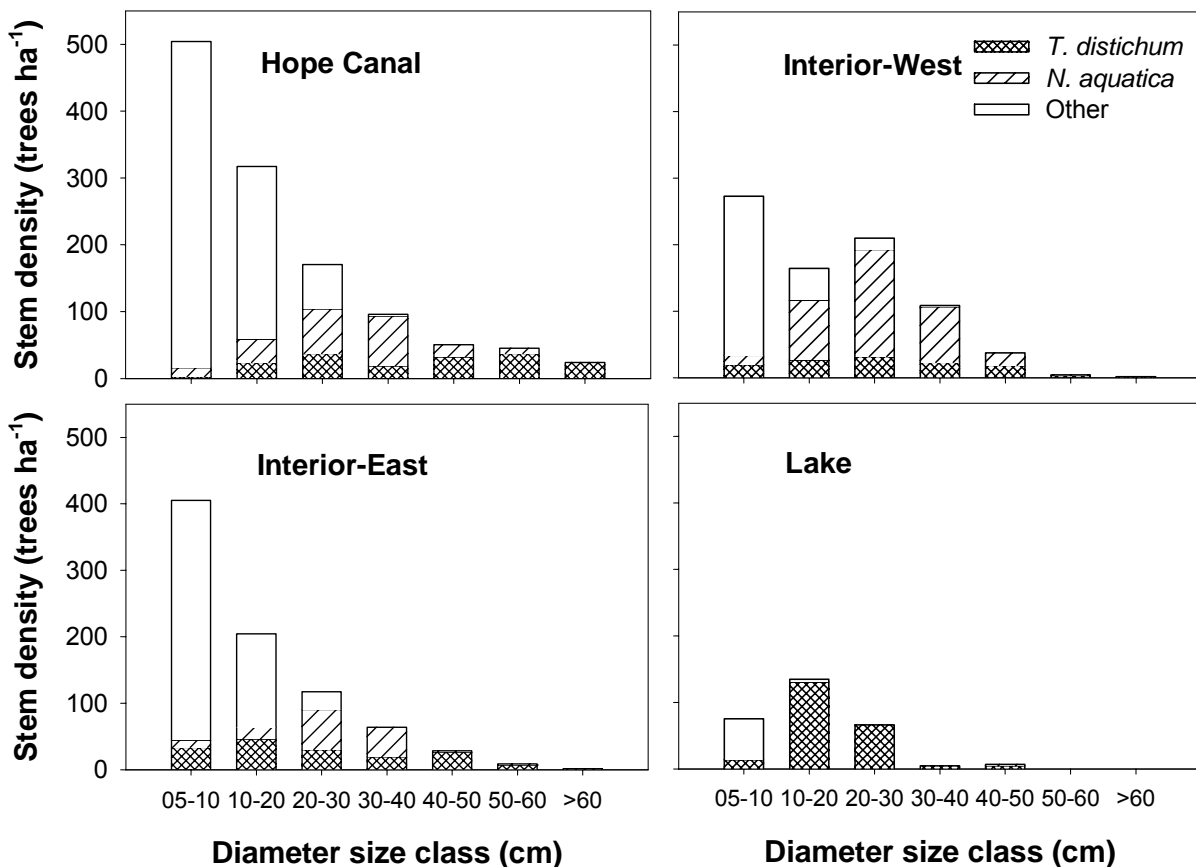


Figure 2.6 - Mean stem density per size-class and species for each of the swamp habitat clusters in 2004.

Cumulative tree mortality varied significantly between swamp habitat clusters ( $F_{3,12.4} = 5.54$ ,  $p = 0.0122$ ), remaining relatively low throughout the western part of the study area and increasing towards Pass Manchac. Cumulative percent mortalities

(Figure 2.7) did not differ significantly between Hope Canal plots (geometric mean = 2.47%) and the Interior-West plots (geometric mean = 6.12%), but were significantly higher at the Interior-East (geometric mean = 10.15%) and Lake plots (geometric mean = 23.75%). Mean cumulative percent mortality at the Interior-West plots did not differ significantly from Interior-East or Lake plots. The two Lake plots located closest to Pass Manchac, which also represented the two most saline plots in the study area, experienced cumulative percent mortalities as high as 75.00% and 61.02%.

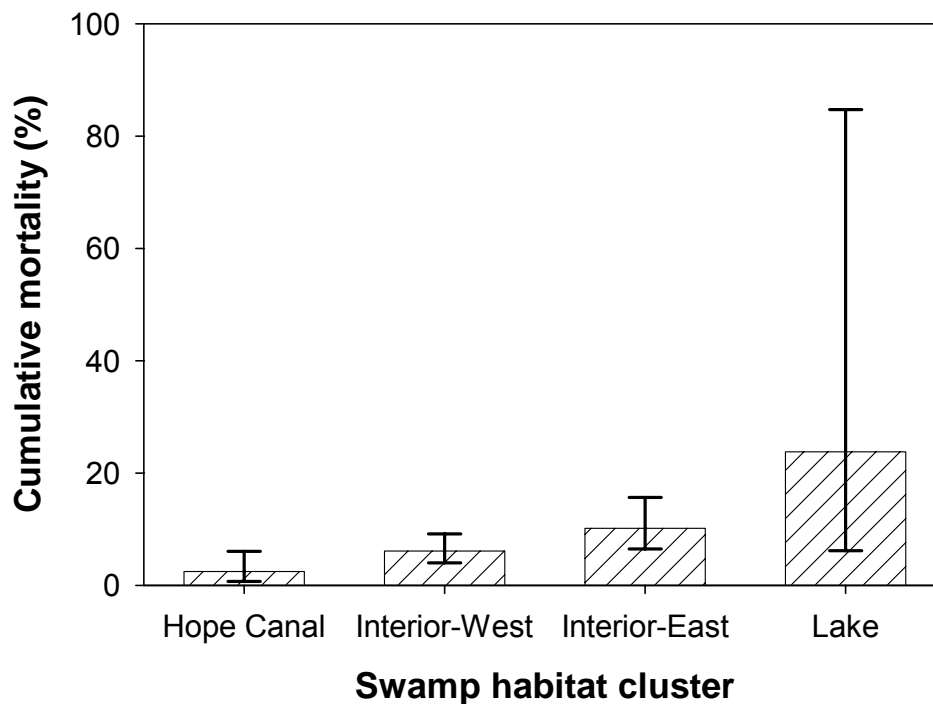


Figure 2.7 - Geometric mean ( $\pm$  95% confidence limits) cumulative percent mortality over 5 years at each of the study plots for all species combined. Shared letters indicate that log-transformed means are not significantly different based on post-hoc pairwise comparisons. Note that confidence limits are unequal as a consequence of back-transforming the log-values used in the ANOVA.

### 2.3.3. Tree Aboveground Biomass Production and Allocation

Tree net annual aboveground biomass production differed significantly between habitat clusters for all species categories, and flooded proportion of the growing season was a significant covariate in the ANCOVA model (Table 2.3). Hope Canal plots had

the highest observed aboveground biomass production for each species category (Figure 2.8). Following observed patterns in standing tree biomass, *T. distichum* annual net aboveground biomass production was significantly lower at the Interior-West, Interior-East, and Lake habitat plots than at Hope Canal plots. Furthermore, *T. distichum* net aboveground biomass production did not differ significantly between the two interior habitat clusters, but was significantly lower at the Lake plots than at the Interior-East plots (Figure 2.8). In terms of *N. aquatica* net aboveground biomass production, both Hope Canal plots and Interior-West plots were not significantly different in production, but both had significantly higher biomass production than Interior-East plots (Lake plots were excluded in this model due to the lack of *N. aquatica* throughout most of this habitat). The combined aboveground biomass production of all remaining tree species was highest at the Hope Canal habitat plots, and continued to decrease significantly from Interior-East plots to Interior-West plots to Lake plots (Figure 2.8).

Of the three tree species categories examined, *T. distichum* was by far the most productive species in the study area (Figure 2.8). Even at the Interior-West plots, where *N. aquatica* had an IVI two to three times greater than *T. distichum*, both species produced nearly equal amounts of aboveground biomass annually. Furthermore, despite being a canopy co-dominant species, *N. aquatica* produced less aboveground biomass annually than the remaining mid-story tree species at all but the Interior-West plots.

Growing season flooding was a significant predictor of net aboveground biomass production by *T. distichum* and *N. aquatica*, but not for the other species combined response variable. Annual variation in aboveground biomass production was modeled

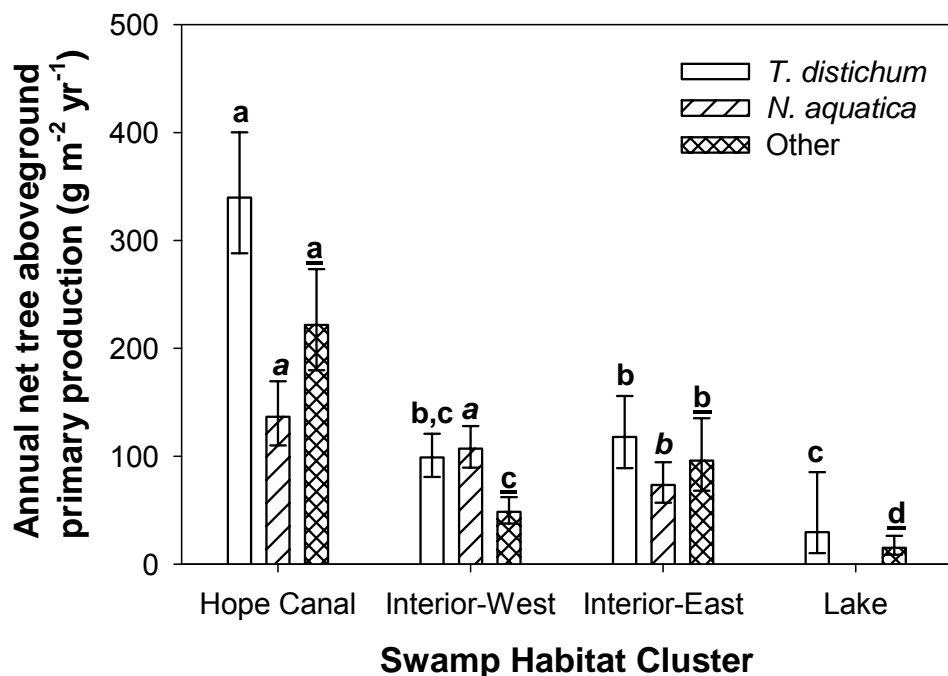


Figure 2.8 - Geometric mean ( $\pm$  95% confidence limits) of annual net tree aboveground biomass production by species for each habitat cluster. 'Other' encompasses all remaining tree species other than *T. distichum* and *N. aquatica* at each plot, primarily *A. rubrum* var. *drummondii* and *F. pennsylvanica*. Note that confidence limits are unequal as a consequence of back-transforming the log-values used in the three separate single-species ANCOVAs. Differing letters indicate significant differences based on post-hoc pairwise comparisons, where simple lower-case letters refer only to the *T. distichum* model, lower-case cursive letters refer to habitat differences in the *N. aquatica* model, and lower-case underlined letters refer to habitat differences in the 'Other' species model.

through the inclusion of annual estimates of the proportion of the growing season flooded (Figure 2.2) in the species-specific ANCOVA models. The proportion of the growing season during which Pass Manchac stage exceeded the average swamp elevation in the Maurepas swamps (i.e., flooding) was a significant negative covariable in the *T. distichum* and *N. aquatica* net aboveground biomass production models (Table 2.3), indicating that these two species had higher net aboveground biomass production in years with reduced flooding. Flooding was negatively correlated with soil salinity ( $r = -0.6195$ ,  $p < 0.0001$ ). Flooding was not a significant predictor in the net tree

Table 2.3 - ANCOVA tests and covariable parameter estimates for net tree aboveground biomass production models by species. Models used log-transformed biomass production estimates as dependent variables, and the percent of the growing season in which Pass Manchac stage exceeded Maurepas swamp mean elevation as a covariate.

Model	Effect	Num. DF	Den. DF	F	P	Estimate	StdErr
<i>T. distichum</i>	habitat cluster	3	22.6	42.61	<0.0001		
	flooding	1	107	24.14	<0.0001	-2.3109	0.4704
<i>N. aquatica</i>	habitat cluster	2	26.6	8.13	0.0018		
	flooding	1	149	25.69	<0.0001	-2.2910	0.4520
Other	habitat cluster	3	25.2	51.92	<0.0001		
	flooding	1	147	0.33	0.5686	n.s.	

Table 2.4 - ANCOVA tests and covariable parameter estimates for aboveground biomass allocation (i.e., leaf litter:total) models by species. Models used estimates of litter proportion of net tree aboveground biomass production as dependent variables, and the percent of the growing season in which Pass Manchac stage exceeded Maurepas swamp mean elevation as a covariate.

Model	Effect	Num. DF	Den. DF	F	P	Estimate	StdErr
<i>T. distichum</i>	habitat cluster	3	67.9	1.50	0.2230		
	flooding	1	188	11.88	0.0007	-0.5691	0.1651
<i>N. aquatica</i>	habitat cluster	2	64.1	7.75	0.0010		
	flooding	1	157	7.54	0.0067	-0.4607	0.1678
Other	habitat cluster	2	54	0.01	0.9910		
	flooding	1	156	7.38	0.0073	-0.4077	0.1501

aboveground primary production model for the collection of all other species.

Flooding during the growing season was a significant predictor of biomass allocation in all species-specific ANOVA models, but only the *N. aquatica* biomass allocation model showed a significant habitat effect. *Taxodium distichum*, *N. aquatica*, and all other species combined produced annually more litter than wood in all swamp habitat clusters included in the ANOVA models. Furthermore, *Nyssa aquatica*

produced a significantly greater proportion of litter at Hope Canal and Interior-East plots than at the Interior-West plots, where it was most prevalent. Inter-annual variation in aboveground biomass allocation to litter was strongly correlated with annual variation in Pass Manchac flooding, indicating a shift from litter to wood production in years with more extensive flooding (Table 2.4).

## **2.4. Discussion**

The Maurepas swamps have been cut off from the sustaining spring floods of the Mississippi River for over a century and are in varying states of decline. Flood control levees, abandoned raised railroad tracks, and spoil banks from oil canal dredging have impounded much of the remaining swamps, so that throughput of water is minimal in most areas. Bulk densities observed throughout most of the Maurepas swamp are low, and indicative of a lack of riverine influence for sediment input and throughput (Hatton et al., 1983). Nitrate concentrations in the surface water collected in rivers and channels in the Maurepas swamp in 2000 by Lane et al. (2003) were less than 1% of those found in Mississippi River water and are, in combination with low phosphate levels found, symptomatic of nutrient limitation throughout the swamp.

Observed tree species compositions throughout the Maurepas swamps are similar to those observed in comparable swamps in the Barataria Basin (Conner and Day, 1976; Visser and Sasser, 1995). *Morella cerifera*, *T. sebiferum*, and *S. nigra* gained importance (Table 2.2) as mid-story species in areas of disturbance, particularly in areas experiencing saltwater intrusion. By contrast, *Quercus* spp. and *F. pennsylvanica* were found in greater abundance at plots characterized by higher bulk densities, and could serve as indicators of increased throughput and generally less flooding. These observations support similar findings from wetland plant ordinations by



White (1983) along the Pearl River, Louisiana, and Rheinhardt et al. (1998) in the forested riverine wetlands of the inner coastal plain of North Carolina.

The forest structure in the interior Maurepas swamps is in the range of stem densities and basal areas reported for several restored, impounded, and stagnantly flooded swamps (Conner et al., 1981; Taylor, 1985; Mitsch et al., 1991; Conner and Day, 1992). Only a few areas in the south-west portion of the study area exhibited dense forest structures with full canopies and large numbers of smaller trees. Previous field studies have found that natural regeneration of *T. distichum* and *N. aquatica* is minimal in many swamp forests in coastal Louisiana due to flooding during germination and early growth stages (e.g., Montz and Cherubini, 1973; Conner and Day, 1976; Visser and Sasser, 1995). Furthermore, while continuous flooding may not be immediately detrimental to cypress-tupelo swamps, flooding will lead to their gradual death over time (Harms et al., 1980; Conner and Brody, 1989). Based on their current low structural complexity, many areas in the interior Maurepas swamps appear to be in various stages along this trajectory of swamp decline.

Average stem densities and basal areas of swamps located around the eastern rim of Lake Maurepas are less than any reported in the previously cited studies, showing that these plots are converting to shrub-scrub, brackish marshes, and open water. Saltwater intrusion into the soils of these swamps, especially during the drought in 2000, was sufficient to kill hundreds of *A. rubrum*, *N. aquatica*, and *F. pennsylvanica*. Conner et al. (1997) and Pezeshki et al. (1989) reported that *N. aquatica*, *F. pennsylvanica*, and *A. rubrum* showed signs of stress and reduced growth even at salinities as low as 2 to 3 psu, which would explain their marked absence and high mortality in the vicinity of Pass Manchac. While soil salinities near Pass Manchac have

gradually decreased from the annual average of 4-5 psu during the unprecedented drought in 2000 (Thomson et al., 2002) back to below 2 psu, many areas were largely deforested by this event, and future saltwater intrusions may complete the conversion of swamp to marsh and open water in this part of the basin in the near future (Barras et al., 1994). Swamp areas on the western margin of Lake Maurepas were not as severely impacted by the salt-water intrusion as swamp areas near Pass Manchac, and seemed to have returned to low ambient salinity levels more quickly.

With the exception of a few areas in the swamp interior south-west of Lake Maurepas, aboveground biomass production throughout the Maurepas swamps was low and in the range of that reported for nutrient-poor, stagnantly flooded swamps (Schlesinger, 1978; Taylor, 1985; Mitsch et al., 1991). Throughout the Maurepas swamps, *Taxodium distichum* generally produced more aboveground biomass than *N. aquatica*, except in areas where *N. aquatica* has a much greater relative structural importance than *T. distichum*. The greater aboveground production by *T. distichum* could be due to flooding conditions being more favorable to *T. distichum* growth than to *N. aquatica* growth. Keeland and Sharitz (1995) found that *N. aquatica* and *N. sylvatica* var. *biflora* grew better than *T. distichum* in deep, periodic flooding, whereas *T. distichum* growth was greater in conditions of shallow, permanent flooding. Both canopy tree species in the Maurepas swamp, *T. distichum* and *N. aquatica*, increased their aboveground biomass production during years with reduced flooding during the growing season. Taken together, these lines of evidence might indicate that the interior Maurepas swamps are near-continuously flooded.

An alternate explanation than flooding for the difference in the productivity of *T. distichum* and *N. aquatica* could be differences in the extent and severity of insect

defoliation experienced by each species. It has been hypothesized that *N. aquatica* herbivory by forest tent caterpillar outbreaks could have been instrumental in the establishment of the nearly pure stands of *T. distichum* that originally dominated swamps in coastal Louisiana (Conner and Day, 1976). Regular outbreaks of this *N. aquatica*-specific pest insect have been recorded since 1948, and can result in the complete defoliation of *N. aquatica* over tens of thousands of hectares, thus giving *T. distichum* a definitive growth advantage. Only fairly recently, the baldcypress leafroller was discovered to be the first serious insect pest species specific to *T. distichum* in 1983 (Goyer et al., 1990). By now, regular outbreaks of baldcypress leafroller infestations defoliate tens of thousands of hectares of *T. distichum* throughout the Louisiana coastal zone, and infestations have spread to the Pontchartrain Basin (Allen et al., 1998). The extent to which either tree species is affected by insect defoliation in the Maurepas basin, as well as the comparative impact the defoliation has on tree growth in both species, remains debatable.

All of the tree species found in the swamps of coastal Louisiana are sensitive to salinity at relatively low concentrations (i.e., 2-10 psu). Most studies investigating the effects of salinity and flooding on tree seedlings also found that there is a synergistically negative effect between salinity and flooding (Conner and Askew, 1992; Conner and Askew, 1993; McCarron et al., 1998). The flooding estimates used in my analysis were based on stage readings at Pass Manchac, which have been found to be affected by local precipitation but also by the wind-driven circulation of the nearby Gulf of Mexico (Thomson et al., 2002). Due to the negative correlation of salinity and flooding, the negative effect of salinity on aboveground biomass production could not be disentangled from concurrent positive effects of reduced flooding during drought years.

It seems likely, however, that a synergistically negative effect of both produced the extremely low aboveground biomass production values at the Lake plots over time.

Increased aboveground biomass allocation to wood production has been noted as a reliable measure for detecting stress in forested wetlands (Brown, 1981; Megonigal et al., 1997). Greenhouse and field investigations have shown that continuously flooded *T. distichum* saplings allocated more carbon to boles (Megonigal and Day, 1992), while mature *T. distichum* had a greater proportion of wood production under continuously flooded conditions (Young et al., 1995). The lower proportion of aboveground biomass production allocated to leaf litter by *N. aquatica* in the Interior-West habitat plots is thus likely an indicator of greater flooding stress in this portion of the basin, as compared to surrounding areas. Throughout the Maurepas swamps, aboveground biomass allocation to leaf litter decreased in response to increases in annual mean stage at Pass Manchac, which lends further evidence to support the hypothesis that biomass allocation can be used as a measure to detect flooding stress.

In summary, the majority of the Maurepas swamp is stressed and seems to be on a trajectory of slow degradation from swamp to marsh. Near-continuous flooding and nutrient deprivation appear to be the largest stressors in the swamp interior. Increasing periods of flooding have been found to decrease the allocation of carbon to the root system (Powell and Day, 1991), so it is likely that swamp interior plots that currently experience near-continuous flooding will experience a greater rate of subsidence than surrounding areas that are flooded less intensely, and will thus undergo an increasingly rapid decline. The combination of observed salt and flooding stress is killing large proportions of the trees located along the lakeshore near Pass

Manchac, and most of these areas are likely to convert to marsh or open water within a few decades.

At present, the Mississippi River diversion into the Maurepas swamp has been approved as a restoration project under CWPPRA, and is currently in Phase 1 (engineering and design) of its implementation. Pulsing events of nutrient and sediment supply to wetlands from river floods or storm events have been found to be essential to the stability of coastal wetlands and the ability of these wetlands to offset RSLR (Day et al., 1995; Odum et al., 1995). Located at the inland edge of the deltaic gradient, the coastal swamps in the Mississippi River Deltaic Plain historically benefited from the pulsing energy of annual river floods in the Mississippi River and its tributaries. Re-establishing the natural hydrology of coastal swamps by reconnecting them even partially to their historic river sources is likely to benefit the persistence and productivity of these subsiding wetlands. Because of the baseline monitoring efforts conducted to date, this restoration effort will provide a unique opportunity to study and model the dynamic ecosystem responses to changes in the current gradients of flooding stress, salinity stress, and nutrient limitation.

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## **CHAPTER 3: INDIVIDUAL-BASED MODELING OF A COASTAL SWAMP FOREST**

### **3.1 Introduction**

Coastal swamps and bottomland hardwood forests are among the rapidly vanishing wetland habitats in Louisiana. Throughout the Mississippi River Alluvial Plain, more than 75% of the original forested wetlands have been lost (Llewellyn et al., 1996). This loss of forested wetlands has serious consequences for wildlife conservation, and threatens the ecosystem functionality of these valuable habitats. The decline of coastal swamps, in particular, has been attributed to three main factors: (1) negative impacts of hydrologic alterations within the swamp following logging in the early 1900s; (2) additional stresses through sea-level rise and subsidence; and (3) the separation of most swamps from riverine inputs (Conner et al., 1981; Conner et al., 1986; Salinas et al., 1986; Myers et al., 1995; Krauss et al., 2000; Conner and Inabinette, 2003). Thus, there is a general consensus that the underlying basic stressors affecting the deterioration of coastal swamps are increased flooding, nutrient and sediment deprivation, and saltwater intrusion. Predicted consequences of global climate change on sea-level rise and renewed logging activities in the coastal zone will likely further accelerate the ongoing decline of coastal swamps. Quantifying the rate at which swamps may convert to marsh or open water, and the threshold levels of flooding and salinity that would cause such conversions, are important for proper management and for ensuring the viability of this habitat.

Many questions remain about the long-term effects of the restoration efforts employed to slow, halt, or reverse wetland loss and improve conditions for coastal swamp forests, as the impact of restoration techniques on a basin-scale may take decades to develop fully (Boesch et al., 1994). Of the many strategies of wetland

restoration or creation in use throughout coastal Louisiana (Underwood et al., 1997; Turner, 1999), only few are applicable to forested wetlands. These restoration efforts include hydrologic restoration, restoration of abandoned agricultural lands, and the construction of controlled and uncontrolled Mississippi River diversions. In many cases, herbivore control of nutria and vegetative plantings are used to supplement these strategies. Our uncertainty regarding the long-term effects of restoration efforts is exacerbated in forested wetlands by canopy tree species living 1,000 years or longer (Wilhite and Toliver, 1990). Our ability to detect significant long-term declines in forested wetlands, and measurement of the responses of forested wetlands to restoration efforts, thus requires decades to centuries of monitoring data. In lieu of sufficient field monitoring data, there has been reliance on predictions from general models of ecosystem behavior that often use many simplifying assumptions that disregard the complex interactions of multiple forcing functions and their resulting biological responses at the varying temporal and spatial scales at which they occur (Costanza et al., 1990; Martin et al., 2002).

One viable approach to investigating the long-term habitat changes of a forested wetland under various environmental and biological conditions is the use of individual-based forest succession models. Individual-based forest succession models describe the habitat as a mosaic of closed tree canopies, and use light availability as the critical limiting factor of tree growth (Botkin et al., 1972; Shugart et al., 1973). Individual trees of different species may be affected differentially by additional stressors (i.e., flooding stress, soil conditions), and are subjected to species-specific mortality and regeneration rates. Individual-based models can simulate the dynamics of forest succession across environmental gradients over time scales ranging from single years to centuries.



While there have been many individual-based forest succession models developed since the early 1970s (Porte and Bartelink, 2002), only a few have been developed specifically for wetland forests (Phipps, 1979; Pearlstine et al., 1985; Xiao et al., 2002) and only one has included the effects of salinity (Chen and Twilley, 1997). Most of the individual-based forest succession models were developed for upland forests. The models that represented multiple growth limiting factors beyond just light generally focused on soil-related variables, such as soil moisture, soil quality, or nutrient gradients. Another limitation of many of the existing models is the simplified approach to reproduction (e.g., randomly selecting new trees from species lists).

In this chapter, I develop an individual-based two-species forest succession model in a dynamic coastal landscape that experiences differential flooding on the scale of 10's of meters and allows for species-specific responses to flooding and to changes in salinity. I used repeating sequences of historical time-series of stage (water levels) and salinity collected within the Maurepas Basin as input for the swamp IBM. The model follows the growth, mortality, and reproduction of individuals of baldcypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*) trees from birth to death on a weekly time step on a spatial grid of 10m x 10m cells. I calibrated the model to stem densities, basal areas, and wood production rates reported in the literature (baseline conditions), and corroborated the model by using the calibrated model to roughly simulate conditions at several plots in the Maurepas swamp and compared predicted and observed stem density, basal area, and wood production across the plots. I then changed the mean elevation of the cells, variability in elevation of the cells, and salinity, and compared predicted responses of basal area, stem density, wood production, and species composition between the altered conditions and baseline conditions. My major

objective was to develop a model that was capable of realistically simulating the dynamics of a forested swamp for the range of environmental conditions observed within the Maurepas Basin, and that was able to accommodate the effects of flooding and salinity, including their possible interactive effects with each other and with other environmental and biological factors. I conclude with a discussion of model performance, the importance of specifying species-specific tolerances, how the final version of my swamp IBM compares to available field data and to some existing models of forested wetlands, and which further model developments would best strengthen the model.

### **3.2 Maurepas Swamp**

The wetlands of Lake Maurepas comprise the northern boundary of the Lake Pontchartrain Basin, a marginal deltaic basin within the Mississippi River deltaic plain in coastal Louisiana, USA. The Maurepas wetlands include approximately 563 km<sup>2</sup> of second-growth *Taxodium distichum* - *Nyssa aquatica* dominated swamps, and 150 km<sup>2</sup> of fresh and intermediate marshes. Extensive logging took place in the Maurepas basin in the early 1900s, and large areas on the eastern part of the basin have not re-grown since then. The swamps in this region are impacted by saltwater intrusion and by elevated levels of subsidence (Pezeshki et al., 1987), while the marshes are generally breaking up into open water (Barras et al., 1994) due to a lack of sediment and nutrient input (Shaffer et al., 2001; Day et al., 2004) and increased flooding (Thomson et al., 2002). Extensive monitoring and experimental studies have been undertaken from 2000 till the present to evaluate the restoration potential of these wetlands through the implementation of a freshwater diversion from the Mississippi River into this region (Chapter 2). Baseline reports identified the need for restoration of the wetland system

and indicated that the Maurepas wetlands would benefit greatly from the infusion of freshwater, sediments, and nutrients by the proposed diversion (Shaffer et al., 2001; Hoeppner, 2002; Day et al., 2004; Shaffer et al., 2007). The Mississippi River diversion into this swamp has been approved as a restoration project under the Coastal Wetlands, Protection, Planning and Restoration Act (CWPPRA, Public Law 101-646, 1990) and is currently in Phase 1 (engineering) of its implementation. The expected ecosystem responses resulting from this restoration effort provide a unique opportunity to study and model the dynamic changes in the current stressor gradients before and after a freshwater diversion. My focus in this chapter is on the development of the individual-based succession model for current conditions, which would set the stage for further application of the model to examine restoration scenarios.

### **3.3 Model Description**

#### **3.3.1. Model Overview**

The swamp individual-based tree model (swamp IBM) simulates the weekly growth, survival, and reproduction of two forested wetland tree species, *Taxodium distichum* (baldcypress) and *Nyssa aquatica* (water tupelo), over a spatial extent of 1-km<sup>2</sup> for up to 1,000 years. Seeds, seedlings, and saplings up to 4 years old are modeled as cohorts associated with their parent trees. At 4 years of age, surviving saplings in each cohort are converted to model individuals and are followed until their death or the end of the simulation. For each individual, the swamp IBM keeps track of its species, spatially-explicit location on the 1-km<sup>2</sup> grid of 10m by 10m (100 m<sup>2</sup>) cells, age, diameter, size class, basal area, and annual diameter growth increment. A 10m resolution is used in the model to capture fine scale variation in flooding and the interactions between individual trees. The individual-level tree attributes are

summarized annually into stand-level forest characteristics, such as stem density, basal area, species composition, recruitment (survivors to age-4 seedlings), and wood production.

Flooding and salinity are driving variables in the model, and a seasonally-specific function that repeats every year is used to adjust the weekly growth rates of the trees. Density-dependence is invoked through shading relationships and seed supply. Tree growth, seed viability, seed germination, and seedling survival are modeled in weekly time-steps, whereas tree mortality due to slow growth, random tree mortality, and seed production are modeled in annual time-steps (Figure 3.1).

### 3.3.2. Flooding

Flooding is determined for each 10m x 10m cell within the 1-km<sup>2</sup> grid based on water depth, which is calculated as the difference between stage (i.e., the water-surface elevation in relation to sea-level) and the assigned elevation of the cell. The model keeps track of the number of weeks each cell is flooded (stage greater than elevation) and the number of weeks of continuous flooding in each cell. If stage is between the elevation and 15 cm below elevation in any given week, the continuous flooding counter for that cell is decreased by one to imitate a slow re-oxygenation of the soil. Once stage decreases to more than 15 cm below the cell's elevation, the cell is considered dry and the continuous flooding counter is reset to zero.

Soil elevations for each cell in the model are specified from a 1-km<sup>2</sup> landscape scene that was selected from a ~ 2,300 km<sup>2</sup> elevation map covering the Maurepas Basin and surrounding area (Figure 3.2). The soil elevations in the Maurepas basin elevation map were estimated from modified digital elevation maps (DEMs), which have a spatial resolution of 5m x 5m and were produced as part of the national remote

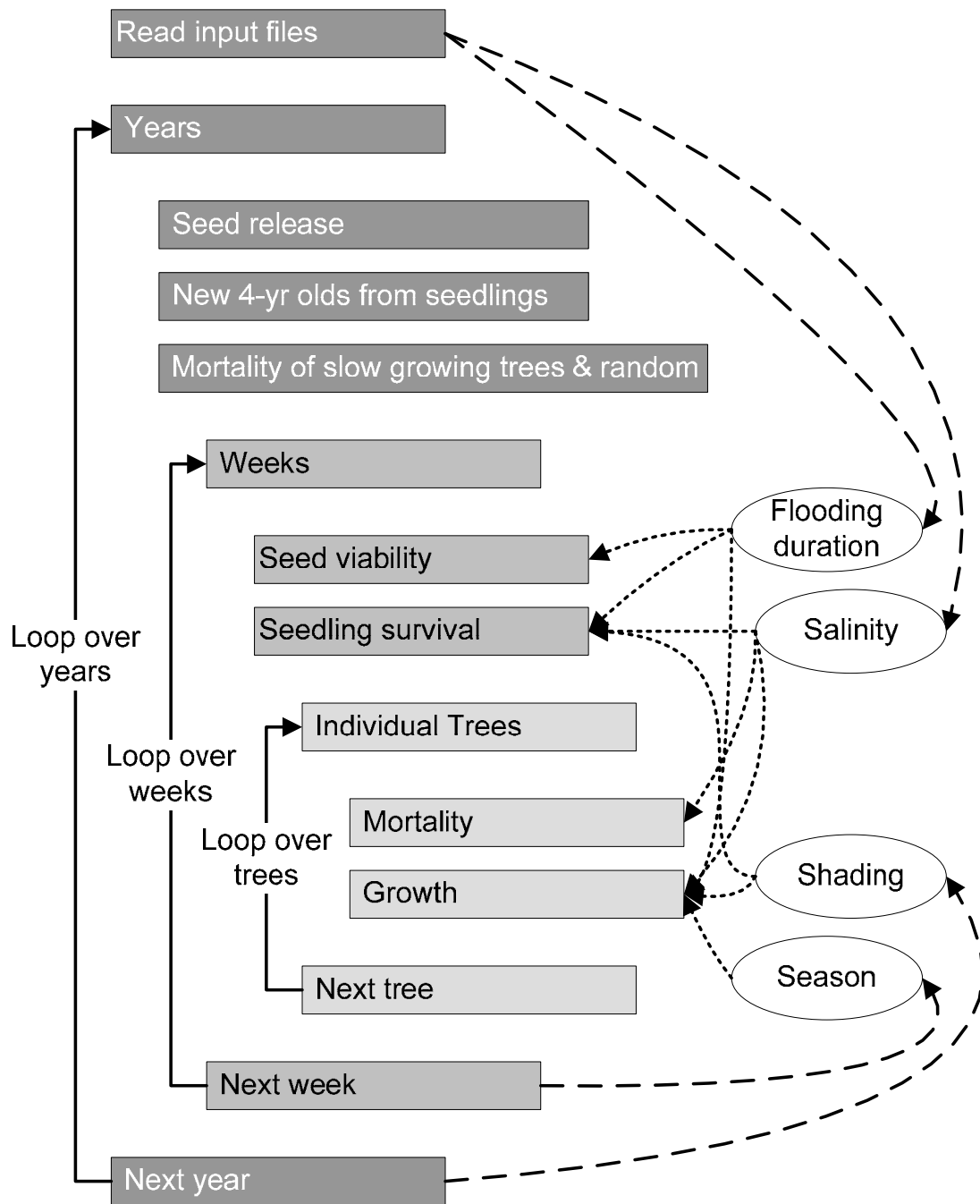


Figure 3.1 - General overview of processes and computations in the swamp forest IBM.

sensing mapping program of Light Detection and Ranging (LIDAR) performed in 1999 (Louisiana statewide GIS database, available online at: <http://atlas.lsu.edu/>). The 5-m resolution soil elevation estimates from the DEMs were aggregated into 10m by 10m cells by averaging four neighboring 5m by 5m cells.

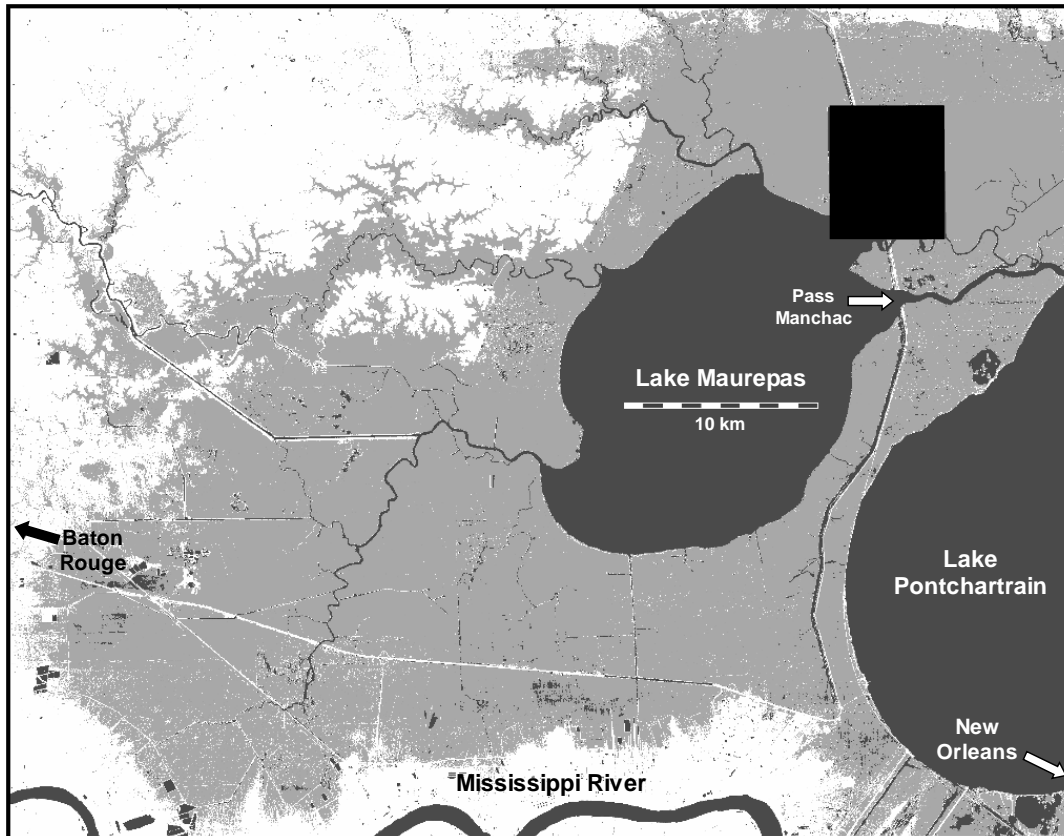


Figure 3.2 - Map of the area of interest from which 1-km<sup>2</sup> scenes were selected to be used as elevation maps in IBM simulations. Open water is shown in dark grey, wetlands in light grey, and uplands in white. The black box denotes an area that has missing elevation data.

The stage data used in the swamp IBM was based on the U. S. Army Corps of Engineers (USACOE) historical records of data collected at Pass Manchac (Figure 3.2). The available 48-year record of daily stage measurements from the Pass Manchac stage gage (USACOE gage ID 85420; gage zero is at the National Geodetic Vertical Datum of 1929) for the time period of 1956-2004 is repeated to produce a 1000-year weekly sequence of stage data that includes observed seasonal and inter-annual correlations. Figure 3.3 shows the long-term average of weekly stage at Pass Manchac with standard deviations to indicate year-to-year variation in reference to the growing season specified in the swamp IBM.

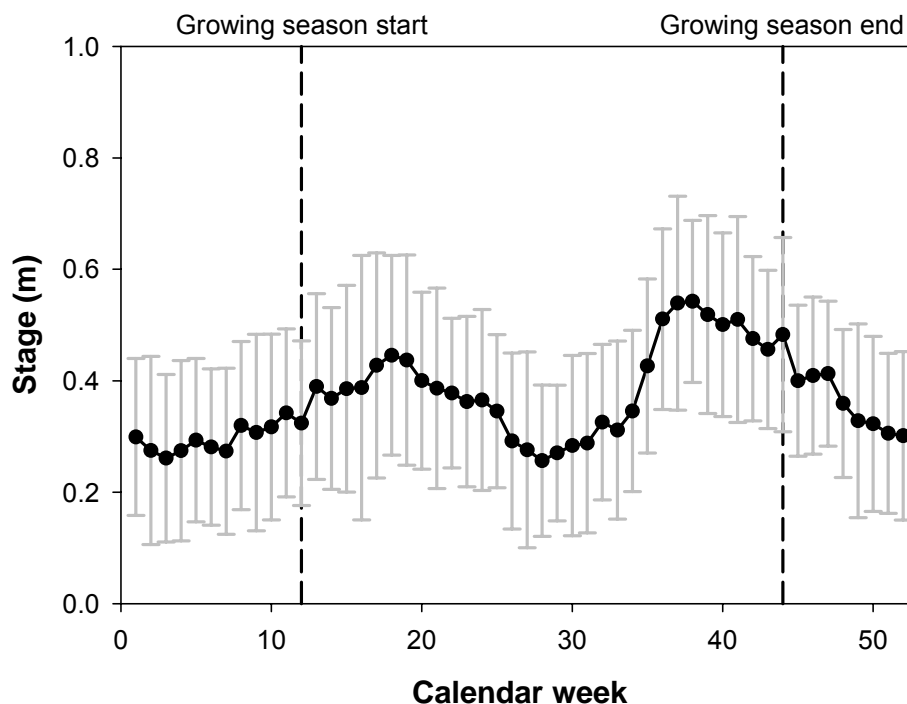


Figure 3.3 - Mean weekly stage (relative to mean sea-level) at Pass Manchac for the 49-year period of 1956 to 2004 used in model simulations. Error bars indicate the annual standard deviation from the long-term weekly means to show inter-annual variation. The 49-year period of record is repeated again and again to produce the 500 or 1,000 year sequences of stage values used in the simulation runs.

### 3.3.3. Salinity

Model simulations were performed under freshwater conditions (0 psu salinity), and under weekly salinity values based on measurements of salinity at Pass Manchac. The available salinity data consisted of hourly salinity readings taken between 1988 and 1996, with several months and years of missing data. I used an analysis of co-variance (ANCOVA) model using SAS software, Version 9.1.2, of the SAS System for Windows (SAS Institute Inc., 2000-2004) to predict salinity for the time periods during which no salinity data was collected. The statistical model was based on 264 co-located readings of salinity and stage at Pass Manchac and indicated that the interaction of week and stage is a significant predictor of salinity ( $F_{51,160} = 1.88$ ,  $p = 0.0017$ ). Figure 3.4 shows

the 48-year average of the predicted weekly mean ambient salinity used in model simulations that involved conditions other than freshwater. Forty-nine years of weekly salinity were generated to match the 49-year time series of weekly stage data.

Salinity levels in each 10m cell in the model were updated weekly using flooding to modify the ambient salinity. Weekly levels of ambient water salinity were assumed to apply to all cells in the model grid. The salinity in each cell was updated to the ambient salinity whenever the cell was flooded. If a cell was not flooded in a given week of the simulation, the cell retained its salinity value.

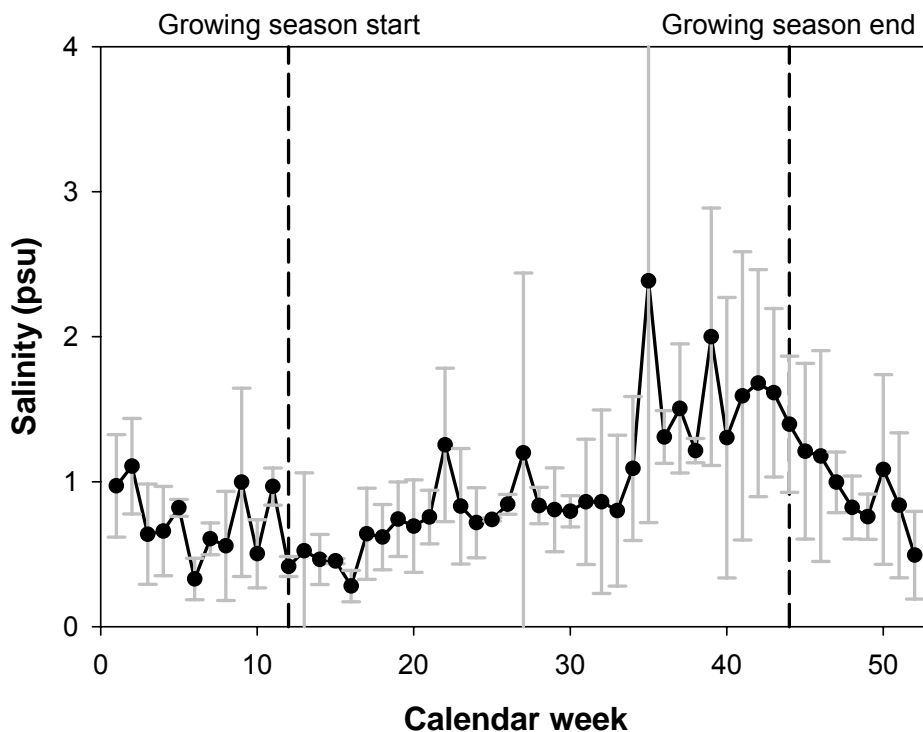


Figure 3.4 - Mean weekly salinity ( $\pm$  SD) at Pass Manchac used in model simulations. The original data was based on salinity records from 1988 to 1996, which were then statistically extrapolated to cover the same 49-year period as the stage data shown in Figure 3.3. Error bars indicate the annual standard deviation from the long-term weekly means to show inter-annual variation. The 49-year period of record is repeated again and again to produce the 500 or 1,000 year sequences of stage values used in the simulation runs.



### 3.3.4. Tree Growth

Tree growth is modeled as a size-dependent maximum annual diameter increment ( $\text{cm year}^{-1}$ ), modified by season, light availability, weeks of continuous flooding, and salinity:

$$\Delta \text{DBH} = \Delta d_{\max} \times g_{\text{season}} \times g_{\text{light}} \times g_{\text{flooding}} \times g_{\text{salinity}}$$

Maximum annual diameter growth ( $\Delta d_{\max}$ ) is modeled the same for both tree species (Figure 3.5), and decreases non-linearly with increasing diameter at breast height (DBH in cm):

$$\Delta d_{\max} = \frac{1}{(0.85 + (0.02 \times \text{DBH}))}$$

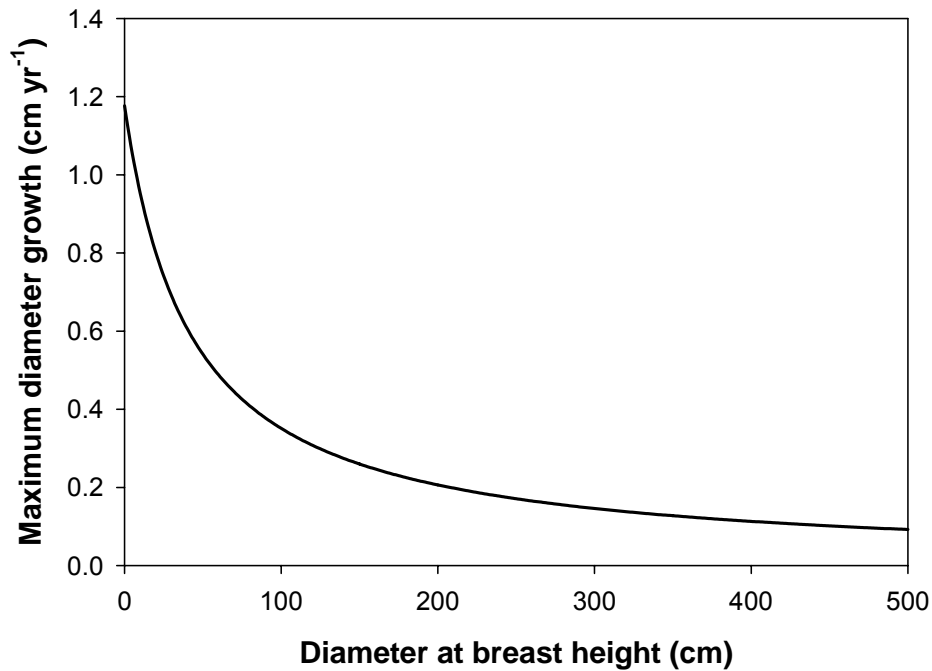


Figure 3.5 - Maximum diameter growth ( $\Delta d_{\max}$ ) decreases with increasing tree diameter at breast height (DBH). The same relationship is used for *T. distichum* and *N. aquatica*.

I used a seasonal growth modifier ( $g_{\text{season}}$ , Figure 3.6) to approximate the effects of seasonal temperature and light intensity on maximum tree growth. The seasonal growth function is a log-normally-shaped function generalized from annual stem-growth

curves for *T. distichum* and *N. aquatica* found in coastal Louisiana and South Carolina (Conner and Day, 1992; Keeland and Sharitz, 1995), and the same function is used for both species:

$$g_{season} = a \times e^{\left( -0.5 \times \left( \frac{\log_e \left( \frac{\text{calendar\_week}}{b} \right)}{c} \right)^2 \right)}$$

where  $a = 0.1217$ ,  $b = 20.3165$ ,  $c = 0.1593$

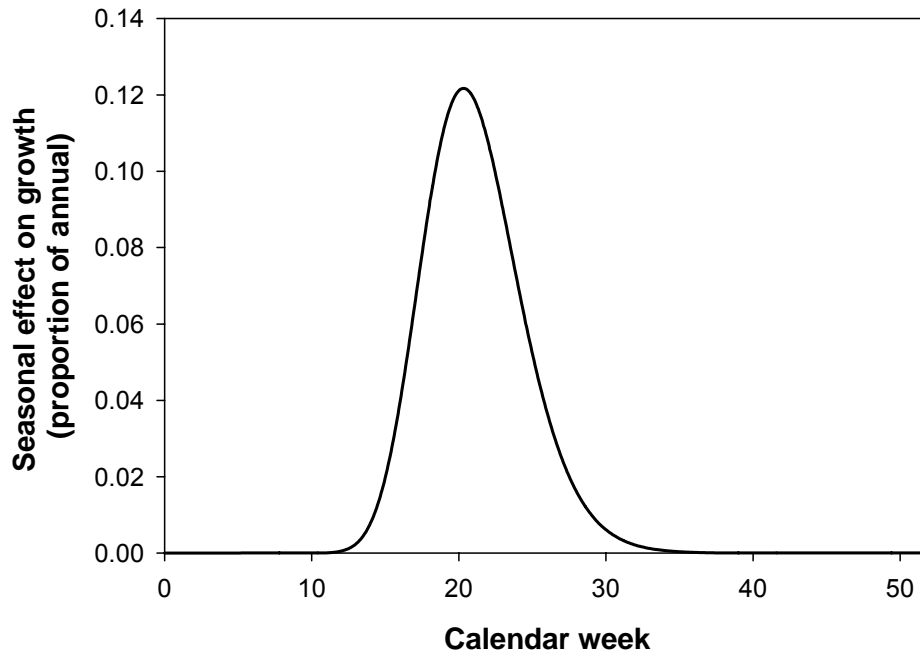


Figure 3.6 - Weekly allocation of annual diameter growth ( $g_{season}$ ). The same relationship is used for *T. distichum* and *N. aquatica*.

The effect of shading on light available for tree growth ( $g_{light}$ ) depends on the sizes of the individual trees within a 10-m radius neighborhood and their effect on light penetration. The amount of light available to each tree is determined for each new year at the end of the growing season of the previous year from the sum total of the basal areas and the stem densities of other individual trees within a 10-m radius of the tree under consideration. Each tree in the neighborhood is evaluated and their stem density

and basal area is summed, with weighting factors based on the DBH size-class bin (2-10 cm, 10-20 cm, 20-30 cm, etc) to which they belong. Each tree is shaded by 100% of the trees that are two diameter size classes larger than itself, by 80% of the trees that are one diameter size-class larger, by 60% of the trees that are of the same diameter size-class, and not at all by trees that belong to smaller size-classes. Trees in the smallest size-class (i.e, 2-10 cm DBH) are treated differently; rather than using a 10-m radius to determine the trees that affect the tree of interest, I used the stem density and basal area of the smallest-sized trees that were in the same cell as the tree of interest and, when summing, weighted their stem density and basal area by 50%. The sum of the basal areas and stem densities of the shading trees are then converted to per-hectare ( $BA_{\text{shading-ha}}$ ,  $SD_{\text{shading-ha}}$ ), and used to determine the amount of light available to each tree based on unpublished data of Dr. Gary Shaffer (Southeastern Louisiana University) (Figure 3.7):

$$\text{light} = 2.6802 - 0.00738 \times BA_{\text{shading-ha}} - 0.3093 \times \log_e(SD_{\text{shading-ha}})$$

where the value of light is truncated below at zero and above at one. The tree growth response ( $g_{\text{light}}$ ) is then computed from the available light and is assumed to be the same for both species and to follow a general sigmoid function (Figure 3.8):

$$g_{\text{light}} = a + \frac{b}{\left(1 + e^{-\left(\frac{(\text{light}-c)}{d}\right)}\right)}$$

$$\text{where } a = -0.0865, \quad b = 1.1303, \quad c = 0.4347, \quad d = 0.1761$$

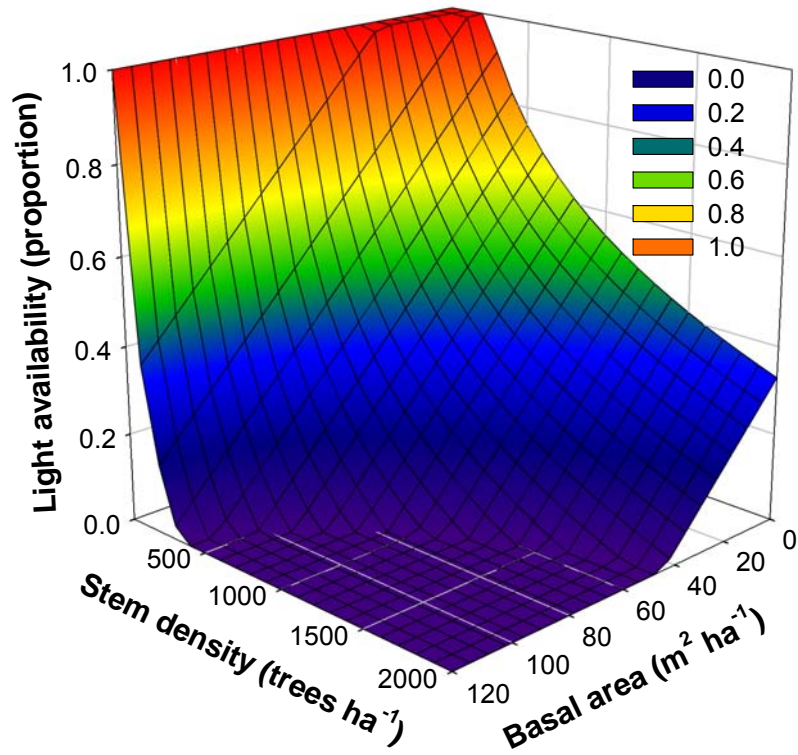


Figure 3.7 - Effect of the basal area ( $BA_{\text{shading-ha}}$ ) and stem density ( $SD_{\text{shading-ha}}$ ) of shading trees on the available light remaining for the tree of interest (light). The value of light is truncated at zero and one. The same relationship is used for *T. distichum* and *N. aquatica*.

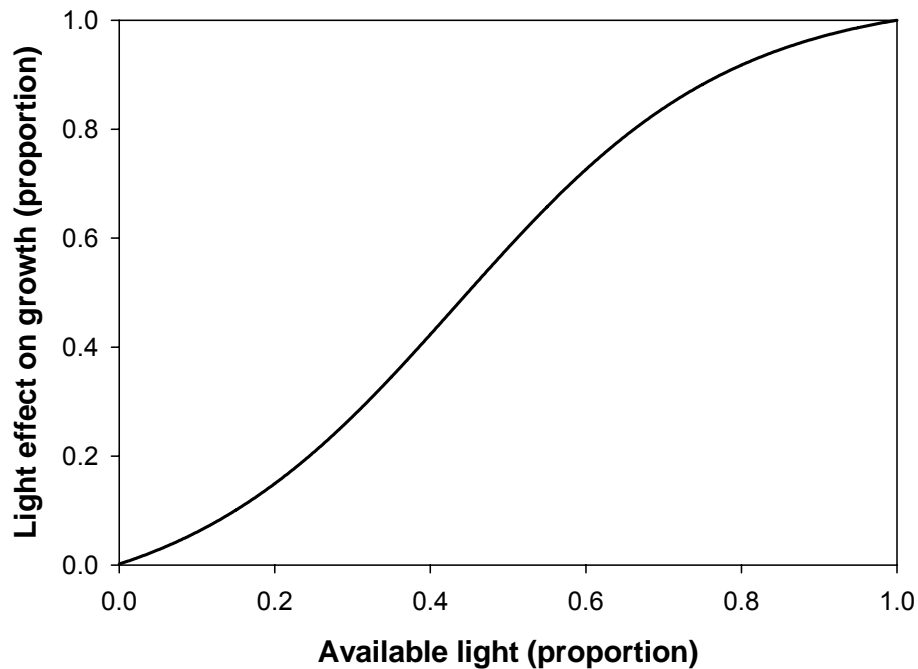


Figure 3.8 - Weekly diameter growth in response to the amount of available light ( $g_{\text{light}}$ ). The same relationship is used for *T. distichum* and *N. aquatica*.

The species-specific growth responses to flooding ( $g_{\text{flooding}}$ , Figure 3.9) are modeled using logistic-shaped functions and are depend on the number of weeks of consecutive flooding (x):

$$g_{\text{flooding}} = a + \frac{b}{\left(1 + \left(\frac{x}{c}\right)^d\right)}$$

where  $a_{T. \text{distichum}} = 0.5013$   $a_{N. \text{aquatica}} = 0.6020$

$b_{T. \text{distichum}} = 0.4987$   $b_{N. \text{aquatica}} = 0.3980$

$c_{T. \text{distichum}} = 3.9779$   $c_{N. \text{aquatica}} = 2.9612$

$d_{T. \text{distichum}} = 4.0767$   $d_{N. \text{aquatica}} = 3.4294$

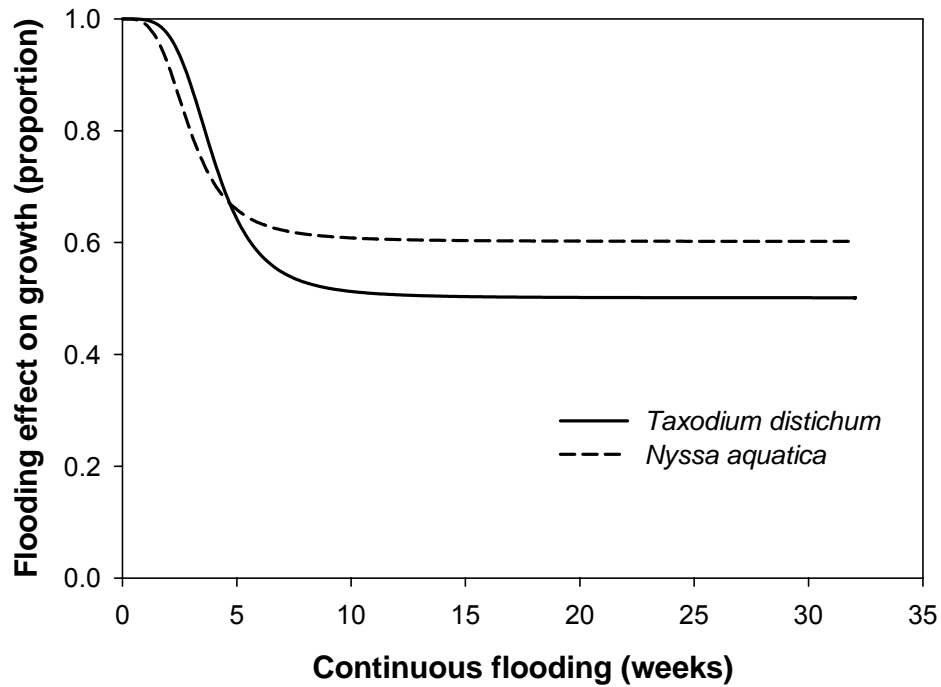


Figure 3.9 - Weekly diameter growth adjustment in response to continuous flooding ( $g_{\text{flooding}}$ ) for *T. distichum* and *N. aquatica*.

As both tree species are tolerant of permanent flooding, flooding effects in the model are assumed to remain constant for flooding beyond 10 to 20 weeks. In their responses to flooding, *T. distichum* and *N. aquatica* have been found to vary significantly. Keeland

et al. (1997) reported that *N. aquatica* grew best in hydrologic regimes of deep, periodic flooding, whereas *T. distichum* growth was greatest under shallow, permanent flooding conditions. Deep, permanent flooding decreased the growth of both *T. distichum* and *N. aquatica* (Keeland et al., 1997).

The salinity effect on growth ( $g_{\text{salinity}}$ ) was configured to have no-effect at 0 psu, and to cause greater reductions in growth with increasing salinity. The effect of salinity on the growth of both *T. distichum* and *N. aquatica* was modeled using species-specific logistic-shaped curves (Figure 3.10):

$$g_{\text{salinity}} = a + \frac{b}{\left(1 + \left(\frac{\text{salinity}}{c}\right)^d\right)}$$

where	$a_{T. \text{distichum}} = -0.17898$	$a_{N. \text{aquatica}} = -0.0087$
	$b_{T. \text{distichum}} = 1.17898$	$b_{N. \text{aquatica}} = 1.0087$
	$c_{T. \text{distichum}} = 6.034$	$c_{N. \text{aquatica}} = 2.6686$
	$d_{T. \text{distichum}} = 1.9151$	$d_{N. \text{aquatica}} = 2.4807$

I used seedling growth data from greenhouse experiments to infer the shape and the species differences in growth responses to salinity. Pezeshki et al. (1989) reported that the photosynthetic rates of *N. aquatica* seedlings decreased by 58% when exposed to salinities as low as 3 psu. In the closely-related species *Nyssa sylvatica* var. *biflora*, seedling biomass production was decreased by 43% after exposure to 2 psu salinity for 2 months (McCarron et al., 1998). Similarly, decreases of 15-30% in net photosynthesis have been reported following the exposure of *T. distichum* seedlings to salinity levels of as little as 2 psu, which intensified to 70-80% decreases at 8 psu (Pezeshki et al., 1988; Allen et al., 1997). By contrast, Conner (1994) found that after a 3-month exposure to a

10 psu salinity regime, *T. distichum* seedlings still achieved roughly 80% of the diameter growth exhibited by seedlings grown at 0 psu.

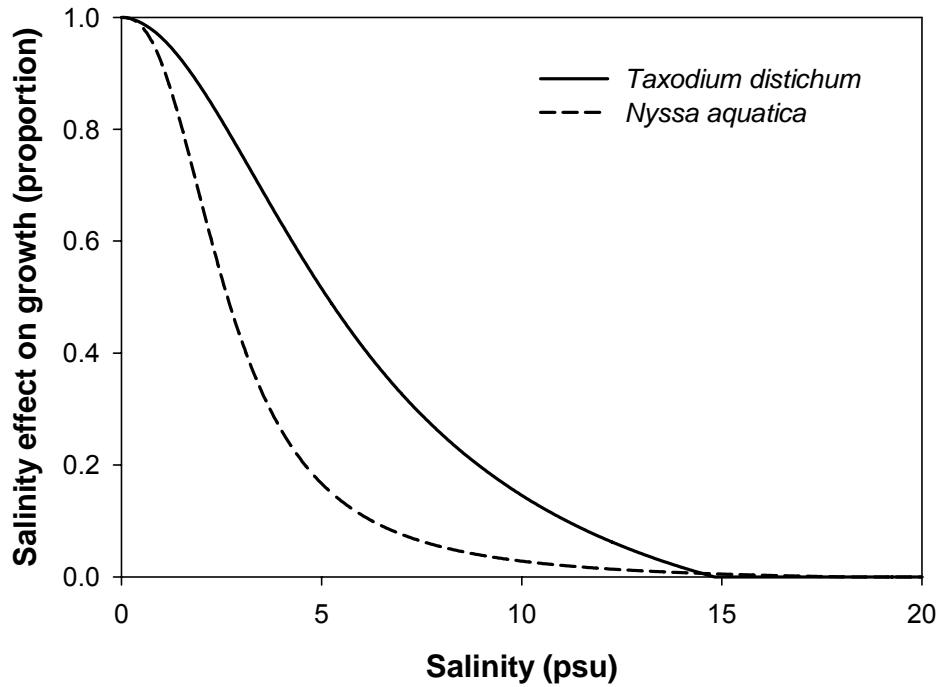


Figure 3.10 - Weekly diameter growth adjustment in response to elevated levels of salinity ( $g_{\text{salinity}}$ ) for *T. distichum* and *N. aquatica*.

### 3.3.5. Tree Mortality

Mortality is the mechanism by which standing biomass is reduced and by which canopy gaps are formed in the swamp. In the model, tree mortality is composed of two components (slow growth and random) that are applied at the end of each year and a salinity-related mortality imposed every week. Slow-growth mortality (Figure 3.11) is invoked equally for both tree species, and is modeled with an exponential function based on realized growth potential:

$$m_{\text{slow growth}} = 0.04 \times e^{(-75 \times g_r)}$$

$$\text{where } g_r = \frac{\Delta \text{DBH}}{\Delta d_{\text{max}}}$$

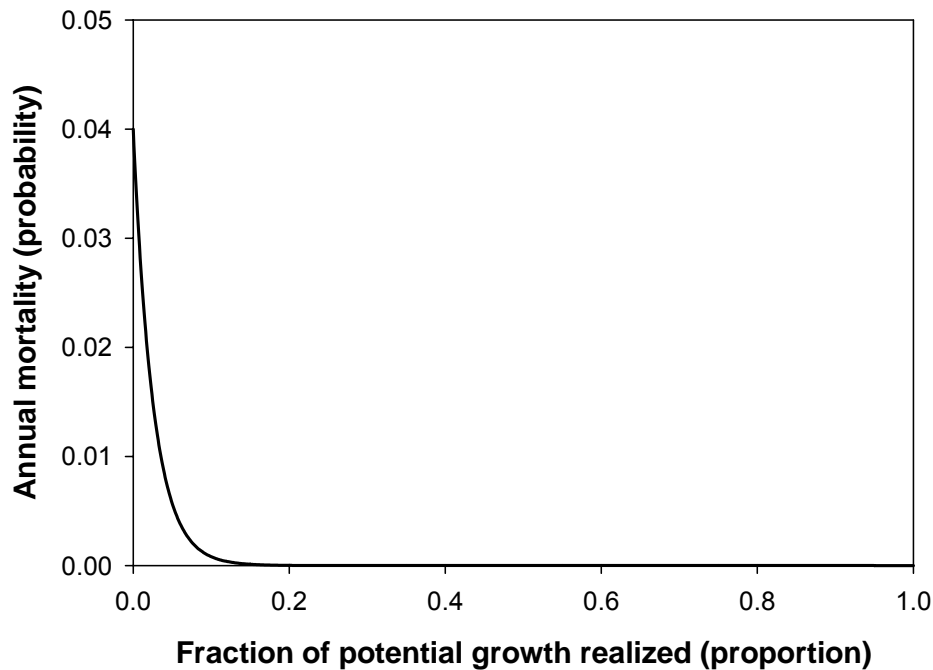


Figure 3.11 - Annual slow-growth mortality ( $m_{\text{slow growth}}$ ) as a function of a tree's realized growth potential. The same relationship is used for *T. distichum* and *N. aquatica*.

The slow-growth mortality function is loosely based on a shade-dependent sapling mortality function for blackgum (*Nyssa sylvatica*) reported by Lin et al. (2001). I adjusted their function from absolute radial growth to a form compatible with the size-dependent maximum growth formulation used in the swamp IBM. The random mortality component is fixed and randomly culls out 1.85% of all trees annually. Random mortality is invoked after slow-growth mortality. A uniform random number is generated for each tree, and compared first to the probability of dying from slow growth. If the tree dies from slow-growth, it is removed from the simulation. If the tree survives slow-growth mortality, then random mortality is evaluated with a new random number.

To include the possibility of mortality due to acute salt stress (i.e., when salinity is greater than 0 psu), salinity mortality for both seedling cohorts and older individuals is incurred weekly in the model. Weekly survival probability ( $s_{\text{salinity}}$ ) is represented by



species-specific logistic dose response equations that depend on the salinity in the cell where the tree or seedlings are located (Figure 3.12):

$$S_{\text{salinity}} = a + \frac{b}{\left(1 + \left(\frac{\text{salinity}}{c}\right)^d\right)}$$

where	$a_{T. distichum} = 0.7887$	$a_{N. aquatica} = 0.7333$
	$b_{T. distichum} = 0.2113$	$b_{N. aquatica} = 0.2667$
	$c_{T. distichum} = 14.103$	$c_{N. aquatica} = 13.863$
	$d_{T. distichum} = 3.4500$	$d_{N. aquatica} = 3.2007$

A uniform random number is generated for each tree on each week and if greater than the survival probability, then the individual tree is killed and removed from the simulation. Salinity-related mortality of seedlings is applied to the cohort as described in Reproduction.

The same functions were used for seedlings and individual trees, and the general shapes of the functions were formulated from available data on seedlings. Salinity tolerance of *T. distichum* has been reported as generally ranging from 2 psu (Chabreck, 1972) to 8.9 psu (Penfound and Hathaway, 1938). Field observations in the Maurepas swamps indicate that chronic exposure to salinity levels ranging from 1 to 4.5 psu caused 10-80% mortality of all prevalent swamp tree species over 5 years, and that *N. aquatica* was notably absent from most of the sites exposed to these salinity levels (Chapter 2). In a greenhouse experiment with a species closely related to *N. aquatica*, *Nyssa sylvatica* var. *biflora* seedlings experienced 100% mortality within 2 months of exposure to a salinity regime of 10 psu (McCarron et al., 1998). In a different experiment, Pezeshki et al. (1989) observed no mortality among *N. aquatica* seedlings during a 6 week exposure to 3 psu. Mesocosm experiments with *T. distichum* seedlings

have shown that seedlings of this species can survive greenhouse-simulated storm surges of up to 10 psu (Campo, 1996) and even 30 psu (Conner and Askew, 1992), albeit the latter only for a few days followed with rapidly decreasing salinity levels.

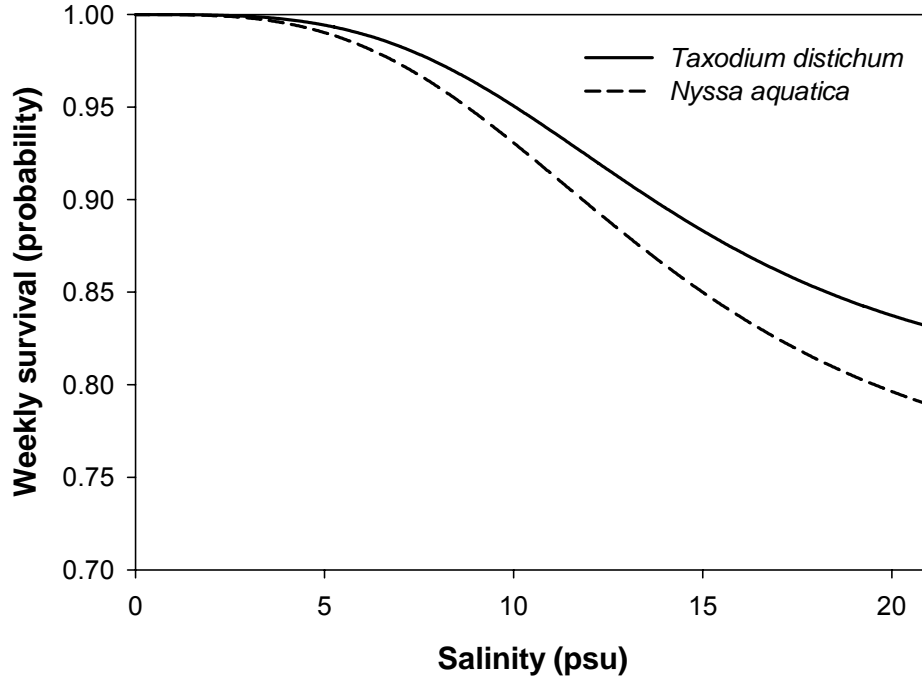


Figure 3.12 - Weekly survival probability ( $s_{\text{salinity}}$ ) of mature trees exposed to elevated salinity levels for *T. distichum* and *N. aquatica*.

### 3.3.6. Reproduction

Seeds can be produced once per year by any individual tree older than 10 years. All seeds are released at the end of November (i.e., in week 48), which roughly represents the peak of seed fall observed in the field (Schneider and Sharitz, 1988). The number of seeds released by each tree is determined as a species-specific maximum number of seeds, modified based on tree size and annual growth (Figures 3.13 and 3.14):

$$\text{seeds} = (0.05 \times d_{\text{canopy}} \times \text{seedmax}) + (0.95 \times g_r \times d_{\text{canopy}} \times \text{seedmax})$$

$$\text{where } d_{\text{canopy}} = \frac{DBH}{40} \quad (\text{constrained between 0 and 1})$$

$g_r$  = realized growth potential,

$\text{seedmax}_{T. distichum} = 750$ ,  $\text{seedmax}_{N. aquatica} = 600$

The maximum number of seeds per parent tree is fixed at 750 for *T. distichum* and at 600 for *N. aquatica* for any individual tree greater than or equal to 40cm DBH, which is the typical diameter at full canopy maturity.

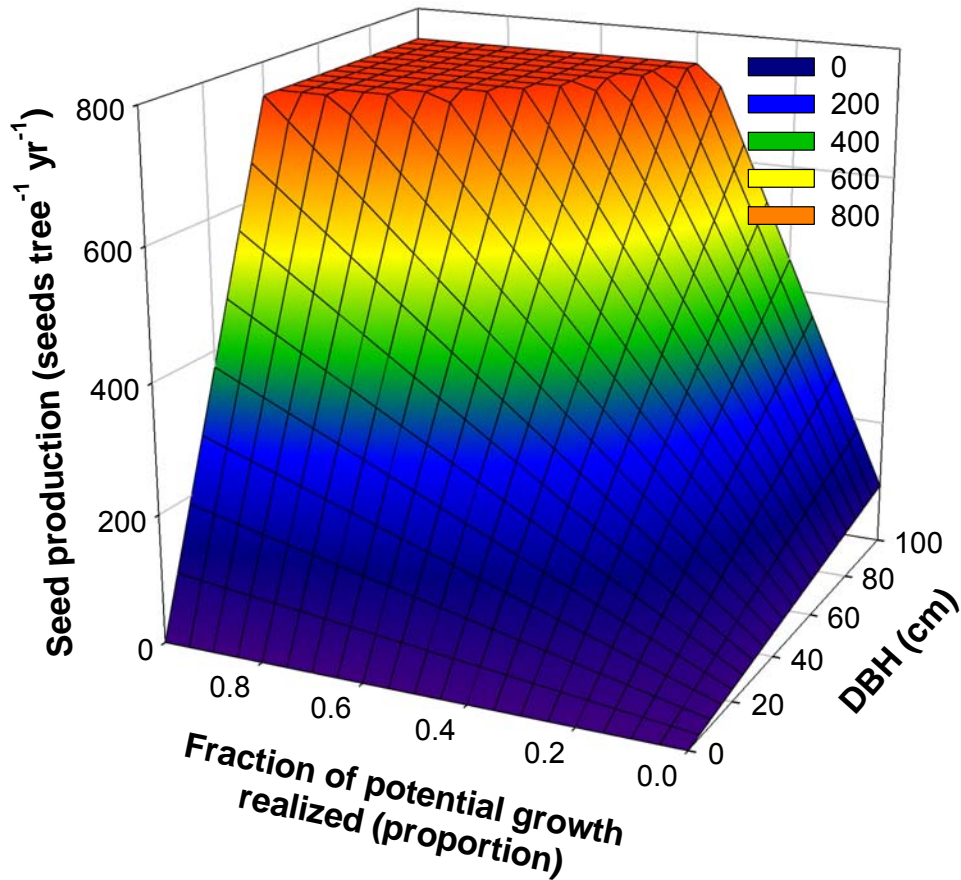


Figure 3.13 - The number of seeds produced per year by each *T. distichum* tree older than 10 years as a function of tree diameter (DBH) and realized growth potential. A maximum value of 750 seeds per tree is imposed.

### 3.3.7. Seedling Germination and Survival

From the time of seed drop at the end of November (i.e, week 48) up to the time of seed germination in spring and early summer of the following year (i.e., no sooner than week 10), the number of viable seeds associated with each parent tree is decremented by 6% each week for *T. distichum* and by 4.5% each week for *N.*

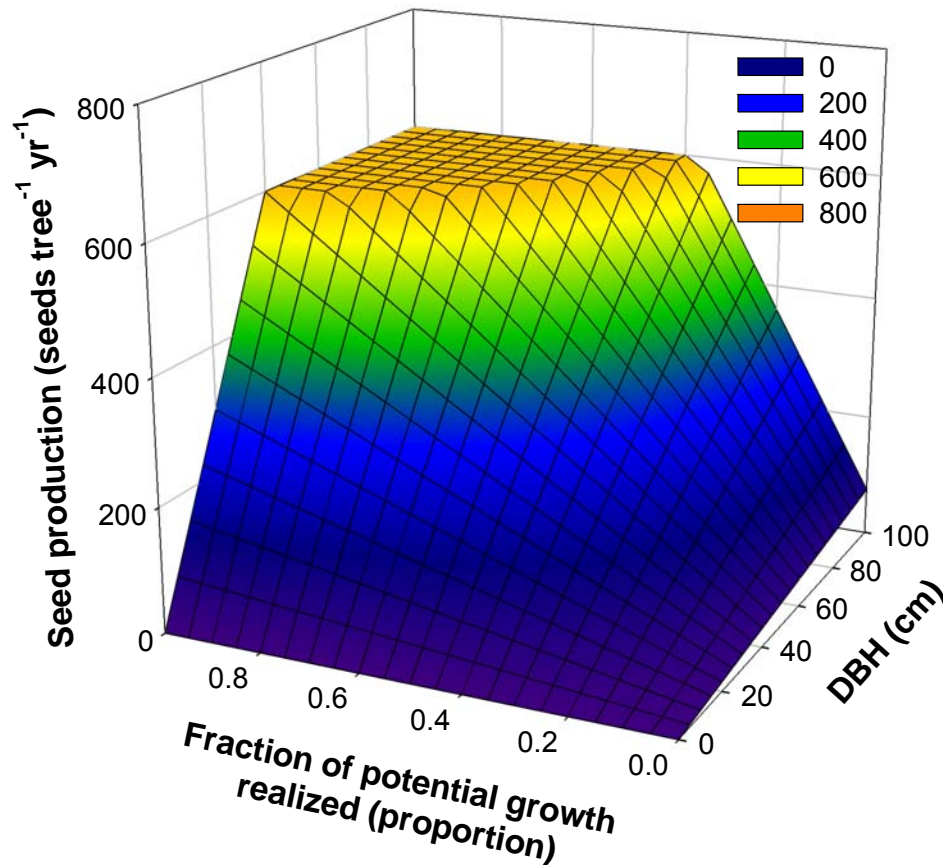


Figure 3.14 - The number of seeds produced per year by each *N. aquatica* tree older than 10 years as a function of tree diameter (DBH) and realized growth potential. A maximum value of 600 seeds per tree is imposed.

*aquatica*. Based on these mortality rates, and the species differences in maximum number of seeds per tree, trees of both species that are of equal size and have the same realized growth potential will have the same number of surviving seeds at the end of winter dormancy (Figure 3.15). For any week that a plot remains flooded after the onset of the germination period, *N. aquatica* gains an advantage in seed survival over *T. distichum*.

Starting at the onset of the model's growing season in mid-March (week 10) and continuing until the end of June (week 26), seed germination is evaluated weekly in each 100 m<sup>2</sup> cell. In the first week in the growing season during which a cell is not flooded, all seed cohorts in that cell germinate and become seedlings. As long as a cell

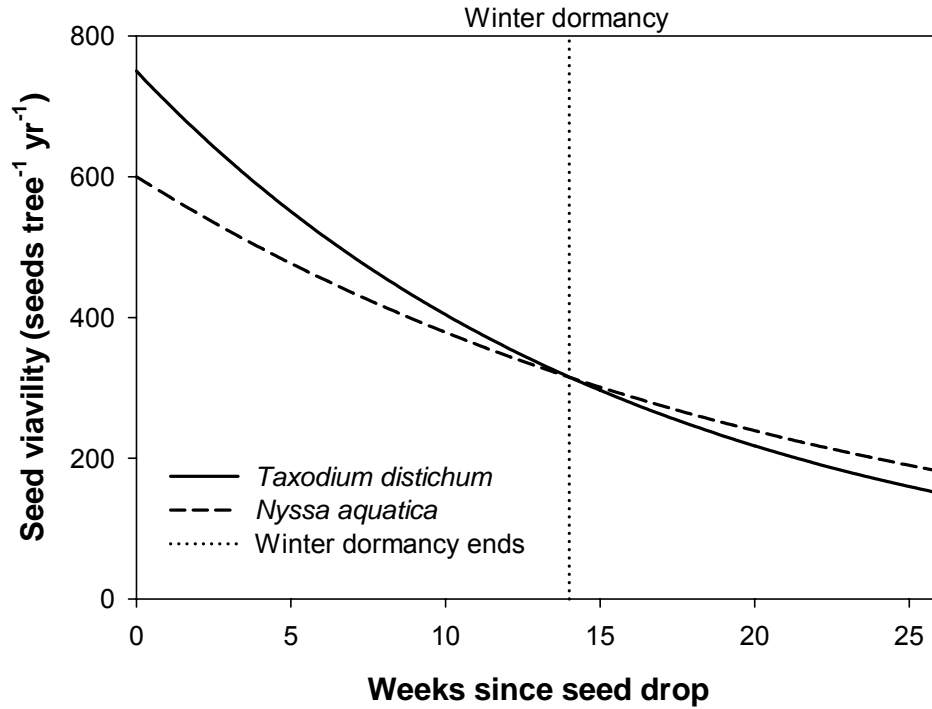


Figure 3.15 - Predicted weekly number of seeds per tree surviving during the winter months and in the time leading up to germination, assuming flooded conditions during the germination season. The initial numbers of seeds per tree are set to the maximum number allowed (750 for *T. distichum* and 600 for *N. aquatica*).

remains flooded, the seeds in that cell continue to decrease at the same 6% or 4.5% mortality rates per week as during the winter period. At the end of the germination period (week 26), any remaining cohorts that are still seeds are presumed dead and are removed. Middleton (2000) found that less than 5% of *T. distichum* seeds were still viable after 300 days in a field study of seed hydrochory in Illinois, and a similar loss of viability was presumed for all seeds in the model.

Once seedlings have germinated, the number of surviving seedlings in each cohort is updated weekly during the growing season (weeks 10 to 44) using survival fractions due to shading ( $s_{\text{light}}$ ), flooding ( $s_{\text{flooding}}$ ), and salinity ( $s_{\text{salinity}}$ ):

$$\text{seedlings}_t = \text{seedlings}_{t-1} \times s_{\text{light}} \times s_{\text{flooding}} \times s_{\text{salinity}}$$

Weekly survival from salinity is the same function as was used for adult trees (Figure 3.12).

The shade tolerance for both species (Figure 3.16) is modeled as an inverse polynomial function based on the survival of *T. distichum* seedlings exposed to five levels of light transmission (Souther and Shaffer, 2000):

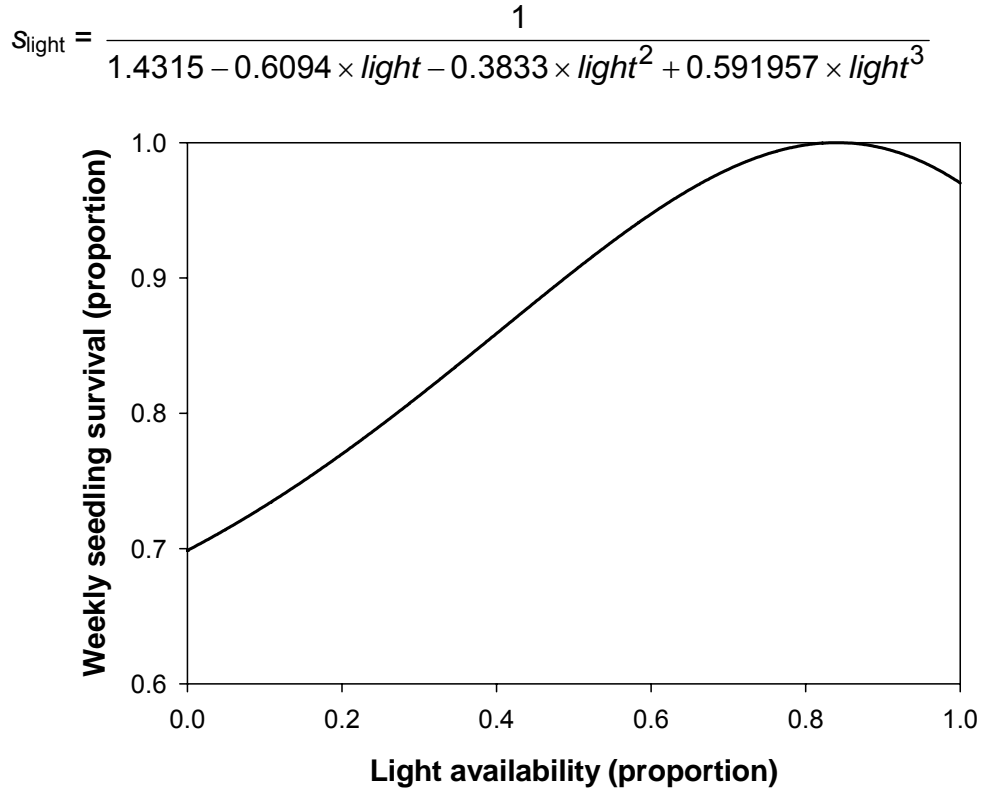


Figure 3.16 - Weekly survival rates of 0-4 year old seedlings in response to light availability. Light availability is evaluated at the end of the growing season of the previous year. The same relationship is used for *T. distichum* and *N. aquatica*. The amount of light available to seedlings is calculated in a similar manner as the light availability for adult trees, with the modification of using 100% of the basal areas and stem densities of larger trees in the light availability calculation, plus the basal areas and stem densities of all seedlings associated with neighboring trees.

The weekly survival of seedlings in response to flooding ( $s_{\text{flooding}}$ , Figure 3.17) is modeled as a single function for first-year seedlings and with species-specific functions for older seedlings. Survival is dependent on the number of weeks of consecutive flooding ( $x$ ) that each cohort experiences during the growing season in its cell:

$$S_{\text{flooding (1st-year)}} = 0.99943 \times e^{(-0.02184 - 0.00035 \times e^x + 0.02276 \times e^{-x})}$$

$$S_{\text{flooding (2nd \& 3rd yr)}} = a + b \times e^{\left( \frac{-\log_e(2) \times \left( \log_e \left( 1 + \frac{(x-c) \times (e^2 - 1)}{d \times e} \right)^2}{\log_e(e)^2} \right)}{\log_e(e)^2} \right)}$$

where	$a_{T. distichum} = 1.0019$	$a_{N. aquatica} = 1.0032$
	$b_{T. distichum} = -0.0779$	$b_{N. aquatica} = -0.0783$
	$c_{T. distichum} = 12.8884$	$c_{N. aquatica} = 9.8272$
	$d_{T. distichum} = 6.7837$	$d_{N. aquatica} = 6.5729$
	$e_{T. distichum} = 0.6933$	$e_{N. aquatica} = 0.7381$

The survival functions for *T. distichum* and *N. aquatica* are based on the results of green-house studies by Souther and Shaffer (2000) and McCarron et al. (1998). I assume that older seedlings of *T. distichum* acclimate to flooding after 12 weeks and older seedlings of *N. aquatica* acclimate to flooding after 17 weeks, after which they no longer suffer any additional flooding-related mortality. In a mesocosm study involving 2-year old seedlings of *T. distichum*, Souther and Shaffer (2000) noticed that survival was lowest (~ 35-50%) in their treatment group exposed to 110-130 days of continuous flooding, and survival was actually higher (~ 75%) in treatment groups that had been subjected to 190 days of flooding. In a greenhouse study with swamp tupelo (*Nyssa sylvatica* var. *biflora*) seedlings, a species closely related to *N. aquatica*, McCarron et al. (1998) found that after withstanding continuous flooding for 2 week, *N. sylvatica* started to experience slowly increasing mortality in their study. By the twelfth week of their study, however, McCarron et al. (1998) did not observe any further cases of mortality despite continued flooding treatment. Observations by Souther and Shaffer (2000) also

indicated that newly germinated *T. distichum* seedlings experienced significantly greater mortality under flooded conditions than 1-year-old seedlings. While newly germinated seedlings showed roughly 90% survival after five weeks of flooding, survival dramatically declined with continued flooding, so that after nine weeks of continuous flooding only 5% of the newly germinated seedlings were still alive.

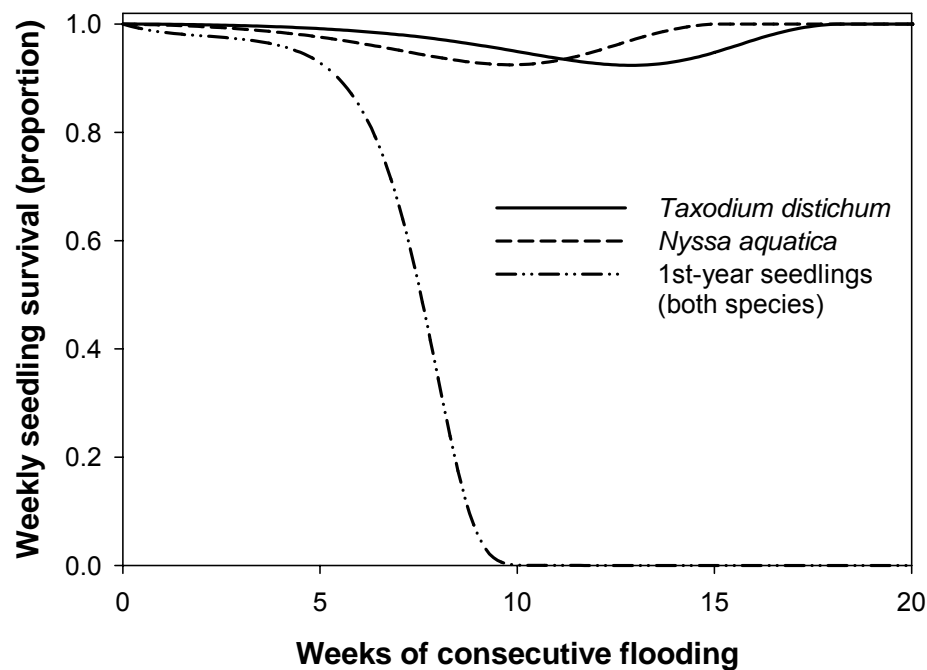


Figure 3.17 - Weekly seedling survival of 1<sup>st</sup> year seedlings (both species) and of 2 and 3 year old seedlings of *T. distichum* and *N. aquatica* in response to continuous flooding.

At the end of the germination period (i.e., week 26), all 4<sup>th</sup>-year seedlings are converted to individual trees and added to the population of individuals. The new individuals are assigned the same species as their parents and are given a diameter drawn from a uniform distribution between 2.0 and 4.0 cm. The location of each new tree is determined as a random distance in both the north-south and east-west directions from its parent's location, and depends on the floating time the seed drifted between seed fall and germination (i.e., the number of weeks of flooding experienced by each tree's seed cohort). The distance in each direction from the parent's location is



comprised of a uniform random distance between -5 m and 5 m to account for a minimum seed fall distance, plus a drift component generated from a normal distribution with a mean equal to the proportion of the time between seed fall and germination that the seed cohort was flooded and thus potentially floating, and a standard deviation equal to 250 m:

$$\text{distance} = (\text{UNIFORM}(-5, +5)) + (\text{NORMAL}(0, 1) \times \text{floating\_time} \times 250.0)$$

New trees that draw a location less than 0.5 m from their parents in either the north-south or west-east direction are placed 0.5 m from their parent in that direction. The tail ends of the normal distribution are folded in by re-sampling from the random distance function if a new tree's distance in either direction exceeds 500 m. The locations of new trees that fall outside the model grid boundaries likewise get re-sampled from the random distance functions. In a seed-trapping experiment in the field, Schneider and Sharitz (1988) found that a distance of 1,800 m was required to trap 90% of the seeds from any given tree in a forested wetland. As this would result in a large seed export from the model domain of 1-km<sup>2</sup>, I used a standard deviation of 250 m to ensure dispersal of roughly 90% of all seeds within 250 meters of their parent tree. Larger grid simulations in further studies would allow for investigation of the effects of longer drifting distances.

### 3.3.8. Numerics

The model simulates true individuals unless the number of new entering trees from surviving 4<sup>th</sup> year seedlings is very high, and then the model switches to a super-individual approach. True individuals mean that all individuals count as one towards the population and when death occurs the individual is removed from the simulation. The use of super-individuals is a way to ensure that arrays in the computer code that store

information on individuals (e.g., DBH, location) can be set to a maximum value that will not be exceeded regardless of recruitment levels (Scheffer et al., 1995). Super-individuals are treated like cohorts; each individual represents some number of population individuals (i.e., a worth). I specified a maximum number of new trees that can be added each year ( $n_{super}$ ). If the new entering number of trees is less than  $n_{super}$ , then each 4<sup>th</sup> year seedling from each cohort (truncated to be an integer value) is represented by a model individual with a worth of one. If  $n_{super}$  is exceeded, then  $n_{super}$  new individuals are added but with a worth equal to the number of new seedlings divided by  $n_{super}$ , so that the sum of the worths over the new super-individuals equals the desired number of new 4<sup>th</sup> year seedlings to be added in that year. In case of the super-individual mode, the list of parents is sorted from highest number of 4<sup>th</sup> year seedlings to least number, and each individual parent's contribution to  $n_{new}$  is determined and scaled to  $n_{super}$ . Each parent tree is assigned a number of recruits equal to its integer-truncated contribution to the pool of new recruits,  $n_{new}$ . If the integer truncation results in an assignment of less than  $n_{super}$  new recruits, single new super-individual recruits are added to the most prolific parent trees in order of their contribution to the pool of new trees until the total number of new recruits is reached.

Because some individuals may be worth more than one, all model output variables are multiplied by their worth when summary statistics are calculated or when tree characteristics are used in model calculations. Density dependence through super-individual self-shading is computed based on first subtracting one from the worth (a true individual tree does not shade itself), and then taking 90% of the remaining worth to calculate the stem density and basal area that counts towards shading. The value of 90% reflects the idea that these other identical trees, which are represented by the

super-individual, would be very close to the tree of interest. All mortality of individual trees in the model is treated probabilistically (random numbers and removal upon death). While probabilistic mortality when worths are much different than one can cause inaccurate representation of population level mortality, this was not a problem in model simulations reported here because the super-individual mode was rarely needed, and when needed, initially assigned worths were always close to one.

### 3.3.9. Model Outputs

At the end of each simulation year, the average annual basal area, stem density, wood production, and stem density by 10-cm diameter classes are determined by species, and for the two species combined, based upon the traits and worths of all living individual trees. Basal area is a common measure of ecological dominance in woody plants, and refers to the stem cross-sectional area at breast height, expressed in m<sup>2</sup> ha<sup>-1</sup>. Individual tree wood production is calculated as the difference in each tree's wood biomass from the beginning to the end of the year, which, in turn, is calculated from the modeled tree diameters using DBH to biomass regression formulas (Muzika et al., 1987):

$$\log_{10} (\text{tree biomass}) = -a + (b \times \log_{10} (\text{DBH}))$$

$$\text{where } a_{T.\text{distichum}} = 0.970 \quad a_{N.\text{aquatica}} = 0.919$$

$$b_{T.\text{distichum}} = 2.340 \quad b_{N.\text{aquatica}} = 2.291$$

The wood production of all trees is summed to yield a total, and then converted to total wood production per square meter per year.

To aid in the explanation of model dynamics for some simulations, additional model output variables are also selectively presented. The additional biological variables include: number of seeds produced per m<sup>2</sup>, the mean number of age-4

seedlings per ha (i.e., recruits), slow-growth deaths per ha, random deaths per ha, and salinity deaths per ha. The additional environmental variables include: the average percent of the grid that was never flooded during the growing season, the average percent of the grid that was always flooded during the germination season (i.e., preventing seed germination), and the mean percent flooding during the growing season. Mean percent flooding during the growing season was computed as the percent of the growing season each cell was flooded, and then averaging the percents over all cells. Unless otherwise indicated, standard deviations (SD) are calculated to represent the variation across years in simulations and are computed based upon annual grid means relative to the overall average of all annual grid means. Standard deviations are used because they represent a consistent measure of inter-annual variation. The degrees of freedom can be artificially controlled with model simulations by simply making longer or shorter simulations that have the same mean values. I used SDs because the mean plus and minus one SD roughly approximates 90% of the values, and because standard errors would be very small and thus difficult to interpret among simulations. In some simulation experiments, coefficients of variance (CV) are calculated based on annual grid means of alternative simulations each year and are then reported as maximum CV for the time period indicated.

#### 3.3.10. Baseline Conditions Selection

Baseline conditions were selected with the goal of simulating representative environmental conditions in the Maurepas Basin. Weekly stage (Figure 3.3) was taken directly from input time-series of monitoring data along with the corresponding time-series of weekly estimates of salinity (Figure 3.4). Elevations for each cell were obtained from a 1-km<sup>2</sup> scene within the re-scaled 1999 surface elevation map of the

Maurepas Basin (Figure 3.2). I selected the scene so that its elevations were similar to elevations of the wetlands portions of the larger elevation map. First, I identified the wetland portions of the map by identifying cells with elevations between 0 and 0.82 m, which was the 99<sup>th</sup> percentile of stage observed at Pass Manchac. Any 1-km<sup>2</sup> landscape scene in the elevation map that contained less than 75% wetland cells was excluded. Based on the remaining scenes, I computed summary statistics of elevation (i.e., median, percentiles, standard deviation, skewness, kurtosis) for each 1-km<sup>2</sup> scene. I selected a particular scene from the map (Figure 3.18) that had summary statistic values of elevation similar to the mean values obtained when all candidate wetland scenes were examined.

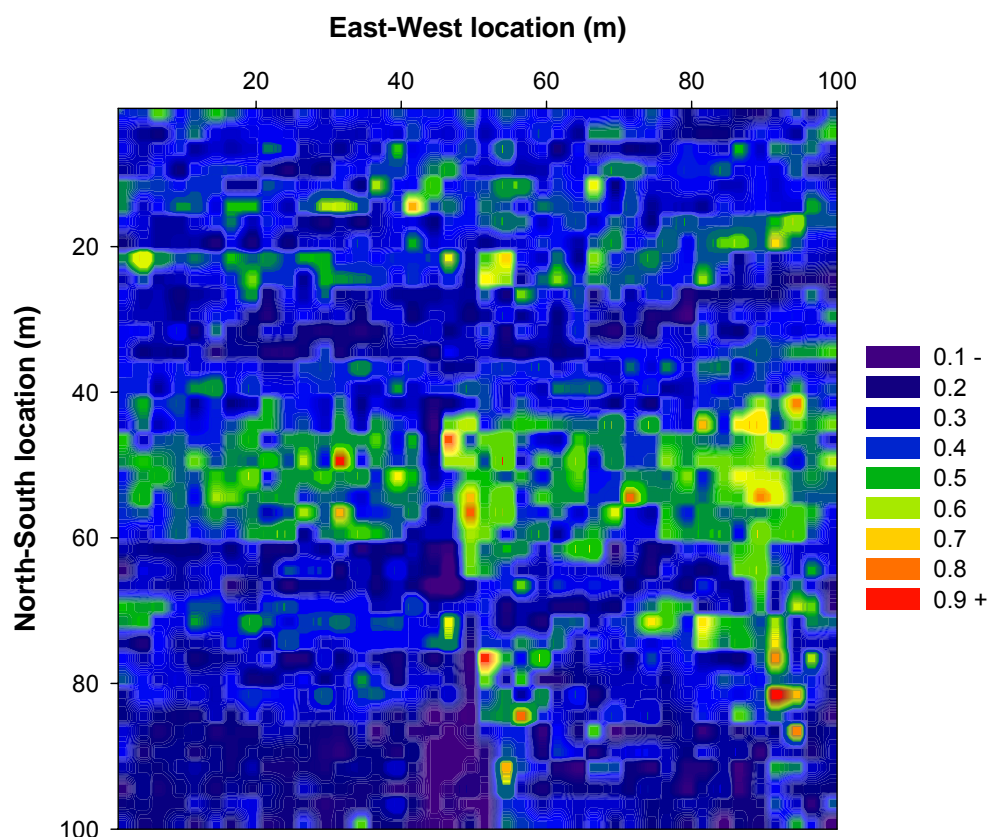


Figure 3.18 - Elevation map used for baseline conditions in the swamp IBM. The minimum elevation of the map is -0.01 m and the maximum elevation is 0.95 m. The scale of the map is truncated at a minimum of 0.1 m and a maximum of 0.9 m for better color differentiation in the center of the range.

Table 3.1 - Overview of the simulations performed with the swamp IBM.

Simulation	Numerics	Duration (years)	Initial condition	Scene	Elevation		Salinity	Clear-cut	Output
					Mean	SD			
True versus Super	True 20,000 40,000 60,000 80,000	1,000	Intact	Baseline	Unflooded	Low	0	Year 300	Time series
Random variation	seed 1 seed 2 seed 3 seed 4 seed 5	500	Intact	Baseline	Baseline	Low	0	None	Time series
Calibration	60,000	500	Intact	Baseline	Baseline High	Low	0	Year 300	Years 365-400
Corroboration	60,000	500	Intact	Baseline	High Baseline Baseline Low	Low Low High High	0 0 PM PM	every 100 years	Years 90-99 after each clear-cut
Initial conditions	60,000	500	Intact Stressed Planted	Baseline	Baseline	Low	0	None	Time series
Mean elevation	60,000	500	Intact	Baseline	Low Baseline High Unflooded	Low	0	None	Time series

Table 3.1 (cont.)

Simulation	Numerics	Duration (years)	Initial condition	Scene	Elevation		Salinity	Clear-cut	Output
					Mean	SD			
Scene selection	60,000	500	Intact	Baseline	Baseline	Low	0	None	Time series
				Scene 2					
				Scene 3					
				Scene 4					
				Scene 5					
Salinity	60,000	500	Intact	Baseline	Low	Low	PM	None	Time series
					Baseline				
					High				
					Baseline	2X PM			

Note: All simulations used seed 1, except where noted; PM=Pass Manchac; all simulations used the same stage time series.

### 3.4. Design of Model Simulations

A variety of simulations were performed for model calibration and corroboration, and to investigate the effects of numerical aspects of the model (super-individuals, random number seeds), initial conditions, mean elevation, standard deviation of elevation, scene selection, and salinity on model dynamics. The design of these simulations is summarized in Table 3.1. All simulations used the calibrated parameter values described under the calibration and corroboration section. Model predictions of annual stem density, basal area, annual wood production, and size-class frequency distributions by species, were compared among simulations.

#### 3.4.1. Numerics: True Individuals versus Super-individuals

In order to select a suitable numeric cap ( $n_{super}$ ), I compared model predictions under true individual mode with runs that used a progression of larger values for  $n_{super}$ . The values of  $n_{super}$  tested were: 20,000, 40,000, 60,000 and 80,000 super-individuals added per year. Model simulations were for 1,000 model years, and used dry (no flooding at all) and zero salinity conditions with a clear-cut event in year 300. The clear-cut removed all trees with DBH > 20 cm, 90% of trees with DBH 5-20 cm, and 50% of the trees with DBH < 5 cm throughout the 1-km<sup>2</sup> baseline scene. The combination of the lack of flooding and clear-cutting created exceptionally large recruitment and a good test of the accuracy of the super-individual approach.

#### 3.4.2. Numerics: The Effect of Random Variation

Several processes in the model make use of random numbers. To test the sensitivity of the model simulations to alternative random number sequences, I performed five identical 500-year simulations that only differed in their random number seeds. The processes that are affected by random numbers are: (1) the selection of the locations



of the initial trees; (2) the size of initial trees within their given size-classes; (3) the assignment of species to each initial tree; (4) which individuals survive the various sources of mortality; (5) the DBH of any new tree introduced into the population; (6) the distance of new trees from its parent tree.

### 3.4.3. Calibration and Corroboration

Selected model parameters were calibrated through trial and error until basal area, stem density, and wood production rates under baseline conditions (relatively high flooding) and under conditions of reduced flooding were qualitatively similar to comparable values reported for swamps in the literature (Table 3.2). Model parameters adjusted during calibration were mortality rate due to random mortality, maximum diameter growth rate, and the combined effect of basal area and stem density on light availability. All other parameters were maintained at their initial values. As none of the swamp forests found in the literature are virgin stands (i.e., none older than 100 years), I added a major disturbance (i.e., simulated logging clear-cut) in year 300 of the 500-year calibration simulations, and then used model outputs from years 365 to 400 to calculate the values of stem density, basal area, and wood production rate.

Reduced flooding was achieved by adjusting the elevations of each cell in the baseline scene so that the mean elevation of the scene equaled the 90<sup>th</sup> percentile elevation of the Maurepas wetlands. Flooding occurred during 44.5% of the growing season in the baseline scene with mean elevation set to the 90<sup>th</sup> percentile Maurepas wetland elevation (mean=0.476 m), compared to an average of 69.5% growing season flooding at baseline (mean=0.356 m) elevations (Table 3). The baseline elevation of each cell was adjusted by adding or subtracting the difference between the target mean elevation and the baseline mean elevation (baseline mean elevation plus the difference

to reach 90<sup>th</sup> percentile elevation in this case). Reduced flooding results was intended for use in comparisons to literature values reported for swamps with natural flooding or periodic flooding, while baseline results were more comparable to impounded or nearly-continuously flooded swamps.

Table 3.2 - Model predicted basal areas, stem densities, and wood production rates for baseline and baseline with reduced flooding conditions compared to values reported in the literature reported for various swamp locations. Model predicted values are the mean values over both species and the spatial grid, and then averaged over 35 years. Maximum and minimum values during the 35 years are shown in brackets.

Location	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	Stem density (trees ha <sup>-1</sup> )	Wood prod. (g m <sup>-2</sup> yr <sup>-1</sup> )
<i>Calibration references</i>			
Cypress – Tupelo (LA) <sup>1</sup>	---	1,730	500
Managed swamp (LA) <sup>2</sup>	35.1	1,564	1,230
Naturally flooded swamp (LA) <sup>2</sup>	38.3	1,303	752
Impounded swamp (LA) <sup>2</sup>	23.1	943	560
Naturally flooded swamp (LA) <sup>3</sup>	---	---	338
Near-continuously flooded Cypress-Tupelo swamp (SC) <sup>3</sup>	---	---	216
Periodically flooded swamp (LA) <sup>4</sup>	50.8	1,568	---
Stagnant Cypress Swamp (KY) <sup>5</sup>	35.9	350	142
<i>Calibration data from the model</i>			
Calibration run: High elevation	35.7 [28.2, 42.2]	1138 [1050, 1227]	510 [379, 545]
Calibration run: Baseline elevation	19.8 [16.0, 23.1]	459 [415, 501]	262 [192, 286]

<sup>1</sup> Conner and Day (1976), <sup>2</sup> Conner et al. (1981), <sup>3</sup> Megonigal et al. (1997),

<sup>4</sup> Dicke and Toliver (1990), <sup>5</sup> Mitsch et al. (1991)

Corroboration of the swamp IBM was achieved by using the calibrated model to simulate conditions approximately corresponding to four well-monitored habitat types within the Maurepas Basin (Chapter 2). The different habitat types were crudely simulated by using the baseline scene with adjusted mean elevations (10<sup>th</sup> percentile for low (0.248 m), median for baseline (0.356 m), and 90<sup>th</sup> percentile for high (0.476 m)) and adjusted standard deviations of elevations (25<sup>th</sup> percentile (0.12 m) for low standard

deviation and 75<sup>th</sup> percentile (0.16 m) for high standard deviation), logging imposed every 100 years, and zero or Pass Manchac salinity values (Figure 3.4). To change the standard elevation of elevation in the scene while keeping the mean elevation constant, each elevation was adjusted using the following equation:

$$elevation_{adjusted} = elevation_{original} \times \frac{sd_{scenario}}{sd_{baseline}} + \left(1 - \frac{sd_{scenario}}{sd_{baseline}}\right) \times \bar{x}_{scenario}$$

where  $sd_{scenario}$  = target standard deviation

$sd_{baseline}$  = baseline standard deviation

$\bar{x}_{scenario}$  = mean elevation of the scenario

The four regions were sampling plots grouped into habitat types based on a cluster analysis (Chapter 2) and were: (1) Hope Canal swamp sites, compared to a simulation using high elevation, low standard deviation of elevation, and zero salinity; (2) Interior-West swamp sites, compared to a simulation using baseline elevation, low standard deviation of elevation, and zero salinity; (3) Interior-East swamp sites, compared to a simulation using baseline elevation, high standard deviation of elevation, and Pass Manchac salinity; and (4) Lake sites, compared to a simulation using low elevation, high standard deviation of elevation, and Pass Manchac salinity. The Maurepas swamps were logged early in the 1900s, and thus would be roughly comparable to a modeled swamp about 90 to 99 years after a clear-cutting. Thus, clear-cutting was imposed in years 100, 200, 300, and 400 of each simulation, and model outputs were recorded only for years 90-99 after each clear-cutting. Means and standard deviations of the field data (stem density, basal area, wood production rate, species composition as percent of counts that were *T. distichum*) were calculated from six plots in the Hope Canal habitat, eighteen plots in the Interior-West habitat, nine plots

in the Interior-East habitat, and seven plots in the Lake habitat, each of which had been measured once annually from 2000 to 2005 (Chapter 2). Means and standard deviations of modeling results were calculated using years 90 through 99 after each of four clear-cutting events, yielding a total of 40 annual model values. Percent of the species counts that were *T. distichum* was computed from the last year of each of the 10-years that followed the clear-cutting events.

#### 3.4.4. The Effect of Initial Conditions

Three alternative initial conditions were simulated for 500 years under baseline conditions with zero salinity to determine the effects of initial conditions on long-term model dynamics. The three initial conditions were: (1) an “intact” swamp with a stem density of 605 trees ha<sup>-1</sup> and a basal area of 60.9 m<sup>2</sup> ha<sup>-1</sup>; (2) a “stressed” swamp with a density of 630 trees ha<sup>-1</sup> and a basal area of 35.5 m<sup>2</sup> ha<sup>-1</sup>; and (3) a “planted” swamp with a stem density of 600 trees ha<sup>-1</sup> and a basal area of 0.3 m<sup>2</sup> ha<sup>-1</sup>. The first set of initial conditions (intact) was the default used in all of the other simulations. All three initial conditions distributed equal numbers of each tree species in each size class at model initiation. In the model runs using intact and stressed swamp initial conditions, the total number of trees in each size class is fixed (Table 3.3), and all trees are dispersed throughout the model domain randomly using the random functions for both their north-south and east-west coordinates. In the model run using planted initial conditions, each 100 m<sup>2</sup> cell in the model domain is assigned three *T. distichum* and three *N. aquatica* trees with a 3 cm DBH each, using the random functions only to determine their exact location within their assigned cells.

Table 3.3 - Initial size-class distributions of trees in the intact and stressed initial conditions. The same size-class distributions are used for *T. distichum* and *N. aquatica*.

Size-class (cm DBH)	Intact swamp		Stressed swamp	
	(total number)	(%)	(total number)	(%)
02-10	3,000	4.96	8,500	13.49
10-20	8,500	14.05	17,500	27.78
20-30	13,500	22.31	21,500	34.13
30-40	16,500	27.27	8,500	13.49
40-50	11,000	18.18	4,500	7.14
50-60	8,000	13.22	2,500	3.97
>60	0	0	0	0

#### 3.4.5. The Effect of Mean Elevation

To assess the effect of differences in elevation alone, I performed simulations that only differed in the mean elevation of the scene. The corroboration simulations involved simultaneous changes in mean and standard deviation of elevations, salinity, and clear-cutting events. The elevation of each 100 m<sup>2</sup> cell in the model affects the amount of flooding the trees and seedlings in that cell experience in any given year and the occurrence or timing of seed germination. I used the same low elevation and high elevation adjusted baseline scene as was used in corroboration, plus a very high elevation adjusted scene (mean elevation of 3.356 m) to simulate no flooding at all (Table 3.4). Figure 3.18 shows each mean elevation level in reference to the long-term mean seasonal pattern of Pass Manchac stage.

#### 3.4.6. The Effect of Elevation Variability

To isolate the effects of elevation variability, I increased the standard deviation of elevations within each of the low elevation, baseline, and high elevation scenes from 0.12 m to 0.16 m. The value of 0.12 m corresponds to the 25<sup>th</sup> percentile of standard deviations of the mean elevations among scenes in the wetland portion of the entire elevation map, and was the same as used for the low variability in elevations case in the

corroboration. The value of 0.16 m is the 75<sup>th</sup> percentile of standard deviations and was used as the high variability case in the corroboration.

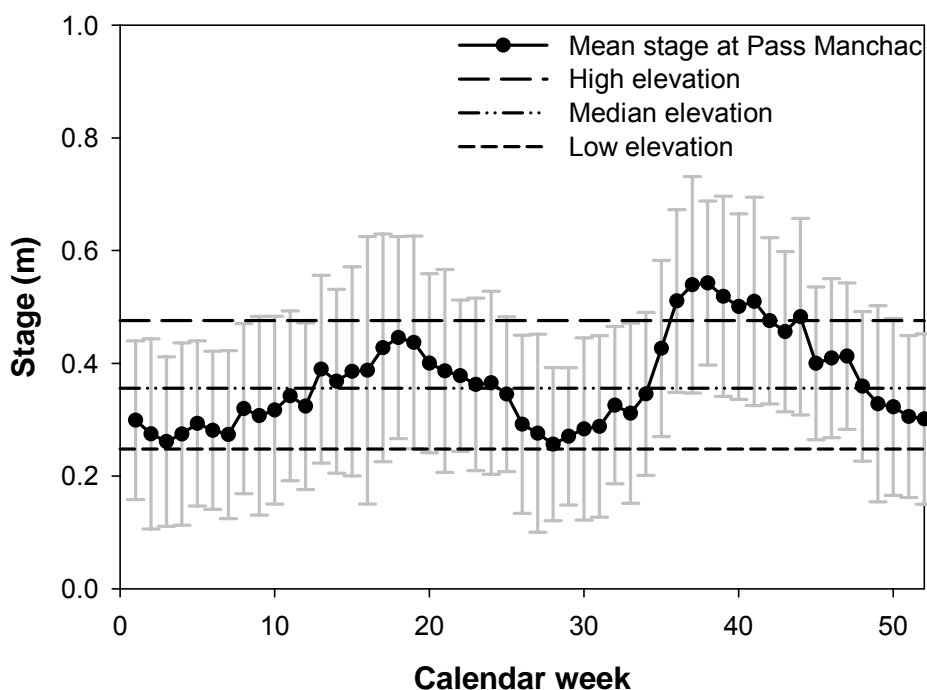


Figure 3.18 - Mean weekly stage ( $\pm$  SD) relative to mean sea-level at Pass Manchac for the 49-year period that is repeated in IBM simulations compared to the mean elevation for the scene under baseline (mean set to median), high elevation (mean set to 90% percentile), and low elevation (mean set to 10% percentile) conditions. The mean elevation for the no-flooding condition was set to 3.356 m (i.e., higher than any possible stage value). Error bars indicate the annual standard deviation from the long-term weekly means to show inter-annual variation.

### 3.4.7. The Effect of Scene-Selection

I selected four other 1-km<sup>2</sup> scenes from the wetland portions of the elevation map to determine the sensitivity of the model to scene selection (Figure 3.19). Each of the four alternative scenes was re-scaled to have mean and standard deviations of elevation similar to the baseline scene (Table 3.5), so that the five-hundred year simulations that were performed only differed in their elevation scenes. Two of the alternative scenes were chosen on the basis of having elevation skewness and kurtosis values close to the baseline map, while the remaining two scenes had higher values for

Table 3.4 - Mean elevation and flooding characteristics of the seven elevation scenarios simulated using the IBM. Flooding was characterized using the estimated percent of the scene modeled that remains dry throughout the whole growing season, the area that remains flooded throughout the whole germination period, and the mean percent flooding experienced during the growing season. All mean values are shown  $\pm$ SD, which is computed as the standard deviation of the 500 annual values around the 500-year mean.

<b>Elevation scenario</b>	<b>Mean elevation (m, <math>\pm</math>SD)</b>	<b>Dry during growing season (% of grid)</b>	<b>Flooded during germination period (% of grid)</b>	<b>Flooded during growing season (% of weeks)</b>
No flooding	3.36 $\pm$ 0.12	100.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0
High elevation	0.48 $\pm$ 0.12	5.3 $\pm$ 7.2	10.2 $\pm$ 14.3	44.5 $\pm$ 15.7
Baseline elevation	0.36 $\pm$ 0.12	1.4 $\pm$ 1.9	31.7 $\pm$ 26.7	69.5 $\pm$ 14.6
Low elevation	0.25 $\pm$ 0.12	0.4 $\pm$ 0.5	58.5 $\pm$ 27.3	86.1 $\pm$ 10.2
High elevation and high variability	0.48 $\pm$ 0.16	8.4 $\pm$ 8.8	14.7 $\pm$ 14.8	46.0 $\pm$ 14.0
Baseline elevation and high variability	0.36 $\pm$ 0.16	3.0 $\pm$ 3.2	35.1 $\pm$ 22.5	67.7 $\pm$ 12.8
Low elevation and high variability	0.25 $\pm$ 0.16	1.2 $\pm$ 1.3	57.6 $\pm$ 22.9	82.9 $\pm$ 9.6

Table 3.5 - Elevation and flooding characteristics of the baseline scene (labeled scene 1) and the four alternate elevation scenes shown in Figure 3.19. Elevation metrics are based on 1,000 elevations in each simulation, while flooding characteristics are based on annual grid means averaged over 500 years of simulation.

<b>Scene</b>	<b>Mean <math>\pm</math> SD (m)</b>	<b>Median (m)</b>	<b>Skew</b>	<b>Kurtosis</b>	<b>Dry growing season (% <math>\pm</math> SD)</b>	<b>Flooded growing season (% <math>\pm</math> SD)</b>
Scene 1	0.36 $\pm$ 0.12	0.35	0.58	1.19	1.35 $\pm$ 1.86	22.75 $\pm$ 20.93
Scene 2	0.36 $\pm$ 0.12	0.34	0.56	0.04	1.20 $\pm$ 2.08	23.83 $\pm$ 21.48
Scene 3	0.36 $\pm$ 0.12	0.35	0.63	2.71	1.20 $\pm$ 1.56	22.25 $\pm$ 20.37
Scene 4	0.36 $\pm$ 0.12	0.36	10.38	237.00	0.77 $\pm$ 0.54	18.67 $\pm$ 23.29
Scene 5	0.36 $\pm$ 0.12	0.34	4.56	55.27	1.45 $\pm$ 1.33	20.24 $\pm$ 24.49

skewness and kurtosis than the baseline scene. The first two alternative scenes have similar probability distributions of elevations as the baseline scene but differ from the baseline scene in their spatial arrangement of these elevations (Figure 3.19). The third

and fourth scenes not only differ in their spatial arrangements but also differ in having more extremely low and high elevation values.

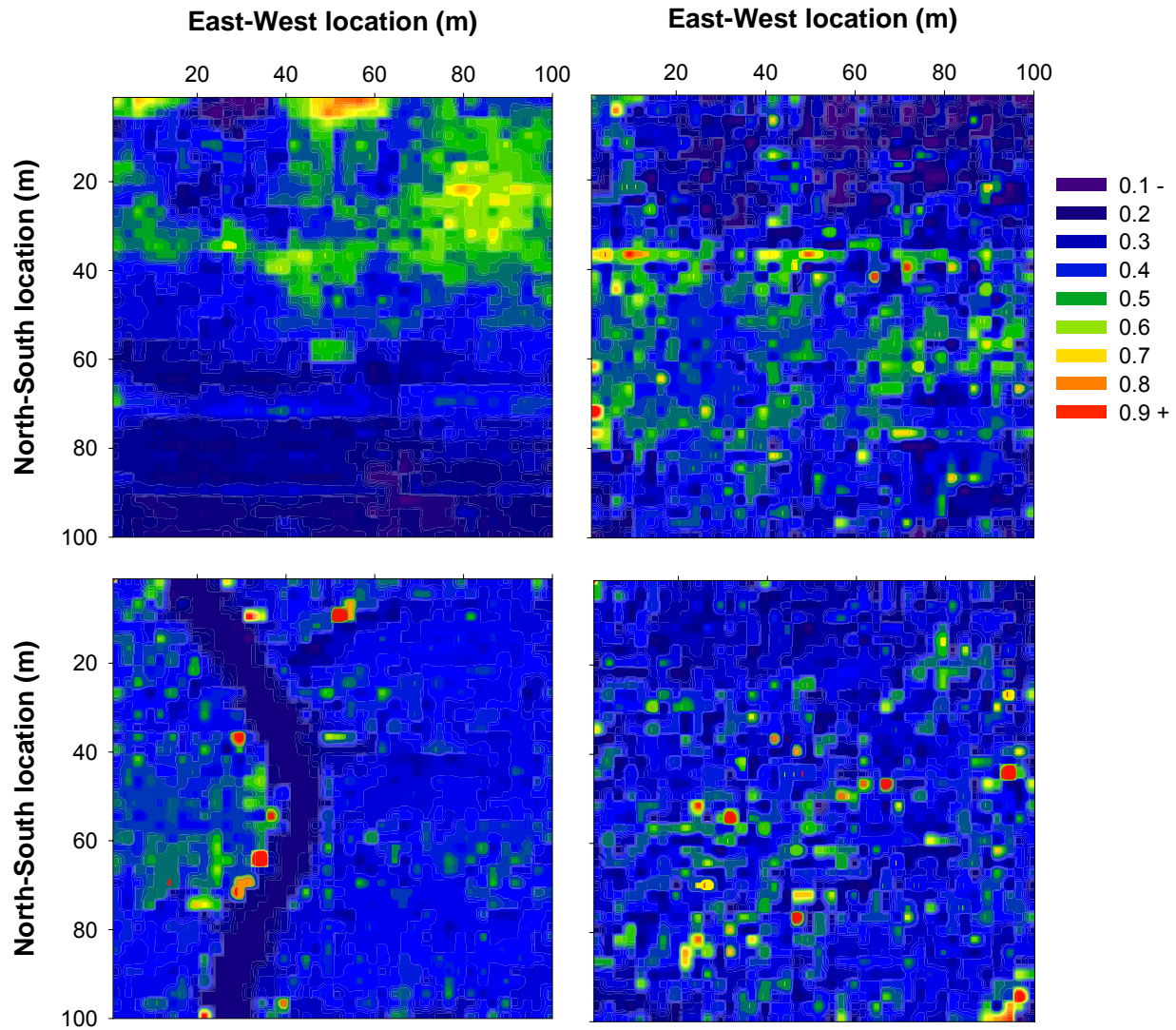


Figure 3.19 - The four alternative elevation scenes used in the IBM simulation experiment. The scale of each map is truncated at a minimum of 0.1 m and a maximum of 0.9 m for better color differentiation in the center of the range. In Map 2 (top left), elevation ranges from 0.05 m to 0.84 m. In Map 3 (top right), elevation ranges from 0.02 m to 1.32 m. In Map 4 (bottom left), elevation ranges from 0.11 m to 3.58 m. In Map 5 (bottom right), elevation ranges from 0.14 m to 2.54 m.

#### 3.4.8. The Effect of Salinity

Five-hundred year baseline simulations were performed that compared zero salinity, Pass Manchac salinity, and doubling of Pass Manchac salinity. The effects of



increased salinity are of interest because of the increasing salinity occurring in many coastal swamps, especially in the Maurepas Basin (Chapter 2). Model predictions were compared between freshwater and Pass Manchac salinity for the low, baseline, and high elevations, all set to the low standard deviation of elevations. Doubled Pass Manchac salinity was simulated with the baseline elevation only.

### **3.5 Simulation Results**

#### **3.5.1. Numerics: Super-individuals and Random Variation**

Model predictions with super-individuals closely mimicked results that used true individuals (Figure 3.20), and different random number seeds had little effect on model predictions (Figure 3.21). The super-individual mode of the model, even with the lowest value of  $n_{super}$  of 20,000, produced stem densities, basal areas, and wood production rates very similar to the true individual results. Super-individuals were not invoked prior to the clear-cutting event in year 300, and then some very small differences occurred after year 400 when high annual recruitments of 4<sup>th</sup> year seedlings occurred.

The effects of different random number seeds on the model output variables were small. The maximum CVs of the five simulations that differed only in random number seeds over 500 years were 6.4% for mean basal area, 5.9% for stem densities, and 2.2% wood production rate, and CVs of the mean stem density by size-category in year 500 were less than 10% in all size classes (Figure 3.22). The largest CVs were found in the smallest size-classes (CV = 9.4% for *T. distichum*, CV = 7.74% for *N. aquatica*), which reflected the random aspects involved with adding new individuals to the model. Based on these results, all subsequent model simulations used an  $n_{super}$  of 60,000 and the results from single random seed simulations are reported.

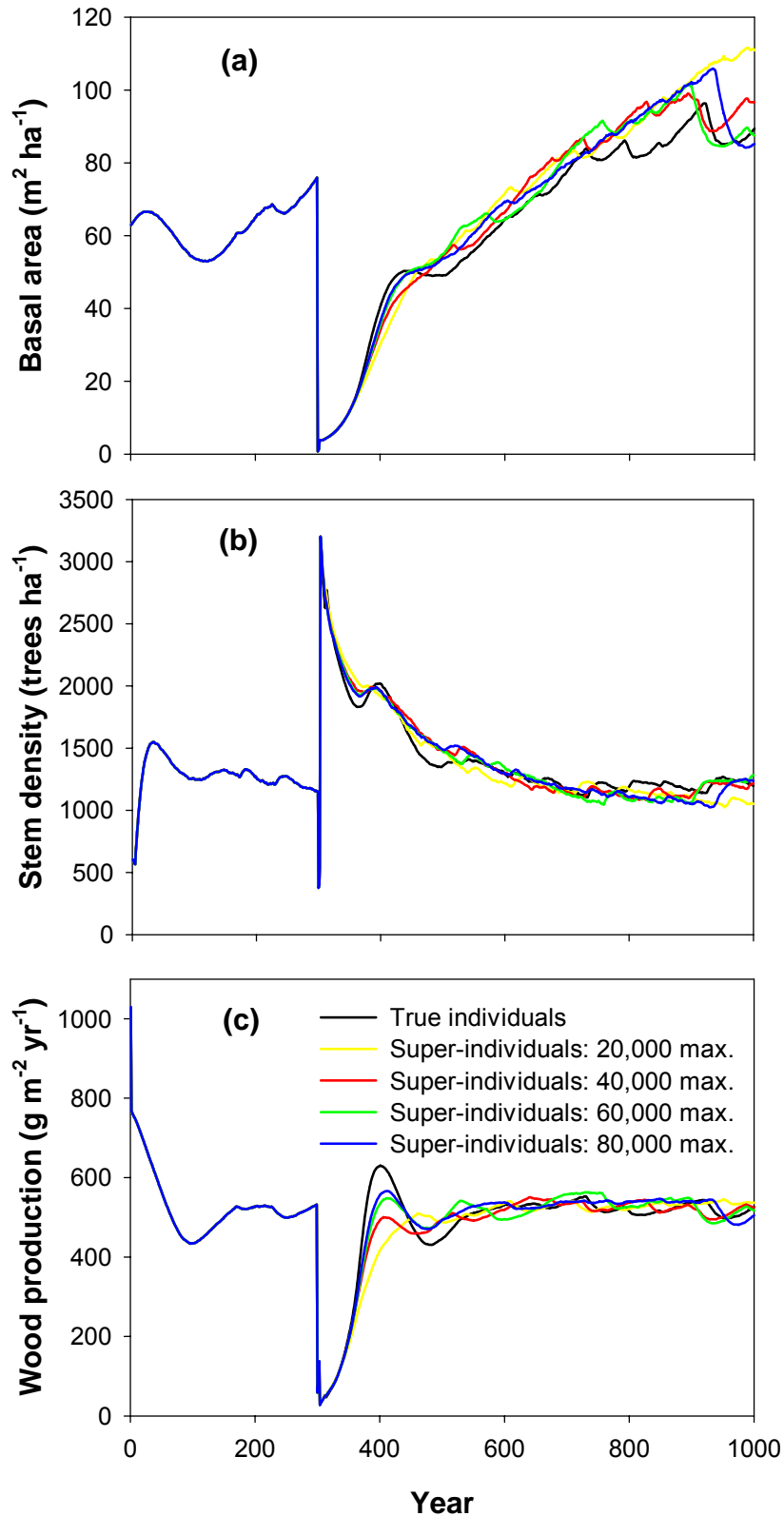


Figure 3.20 – Mean basal area (a), stem density (b), and wood production (c) over 1,000 years in baseline simulations using super-individuals with four different annual recruitment caps and no recruitment cap (true-individuals). A clear-cut disturbance is invoked in year 300 to force high recruitment.

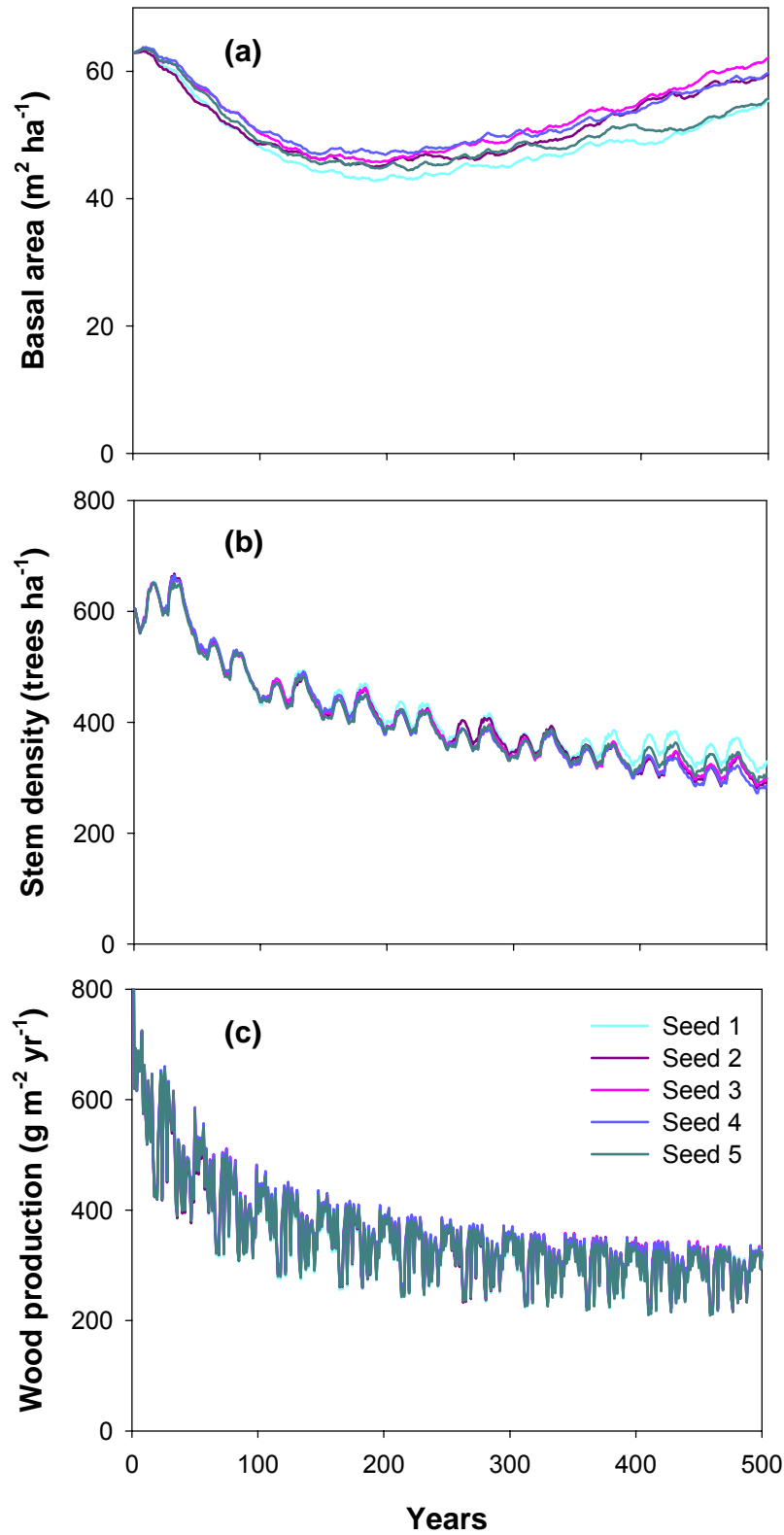


Figure 3.21 – Mean basal area (a), stem density (b), and wood production (c) over 500 years in baseline simulations differing only in their random number sequences.

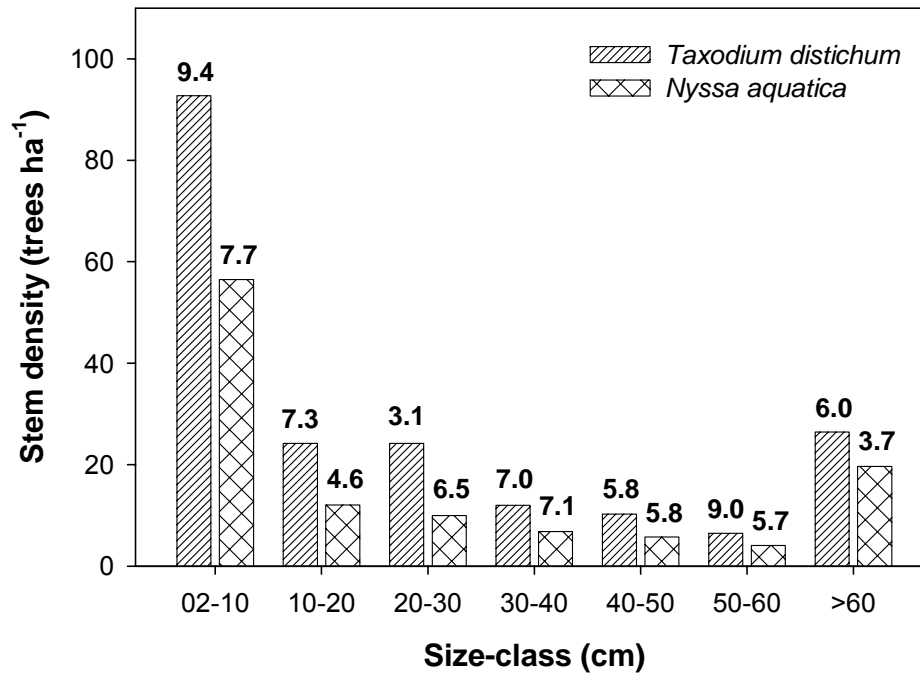


Figure 3.22 - The size-class distribution of trees in year 500 from five baseline simulation runs differing only in their random numbers sequences. The CV of tree density for each size-class is shown on the top of each bar.

### 3.5.2. Model Calibration and Corroboration

Model predicted mean basal areas, stem densities, and wood production rates for years 365 to 400 for the baseline and high elevation scenes were roughly comparable to the range of values reported in the literature (Table 3.2). Model predicted mean values for basal area were 19.8 m<sup>2</sup> ha<sup>-1</sup> for baseline and 35.7 m<sup>2</sup> ha<sup>-1</sup> for high elevation versus 23.1 to 50.8 m<sup>2</sup> ha<sup>-1</sup> reported in the literature, for stem density were 459 and 1,138 trees ha<sup>-1</sup> versus 350 to 1,730 trees ha<sup>-1</sup> in the literature, and for annual wood production were 262 and 510 g m<sup>-2</sup> yr<sup>-1</sup> versus 142 to 752 g m<sup>-2</sup> yr<sup>-1</sup> in the literature, with one managed swamp reaching an annual wood production of 1,230 g m<sup>2</sup> yr<sup>-1</sup>.

In terms of model corroboration, the model successfully replayed the general decrease in basal area, stem density, and wood production rate apparent in the data as

one proceeds from Hope Canal, to Interior-West, to Interior-East, and finally to the Lake habitat (Figure 3.23). Model predictions of basal area and stem density expressed as the mean plus and minus one SD, overlapped with observed data, also expressed as the mean plus and minus one SD. The greatest difference in mean stem density and basal area was for stem densities at the Interior-West and Interior-East habitats, where the model underestimated mean stem density compared to the field data. In contrast to good agreement with stem density and basal area, the model consistently overestimated wood production rate for all four habitats. The model did produce generally declining wood production rate from Hope Canal to the Interior habitats to the Lake habitat, but with mean values 40-50% higher than observed. Annual wood production is strongly affected by inter-annual variation in environmental conditions. With only six years of field data, during which a severe drought with higher than normal salinity levels occurred and wide-spread occurrences of for insect defoliation affected both *T. distichum* and *N. aquatica*, mean wood production from the field data could be reflecting conditions not included in the model simulations. Alternatively, the mismatch between predicted and observed wood production rates could suggest a deficiency in the model's representation of growth and mortality.

The model had more difficulty capturing the differences in species composition among the four habitats (Table 3.6). Both the model and the field data had stem density and basal area for the Lake sites very much dominated by *T. distichum*, and ignoring the Interior-West habitat, both had the Hope Canal as less dominated by *T. distichum*. However, the model overestimated the dominance of *T. distichum* for the Interior-East habitat (~87% versus ~55%), and for the Interior-West habitat, which the data had as dominated by *N. aquatica* (64% *T. distichum* by model versus 25-29% for the data).

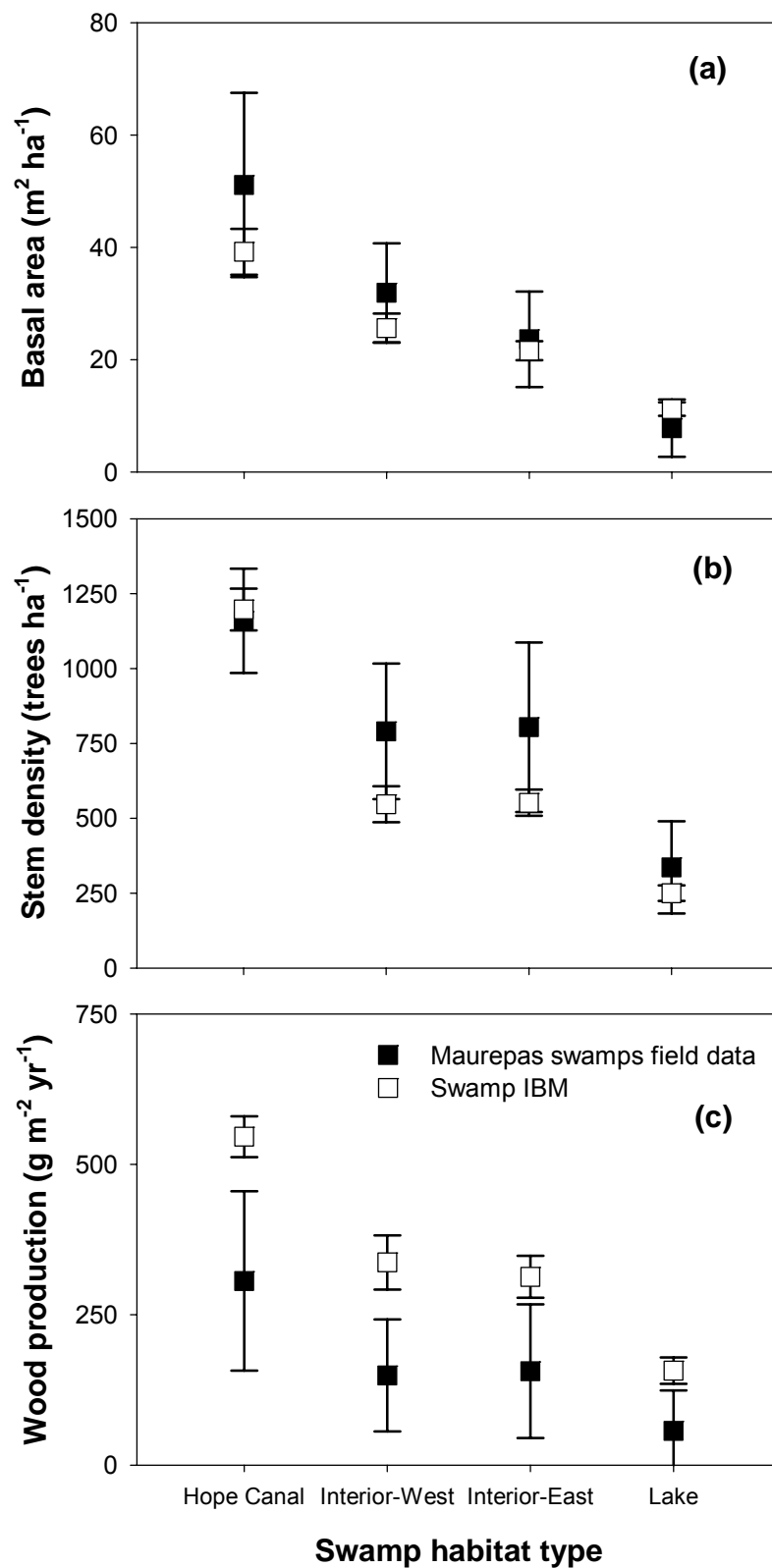


Figure 3.23 - Comparison of model predicted and observed mean ( $\pm$  SD) basal area (a), stem density (b), and annual wood production (c) for the four swamp habitat types identified in the Maurepas basin using data from 2000 to 2005. IBM simulations differed among habitat types by the mean elevation and salinity values used.

The potential effects of local differences in the field sites not included in the model can contribute to these differences, and the model may not sufficiently distinguish between the tolerances of the two species.

Table 3.6 - Comparison of 2004 Maurepas field data and swamp IBM results 90 years after disturbance (i.e., simulated logging) mean ( $\pm$  SD) percent *T. distichum* of combined *T. distichum* and *N. aquatica* stem density and basal area.

Corroboration scenario	% <i>T. distichum</i> of stem density		% <i>T. distichum</i> of basal area	
	Field data 2004	Swamp IBM	Field data 2004	Swamp IBM
Hope Canal	46.1 $\pm$ 13.6	59.6 $\pm$ 2.6	65.2 $\pm$ 14.9	60.4 $\pm$ 2.6
Interior-West	25.3 $\pm$ 11.0	64.3 $\pm$ 4.1	29.5 $\pm$ 13.3	64.8 $\pm$ 4.8
Interior-East	55.3 $\pm$ 13.7	88.4 $\pm$ 6.8	57.7 $\pm$ 12.1	87.7 $\pm$ 7.3
Lake	99.4 $\pm$ 1.7	88.1 $\pm$ 6.5	98.2 $\pm$ 4.8	87.3 $\pm$ 6.5

### 3.5.3. The Effect of Initial Conditions

Despite the large range in initial conditions used, the modeled swamp forests grown from basal areas of either 60.93 m<sup>2</sup> ha<sup>-1</sup> (intact), 35.49 m<sup>2</sup> ha<sup>-1</sup> (stressed), or 0.28 m<sup>2</sup> ha<sup>-1</sup> (planted) at the onset of the model all converged to similar basal area, stem density, and wood production rate within 120 to 150 years (Figure 3.24). The simulation that started with the lowest initial basal area (planted) slightly overshot the stem densities predicted from the stressed and intact initial conditions, and predicted slightly higher basal areas throughout the 500-year model run (Figure 3.24-b). However, the maximum coefficients of variation between the scenarios throughout the last 350 years were quite low (7.4% for basal area, 4.1% for stem density, 4.0% for wood production rate). Thus, the effects of initial conditions disappear within the first 150 years of simulations.

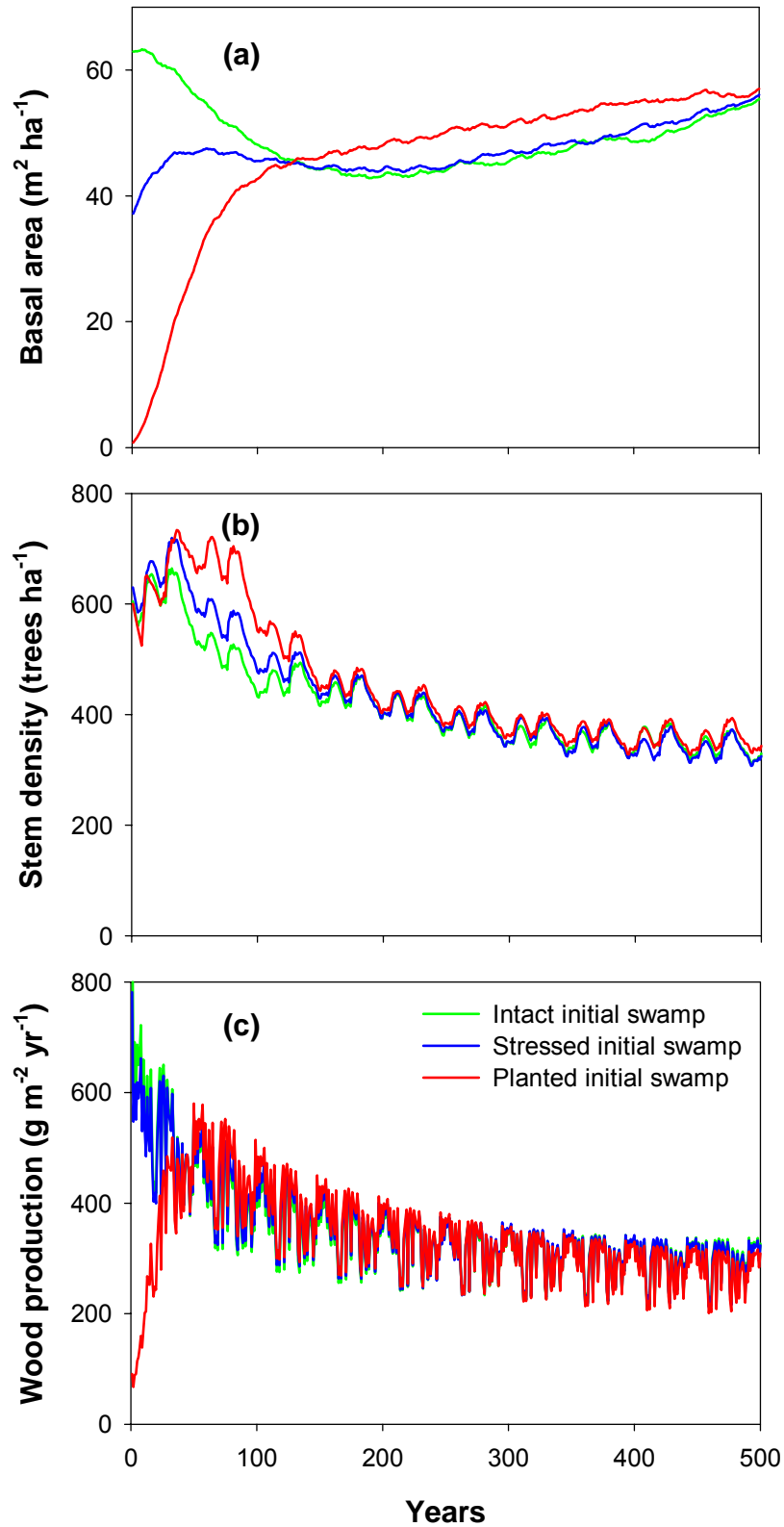


Figure 3.24 - Mean basal area (a), stem density (b), and wood production (c) over 500 years in baseline simulations differing only in the initial conditions assumed for the trees (intact, stressed, planted).



#### 3.5.4. The Effect of Mean Elevation

Mean elevation of cells in the baseline scene had a very strong effect on basal area, stem density, and wood production rate, due to its effect on the duration of flooding in model cells (Figure 3.25). The mean percent flooding during the growing season was 0.0% under no flooding, 44.5% under the high mean elevation, 69.5% under baseline elevations, and 86.1% under the low elevation (Table 3.4). Basal area, stem density, and annual wood production were highest under conditions of no flooding and lowest at the low elevation (highest flooding). For the first 150 years of each model run, the swamp forests at all elevations adjusted to their different mean elevations and flooding patterns. After about 150 years, the simulated swamp forests underwent a gradual process of self-thinning, as basal areas slowly increased and stem densities slowly decreased in response to increased density-dependent shading. By year 500, the modeled swamps had reached mean basal areas of  $98.37 \text{ m}^2 \text{ ha}^{-1}$  under non-flooded conditions,  $81.97 \text{ m}^2 \text{ ha}^{-1}$  at high elevation,  $55.38 \text{ m}^2 \text{ ha}^{-1}$  at baseline elevation, and  $32.69 \text{ m}^2 \text{ ha}^{-1}$  at low elevation (Figure 3.25-a). Stem density and wood production also showed similar decreases with increasing flooding (Figure 3.25-b, 3.25-c).

Decreasing elevation (increased flooding) also caused higher inter-annual variation in stem density and wood production but not in basal area (Figure 3.25). Inter-annual variation in stem density and wood production progressively increased with decreasing elevation reflective of the effects of flooding on 4<sup>th</sup> year seedling recruitment. The CV of annual recruitment, which in this case was calculated based on the annual grid means over 500 years, was 43% under the high elevation, 67% under baseline, and 90% under low elevation. Basal area showed much less variation year-to-year because it is roughly a measure of standing biomass that is very sensitive to the

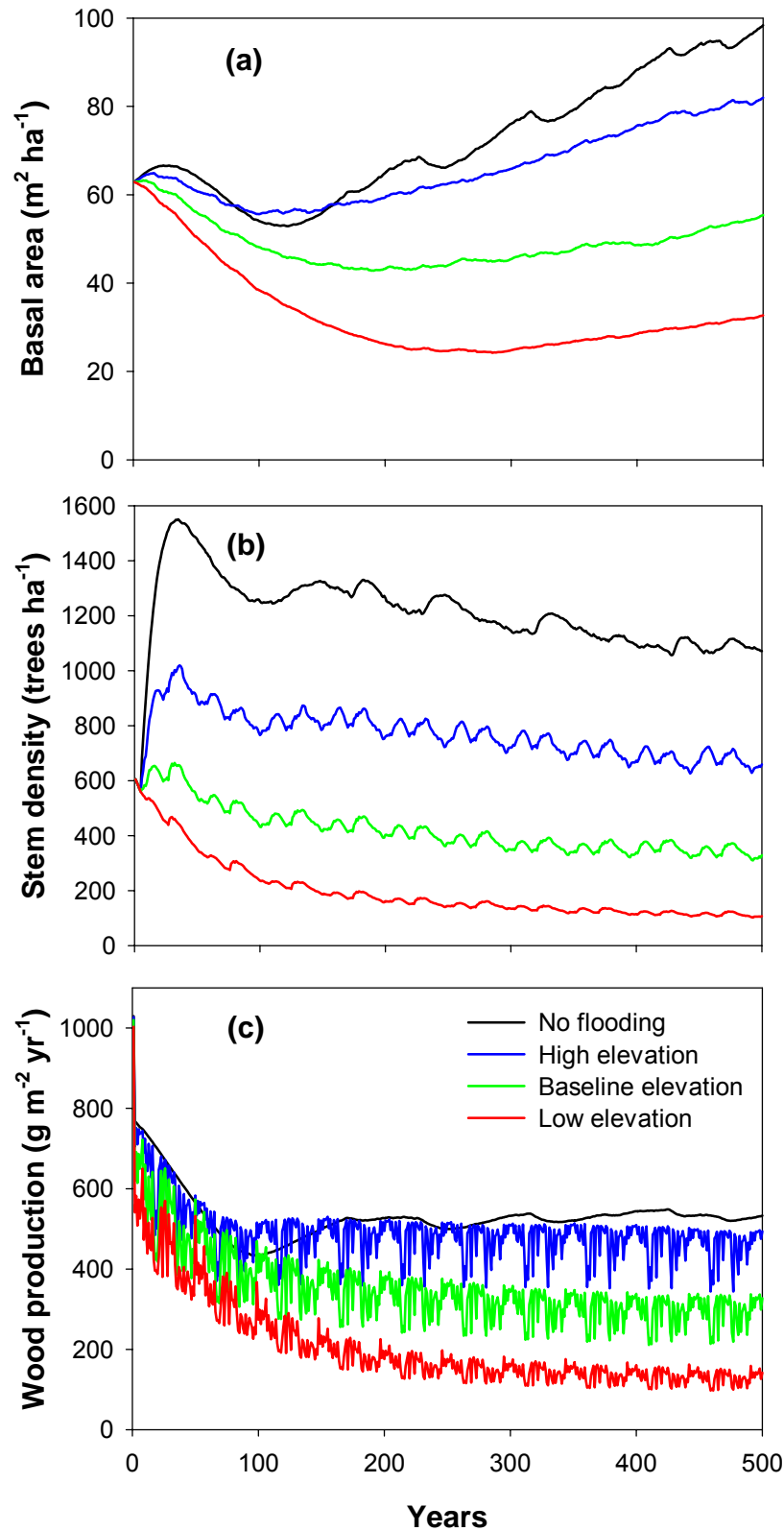


Figure 3.25 - Mean basal area (a), stem density (b), and wood production (c) over 500 years in simulations under non-flooded conditions, high mean elevation, baseline elevation, and low mean elevation.

presence or absence of large canopy trees, but is impacted only little by annual growth variations and small changes in recruitment (Figure 3.25-a).

Intermediate flooding associated with the baseline elevation gave *T. distichum* the greatest competitive advantage over *N. aquatica* (Figure 3.26-3.29). By year 500, the size-class histograms of the swamp forests at each elevation were indicative of old-growth forests with high numbers of large, old trees (> 60 cm DBH). Stem densities at all size-classes generally decreased with increasing flooding, with the difference between *T. distichum* and *N. aquatica* densities being greatest under the baseline elevation (intermediate flooding). Under no flooding, the two species occurred in equal numbers, while high flooding caused large decreases in both species' densities.

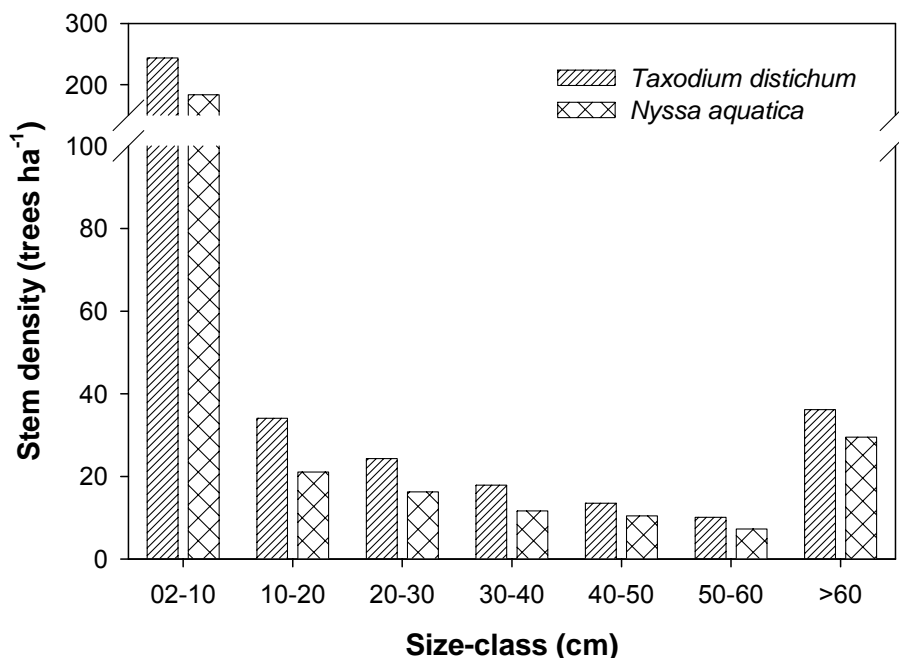


Figure 3.26 - The size-class distribution of trees after 500 years in a high-elevation swamp with low elevation heterogeneity (mean = 0.48 m, SD = 0.12 m). Note the broken y-axis denoting high stem densities of young recruits.

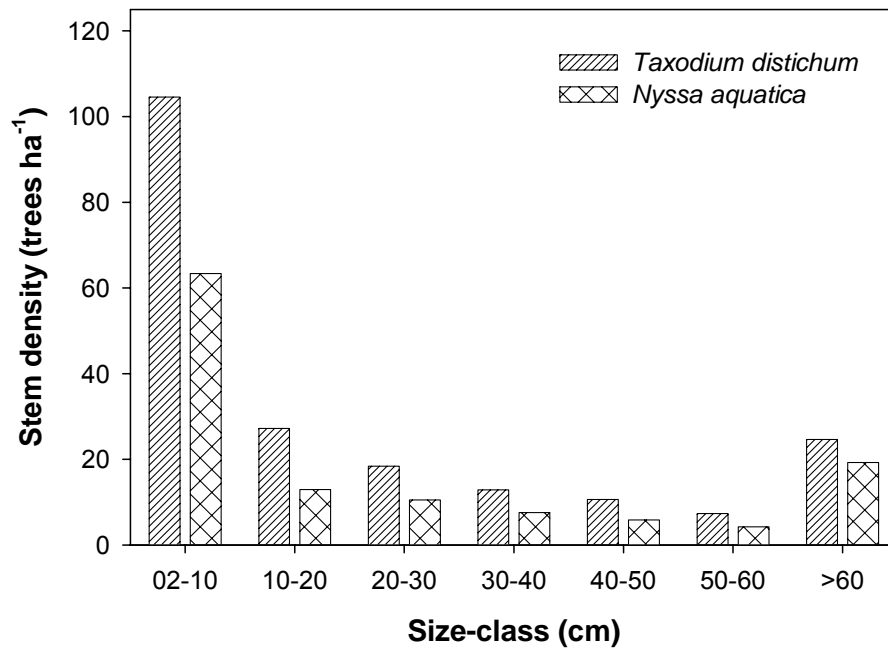


Figure 3.27 - The size-class distribution of trees after 500 years in a baseline elevation swamp with low elevation heterogeneity (mean = 0.36 m, SD = 0.12 m).

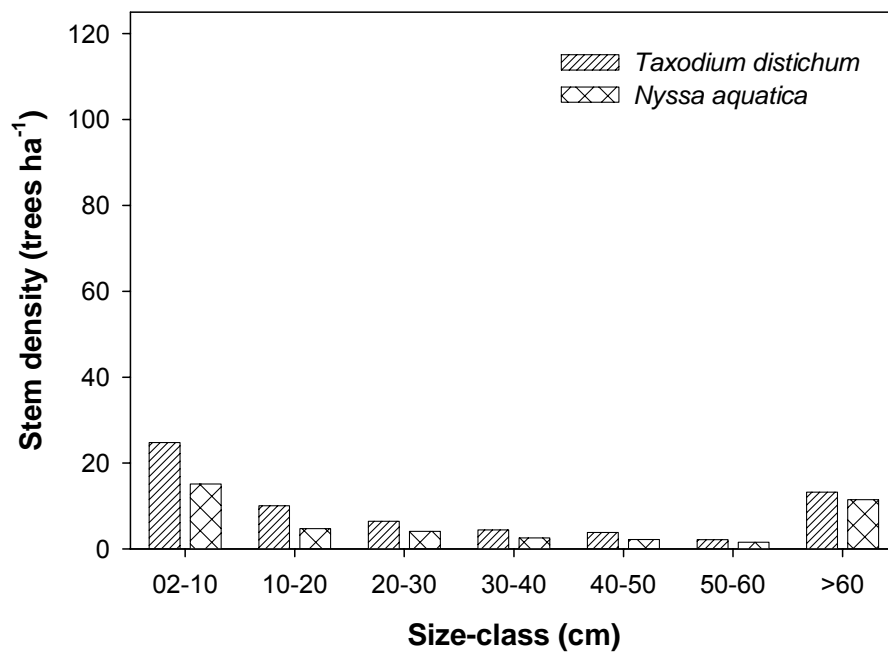


Figure 3.28 - The size-class distribution of trees after 500 years in a low elevation swamp with low elevation heterogeneity (mean = 0.25 m, SD = 0.12 m).

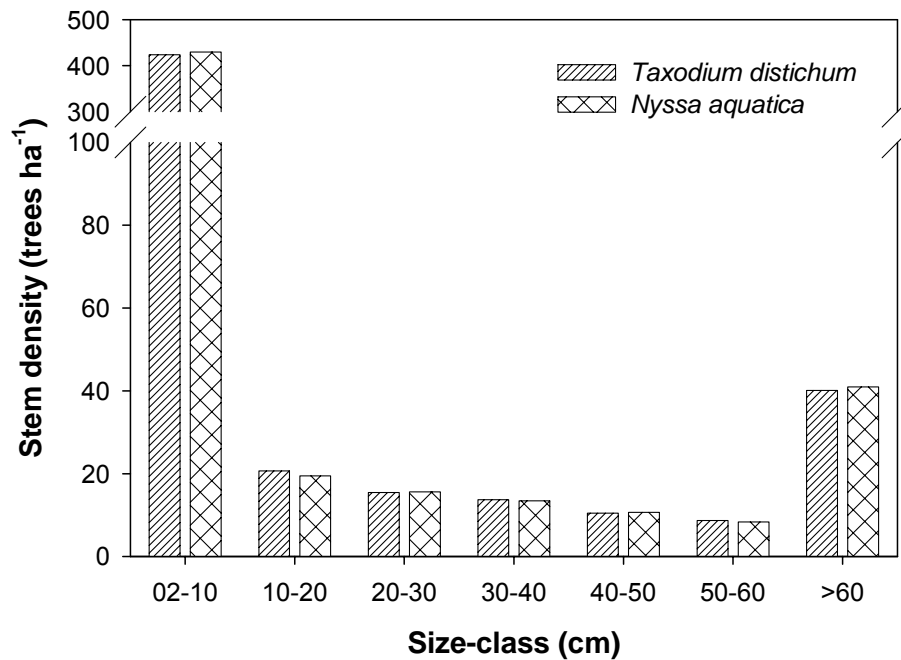


Figure 3.29 - The size-class distribution of trees after 500 years in a non-flooded swamp. Note the broken y-axis denoting high stem densities of young recruits.

*Taxodium distichum*'s dominance over *N. aquatica* developed gradually in model simulations (baseline case shown in Figure 3.30), based on small differences in the species' flooding tolerances causing differential survival in the seed and seedling stages that get amplified over time. Seed production during the first 50 years of the simulations decreased with increasing flooding, but was similar between species for each elevation scenario, with *N. aquatica* even having slightly higher mean values for several scenarios (Table 3.7). The basal area and stem density for the two species during the first 50 years of the simulations were similar; thus seed production on a per area basis is also indicative of the similarity between the two species in their per capita rates of seed production. Similar to seed production, the recruitment of age-4 seedlings of both species to adults decreased with increased flooding. However, in contrast to seed

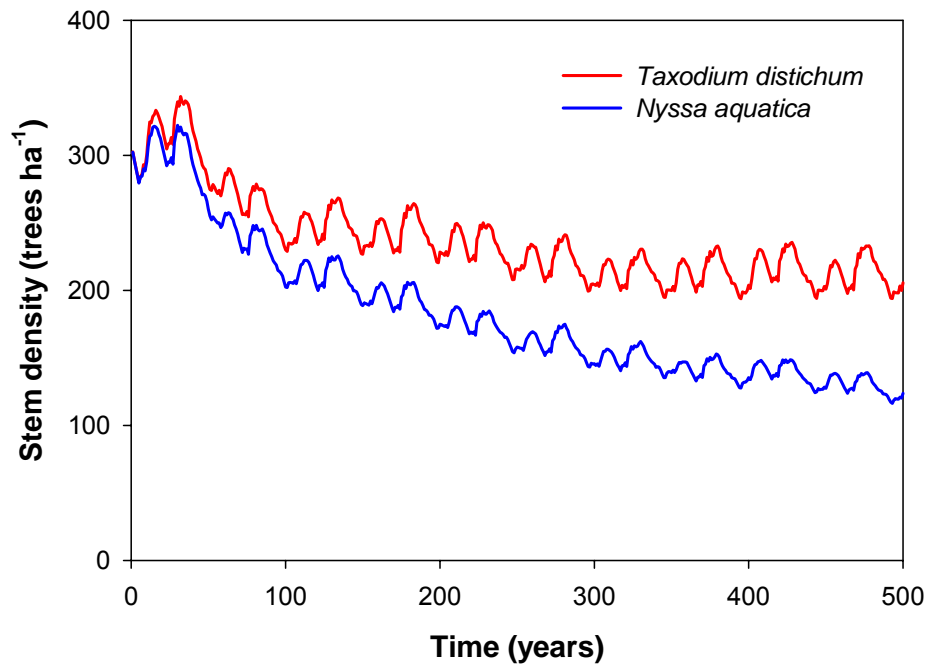


Figure 3.30 - Mean stem density of *T. distichum* and *N. aquatica* for the 500 years in the baseline simulation.

production, the average recruitment of *T. distichum* was higher than the recruitment of *N. aquatica* under all flooding conditions, and the difference was largest under the baseline elevation scenario (Table 3.7). *Nyssa aquatica* had a growth advantage over *T. distichum* after flooding exceeds 5 consecutive weeks (Figure 3.9), while *T. distichum* retained a seedling survival advantage over *N. aquatica* for up to twelve weeks of consecutive flooding (Figure 3.17). These small differences in seed production and seedling survival due to flooding got amplified year after year by slowly increasing densities of *T. distichum* relative to densities of *N. aquatica*, resulting in the slow development of *T. distichum* dominance over *N. aquatica*. For example, average recruitment for the last 350 years of the simulations was 5.4 trees ha<sup>-1</sup> for *T. distichum* and 3.6 trees ha<sup>-1</sup> for *N. aquatica* for baseline (versus 6.78 trees ha<sup>-1</sup> and 5.88 trees ha<sup>-1</sup> for the first 50 years). In contrast, averaged recruitment of the two species during the

last 350 years of the low elevation simulations remained much more similar (1.7 trees ha<sup>-1</sup> for *T. distichum* and 1.2 trees ha<sup>-1</sup> for *N. aquatica*), as recruitment was very low for both species throughout the whole simulation.

Table 3.7 - Mean ( $\pm$  SD) number of seeds that survive winter dormancy and numbers ( $\pm$  SD) of 4-year old seedlings that survive to recruitment for *T. distichum* and *N. aquatica* during the first 50 years under no-flooding, high mean elevation, baseline elevation, and low mean elevation conditions.

Elevation	Seeds surviving winter dormancy (seeds m <sup>-2</sup> yr <sup>-1</sup> )		Recruits (trees ha <sup>-1</sup> yr <sup>-1</sup> )	
	<i>T. distichum</i>	<i>N. aquatica</i>	<i>T. distichum</i>	<i>N. aquatica</i>
No flooding	10.2 $\pm$ 2.2	10.2 $\pm$ 2.2	32.2 $\pm$ 12.7	32.2 $\pm$ 12.6
High	9.4 $\pm$ 2.3	9.5 $\pm$ 2.3	15.9 $\pm$ 8.5	14.3 $\pm$ 8.5
Baseline	8.3 $\pm$ 2.4	8.5 $\pm$ 2.3	6.8 $\pm$ 5.7	5.9 $\pm$ 5.1
Low	7.0 $\pm$ 2.2	7.6 $\pm$ 2.1	2.3 $\pm$ 2.7	2.1 $\pm$ 2.6

### 3.5.6. The Effect of Elevation Variability

Increasing the variability in elevation for a given mean elevation had a much smaller effect on stem density, basal area, and wood production rate than the changes from low to baseline to high mean elevations (Figure 3.31). Higher variability in elevation eventually resulted in higher stem densities, basal areas, and wood production for the low mean elevation, with higher basal area also predicted for the high variability under the baseline elevation. Little long-term effect was predicted between the high and low variability for the high mean elevation. The greatest difference between high and low elevation variability was for the low mean elevation. Averaged annual wood production over the last 350 years for high versus low variability with low mean elevation for wood production was 188  $\pm$  29 versus 149  $\pm$  28 g m<sup>-2</sup> yr<sup>-1</sup>, with stem density decreasing from 202  $\pm$  30 to 140  $\pm$  24 trees ha<sup>-1</sup>, and for basal area declining

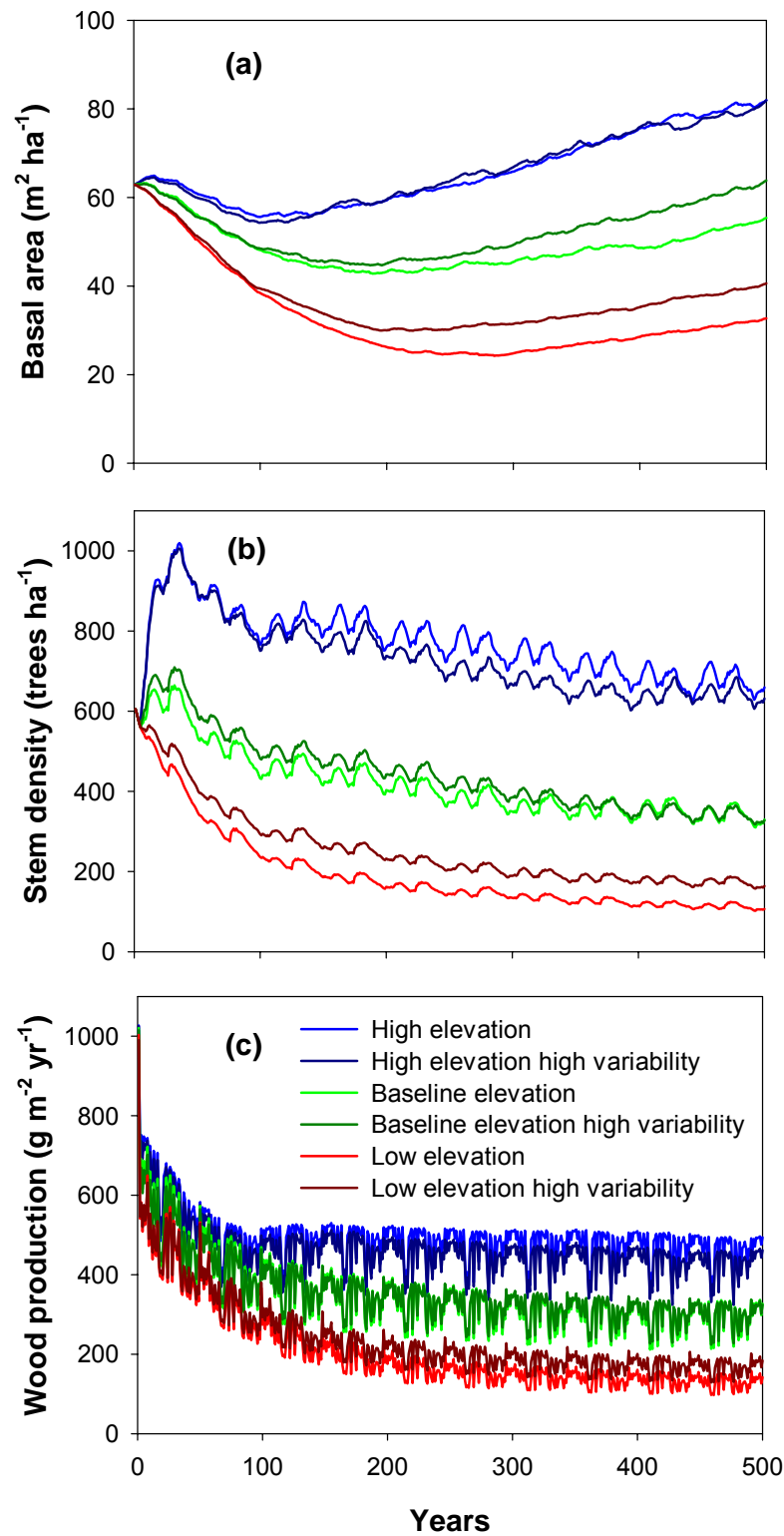


Figure 3.31 - Mean basal area (a), stem density (b), and wood production (c) over 500 years in simulations under high mean elevation, baseline elevation, and low mean elevation, each at low ( $\text{SD}=0.12 \text{ m}$ ) or high variability ( $\text{SD}=0.16\text{m}$ ).



from  $33.6 \pm 3.1$  to  $27.5 \pm 2.4 \text{ m}^2 \text{ ha}^{-1}$ . The dynamics of flooding were similar between the high and low elevation variability for any given mean elevation (Table 3.4), with perhaps the low mean elevation showing slightly larger responses in flooding to higher variability in elevation. Mean percent of the growing season that was flooded for the high and low variability scenarios was 46% versus 44.5% for the high mean elevation, 67.7% versus 69.5 for the baseline elevation, and 86.1% versus 82.9% for the low mean elevation (Table 3.4).

#### 3.5.7. The Effect of Alternative Scenes

Use of alternative 1-km<sup>2</sup> scenes from the basin-wide elevation map, once adjusted to have the same mean and standard deviation of elevations, had little effect on stem density, basal area, and annual wood production (Figure 3.32). Model simulations were robust to which particular 1-km<sup>2</sup> portion of the Maurepas elevation map was selected (alternative scenes 2-4), and even to scenes that had higher proportions of extreme values of elevation (alternative scenes 4 and 5) (Figure 3.19). An important caveat is that each of alternative scenes was adjusted to have the same mean and standard deviation of elevations as the baseline scene (Table 3.5). Mean elevation had a very large effect on model predictions (Figure 3.25).

#### 3.5.8. The Effect of Salinity

Even at the low concentrations observed at Pass Manchac (Figure 3.5), salinity had a strong negative impact on the simulated swamp forest (Figure 3.33). For each mean elevation, basal area was approximately 50 to 60% of the value predicted under freshwater (baseline) conditions (Figure 3.33-a), while stem density and annual wood production were much less affected by higher salinity (Figure 3.33-b and -c). Mean basal area with Pass Manchac salinity versus freshwater was  $41.1 \text{ m}^2 \text{ ha}^{-1}$  versus  $69.0$

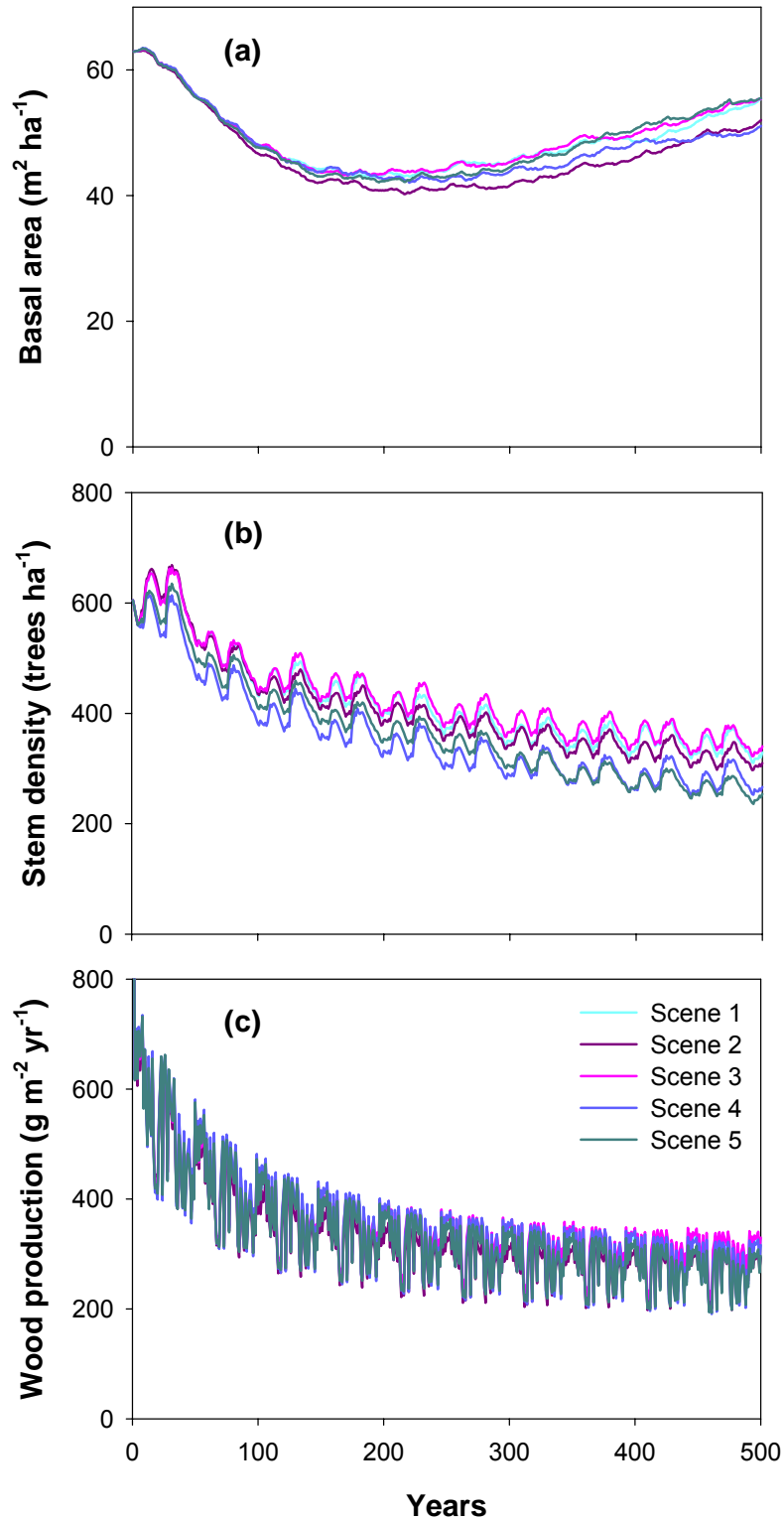


Figure 3.32 - Mean basal area (a), stem density (b), and wood production (c) over 500 years in simulations using 5 different 1- $\text{km}^2$  landscape scenes selected from the Maurepas Basin map. Scene 1 is the baseline scene. All maps were scaled to a mean elevation of 0.36 m, with a standard deviation of 0.12 m to allow isolation of the effects of the spatial arrangement of elevation heterogeneity.

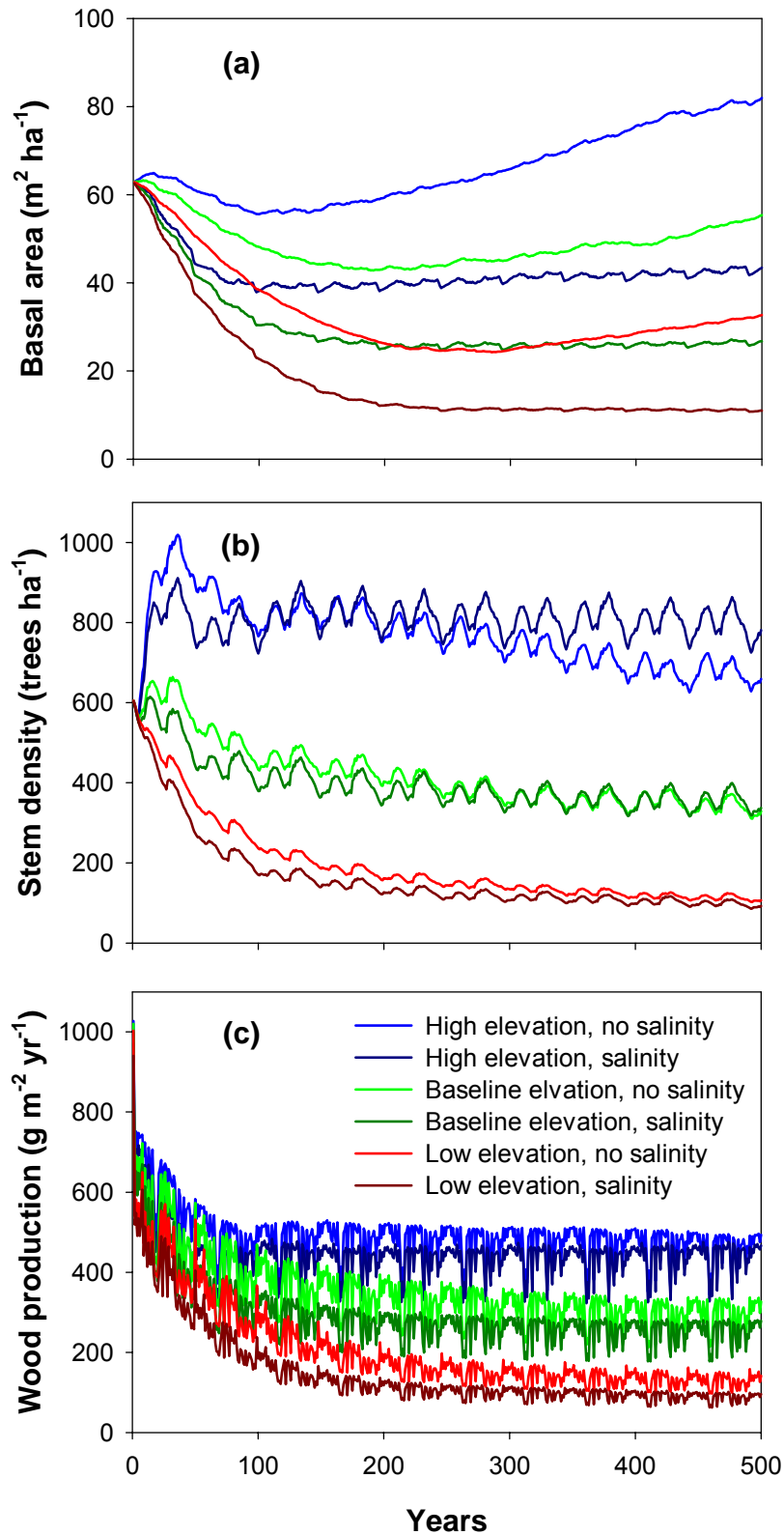


Figure 3.33 - Mean basal area (a), stem density (b), and wood production (c) over 500 years in simulations under high mean elevation, baseline elevation, and low mean elevation, each with no salinity or Pass Manchac salinity levels.

$\text{m}^2 \text{ha}^{-1}$  at high mean elevation,  $26.0 \text{ m}^2 \text{ha}^{-1}$  versus  $47.3 \text{ m}^2 \text{ha}^{-1}$  at baseline mean elevation, and  $11.6 \text{ m}^2 \text{ha}^{-1}$  versus  $27.5 \text{ m}^2 \text{ha}^{-1}$  at low mean elevation.

Mean annual percent mortality (i.e., % of population dying annually) only changed slightly between no salinity and Pass Manchac salinity conditions for a given mean elevation across salinity levels (changes of  $\sim 0.2 - 0.4\%$ ; Table 3.8), but salinity caused a greater proportion of larger individual trees to die and thus affected basal area more than stem density. In simulations that used Pass Manchac salinity, salinity caused roughly 20% of all tree deaths per year at each mean elevation, and roughly replaced slow-growth as the main causation of non-random deaths (Table 3.8). While slow-growth mortality generally targets small trees affected by density-dependent shading, salinity mortality equally affects trees of all sizes. Thus, a greater proportion of large trees died in each model run that used Pass Manchac salinity, and prevented the swamp from reaching the self-thinning old-growth structure it had achieved under freshwater conditions.

Stem densities and wood production (Figure 33.3-b and -c), while moderately lower, appeared eventually to become stable for the high and baseline mean elevations in the simulations that used Pass Manchac salinity, indicating that swamp forests can achieve a stable equilibrium under low salinity values if recruitment is sufficiently high. However, the swamp forest with Pass Manchac salinity was dominated by *T. distichum* (Figure 3.34), and *T. distichum* had a size-distribution dominated by the smallest size-class beyond that predicted under freshwater conditions (compare Figure 3.35 to Figure 3.27). Recruitment of age-4 seedlings of *T. distichum* (i.e., the smallest size class) was slightly increased at the high elevation from an annual mean ( $\pm$  SD) of  $11.2 \pm 5.1$  to  $19.8 \pm 8.2$  trees  $\text{yr}^{-1}$  and at baseline elevations from an annual mean ( $\pm$  SD) of  $5.4 \pm 4.0$  to

Table 3.8 - Mean percent mortality (% of population dying annually) and mean total mortality (trees dying ha<sup>-1</sup> yr<sup>-1</sup>) by causes of death for the high, baseline, and low mean elevations, each simulated with zero salinity, Pass Manchac salinity, and doubled Pass Manchac salinity. Percent mortality and total mortality is based on the trees of both species combined. Means and SD are based on 500 annual estimates per simulation.

Elevation	Cause of death	No salinity (mean ± SD)	Pass Manchac salinity (mean ± SD)	Double Pass Manchac salinity (mean ± SD)
High	Slow-growth (%)	0.92 ± 0.19	0.44 ± 0.13	
	Random (%)	1.81 ± 0.09	1.81 ± 0.09	
	Salinity (%)	0.00 ± 0.00	0.67 ± 0.53	
	Total (%)	2.73 ± 0.22	2.92 ± 0.58	
	Total (n)	21.11 ± 3.23	23.56 ± 4.81	
Baseline	Slow-growth (%)	0.52 ± 0.12	0.25 ± 0.08	0.02 ± 0.02
	Random (%)	1.88 ± 0.09	1.89 ± 0.09	1.93 ± 0.14
	Salinity (%)	0.00 ± 0.00	0.58 ± 0.48	5.09 ± 4.06
	Total (%)	2.41 ± 0.17	2.72 ± 0.51	7.04 ± 4.14
	Total (n)	10.08 ± 1.95	10.86 ± 2.64	13.70 ± 7.80
Low	Slow-growth (%)	0.30 ± 0.10	0.14 ± 0.07	
	Random (%)	1.91 ± 0.09	1.92 ± 0.10	
	Salinity (%)	0.00 ± 0.00	0.57 ± 0.48	
	Total (%)	2.21 ± 0.15	2.63 ± 0.51	
	Total (n)	4.25 ± 2.13	4.25 ± 2.62	

8.3 ± 5.8 trees yr<sup>-1</sup> with Pass Manchac salinity, due to few larger trees resulting in less density-dependent shading. *N. aquatica* was characterized as having lower salinity tolerance than *T. distichum* in the model (Figures 3.10 and 3.12), and *N. aquatica* slowly disappeared from the swamp when Pass Manchac salinity was used (Figure 3.34 and 3.35).

Doubling the historic Pass Manchac salinity caused declines in both species, resulting in the swamp becoming so low in tree biomass that it could be considered a marsh. Basal areas approached zero for the doubled salinity under baseline elevation within 50 years (Figure 3.36), and *N. aquatica* disappeared in almost half that time

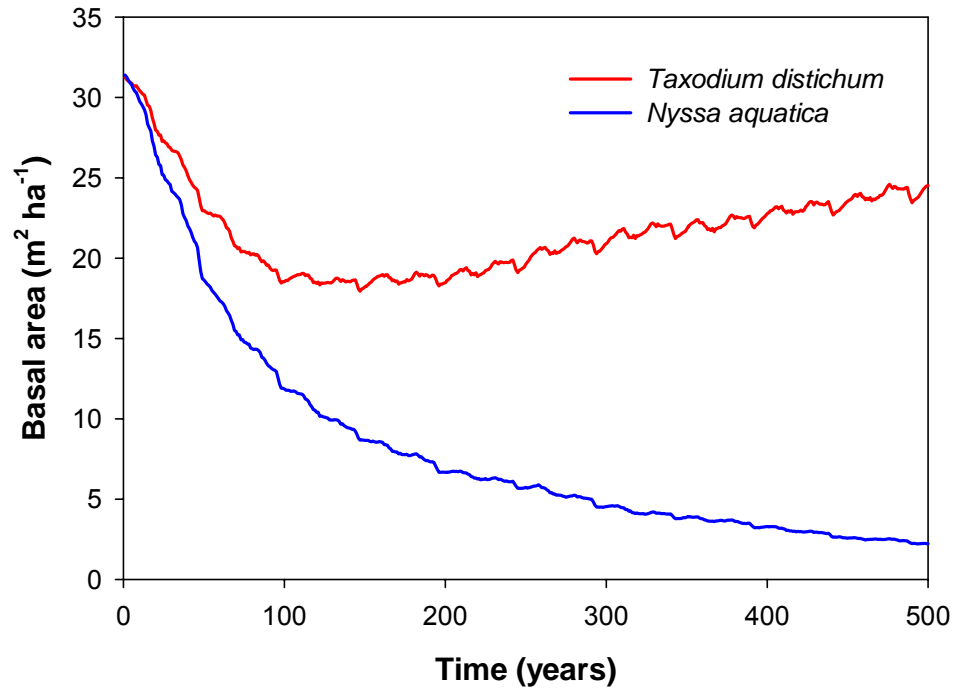


Figure 3.34 - Mean basal area of *T. distichum* and *N. aquatica* over 500 years in simulations at baseline elevation (mean = 0.36 m, SD = 0.12 m) and Pass Manchac salinity levels.

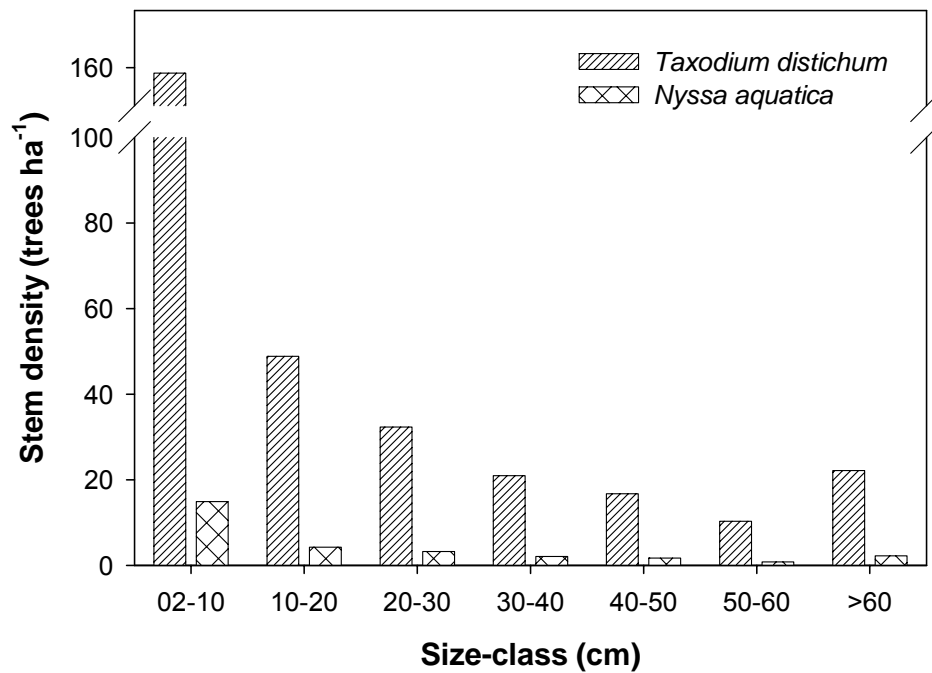


Figure 3.35 - Size-class histograms of *T. distichum* and *N. aquatica* after 500 years under baseline elevation and Pass Manchac salinity levels.

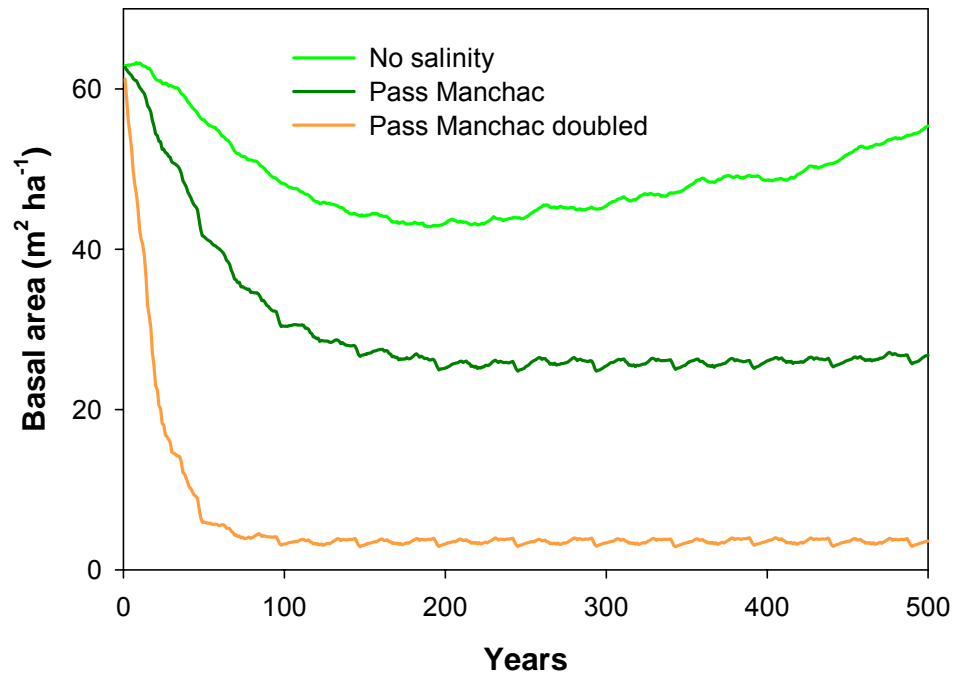


Figure 3.36 - Mean basal area over 500 years in simulations at baseline elevation (mean=0.36 m, SD=0.12 m) with no salinity, Pass Manchac salinity levels, and doubled Pass Manchac salinity levels.

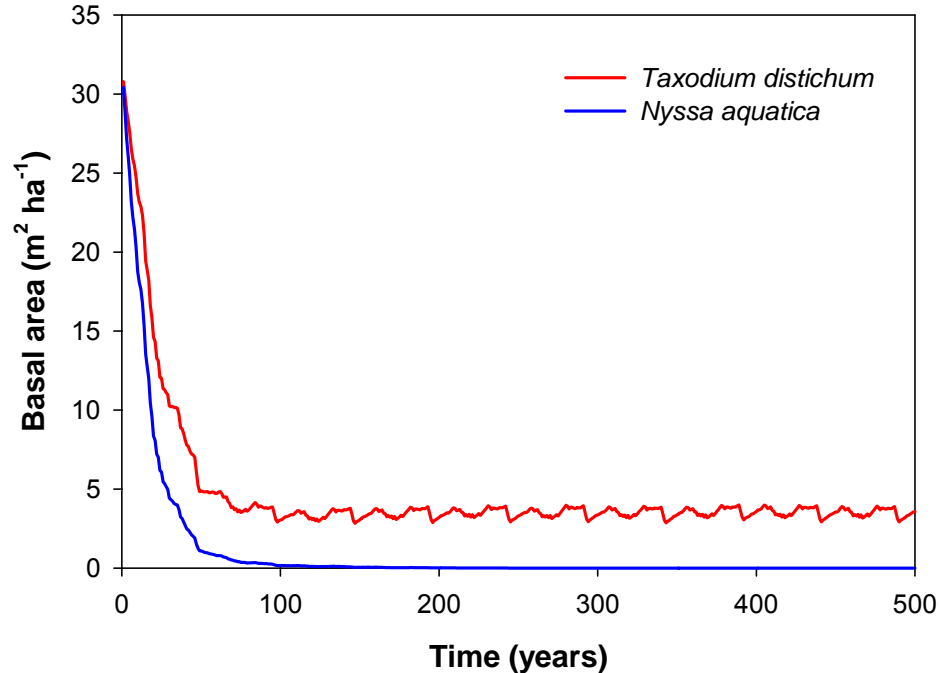


Figure 3.37 – Mean basal area of *T. distichum* and *N. aquatica* over 500 years in simulations at baseline elevation (mean = 0.36 m, SD = 0.12 m) and doubled Pass Manchac salinity levels.

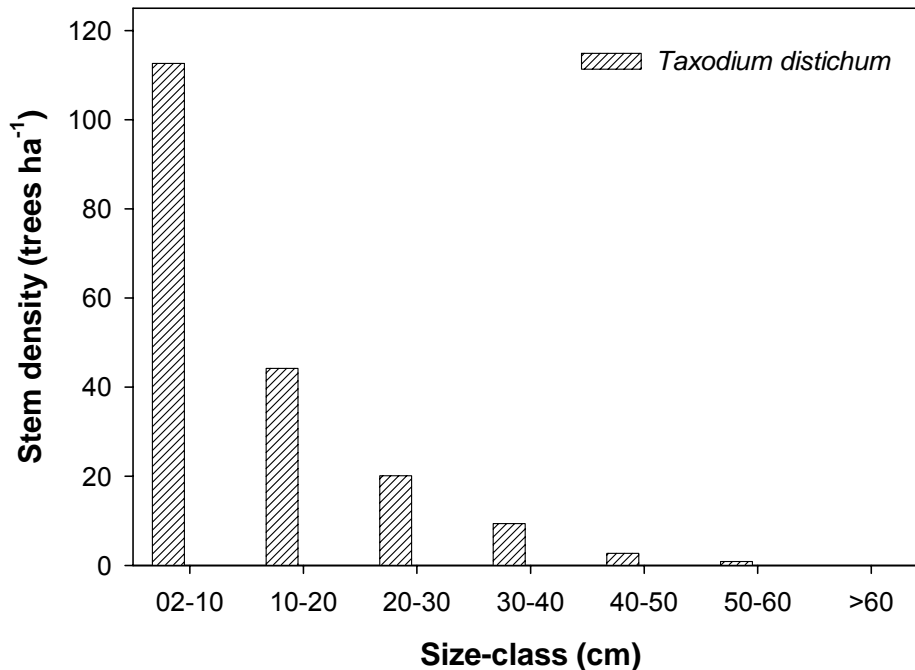


Figure 3.38 - Size-class histogram of *T. distichum* after 500 years under baseline elevation and doubled Pass Manchac salinity levels. *N. aquatica* has long since disappeared from the swamp.

(Figure 3.37). Due to continued high recruitment, a small population of small *T. distichum* trees manages to survive until year 500. The size-class histogram of this highly disturbed forest is characteristically dominated by the smallest size-class, with sharply declining frequencies of larger individuals (Figure 3.38).

### 3.6 Discussion

#### 3.6.1. Calibration and Model Sensitivity

The swamp IBM appears quite robust in its predictions. The model was insensitive to the random number seeds that are employed, the selection of alternative landscape scenes from the Maurepas basin elevation map (scaled to same mean and standard deviation), and to initial densities and biomass of the two tree species. Use of five different random number sequences, and four alternative 1 km<sup>2</sup> scenes from the elevation map resulted in nearly identical simulations results (Figures 3.21 and 3.32).



The model converged in its predictions of basal area, stem density, and annual wood production within 150 years for initial conditions ranging from an intact forest to a planted swamp (Figure 3.24). If *a priori* initial conditions are unknown, long-term model simulations (ignoring the first 150 years) can still generate robust predictions. The model showed small responses to changes in the standard deviation of elevation. Given the same mean elevation, a 25% increase in the standard deviation of elevation resulted in less than 20% changes in the predictions of basal area, stem density, and annual wood production (Figure 3.31). Based on the good agreement during model corroboration between model predictions and field observations of basal areas and stem densities, particularly in comparisons with the fairly intact Hope Canal habitat and the generally degraded Lake habitat (Figure 3.23), the swamp IBM seemed to capture the flooding gradient and its effects on trees found within the Maurepas swamp quite well.

#### 3.6.2. Flooding and Salinity

The model predicted large responses to changes in elevation (i.e., flooding duration) and to increases in salinity. Simulations used a broad range of mean elevations, ranging from the 10<sup>th</sup> to the 90<sup>th</sup> percentile of wetland elevations found in the Maurepas Basin. These extremes in mean elevations resulted in large differences in the percent of the growing season that was under flooded conditions (44.5% for the 10<sup>th</sup> percentile versus 86.1% for the 90<sup>th</sup> percentile). The increase in flooding from high (90<sup>th</sup> percentile) to low (10<sup>th</sup> percentile) mean elevation caused declines in average seed survival to germination, and drastic reductions in seedling survival in both *T. distichum* and *N. aquatica* (Table 3.7). Basal area, stem density, and wood production also

decreased with increasing degree of flooding caused by lowering the mean elevation (Figure 3.25).

The no-flooding scenario at the very high mean elevation was included strictly for comparative purposes and is not meant to imply that swamps would grow best under fully drained and potentially even water-limited conditions (Figure 3.25). Even at slightly increased elevations, both *T. distichum* and *N. aquatica* are replaced by less flood-tolerant species that make up bottomland hardwood forests (Mitsch and Gosselink, 2000), and tree productivity is expected to decrease in response to water limitations. The no-flooding scenario provides an extreme basis for comparing the predictions of simulations with low and moderate levels of flooding, and also illustrates a limitation in the two-species model that other species, not represented, can become important under some environmental conditions.

While both species decreased with increasing flooding, *T. distichum* did relatively better than *N. aquatica*. Species differences in seed flood tolerance (Figure 3.15) first gave *N. aquatica* a slight advantage in potential regeneration (viable seeds annually). However, the greater seedling flooding tolerance of *T. distichum* seedlings for up to 12 weeks of continuous flooding (Figure 3.17) ultimately shifted the species dominance towards *T. distichum* by the end of the 500-year simulations (Figures 3.26-3.28 contrasted with Figure 3.29).

The swamp IBM was very sensitive to salinity. Even relatively low levels of salinity in the model (~1-3 psu observed at Pass Manchac, Figure 3.4) greatly decreased basal areas and slightly decreased wood growth; salinity had a very small effect on stem density (Figure 3.33). Initial fast declines in basal area and stem density were mostly due to the fairly rapid death of *N. aquatica* throughout the modeled spatial

grid (Figure 3.34). Throughout the 500-year simulations that included Pass Manchac salinity, salinity mortality became more important than slow-growth mortality, resulting in a shift from mortality culling out smaller, slowly growing trees to mortality affecting trees of all size-classes (Table 3.8). The indiscriminate culling of trees of all sizes due to shift of mortality to salinity, in turn, caused a population shift towards a greater relative abundance of small trees (Figure 3.35). Thus, increased salinity caused reductions in basal area while stem density was relatively unaffected.

The salinity results are consistent with the corroboration results. Basal area, the summary forest characteristic that was most sensitive to salinity (Figure 3.33), performed very well in the corroboration comparisons that relied heavily on salinity to differentiate among the habitats (Figure 3.23-a).

In a further simulation, increasing salinity to twice the salinity observed at Pass Manchac (range ~ 2-4 psu) resulted in a swift degradation of the modeled forest, first eliminating *N. aquatica*, and even leading to the disappearance of *T. distichum* within 50 years (Figure 3.37). Mean monthly salinities in the range of 0.57 to 3.21 psu (USGS gage #301748090200900) have already been observed in Pass Manchac in recent years (i.e., in 2005 and 2006), and thus are likely indicative of future salinity levels in the southeastern most parts of the Maurepas Basin. While the model response to salinity in the range of 2-4 psu looked somewhat extreme, it matched well with the observed high cumulative percent mortalities of trees at the Maurepas Lake sites (Chapter 2, Figure 2.6), which did experience salinities in the approximate range of 2 to 4 psu during the 5-year field study (Chapter 2, Figure 2.3).

Taken together, the results of the corroboration, the mean elevation, and the salinity simulations indicate that the swamp IBM is capable, with a fair degree of

reliability, of modeling the dynamics of basal area and stem density under a wide range of environmental conditions found in the Maurepas Basin. As discussed below, more caution is needed in interpreting model predictions of the response of wood production to mean elevation (flooding) and salinity.

### 3.6.3. Caveats

While the swamp IBM appears to simulate total stem density and basal area quite well, some caution is needed in interpreting annual wood production and in interpreting all three variables on a species-specific basis. The IBM was able to be calibrated so that basal area, stem density, and wood production all remained well within literature reported minimum and maximum values (Table 3.2, Figure 3.39). In the corroboration analysis, however, the model showed a consistent tendency to overestimate annual wood production compared to estimated values in the four distinct habitats that were monitored in the Maurepas swamp (Chapter 2) and that were used as corroboration benchmarks (Figure 3.23). In comparison to wood production data collected in field studies throughout a wide variety of hydrological and nutrient conditions, the wood production values estimated for the Maurepas swamps are low relative to their measured basal areas and stem densities, while model simulated wood production values are similar to the reported values (Figure 3.39). This suggests that the model, which was based on literature-reported values for parameters and relationships, realistically simulates wood production under averaged and generalized conditions, and that there are factors specific to the Maurepas swamp that are not included in the model.

Possible site-specific factors that could cause overestimation of wood production in the model predictions relative to the observed Maurepas data include the use of

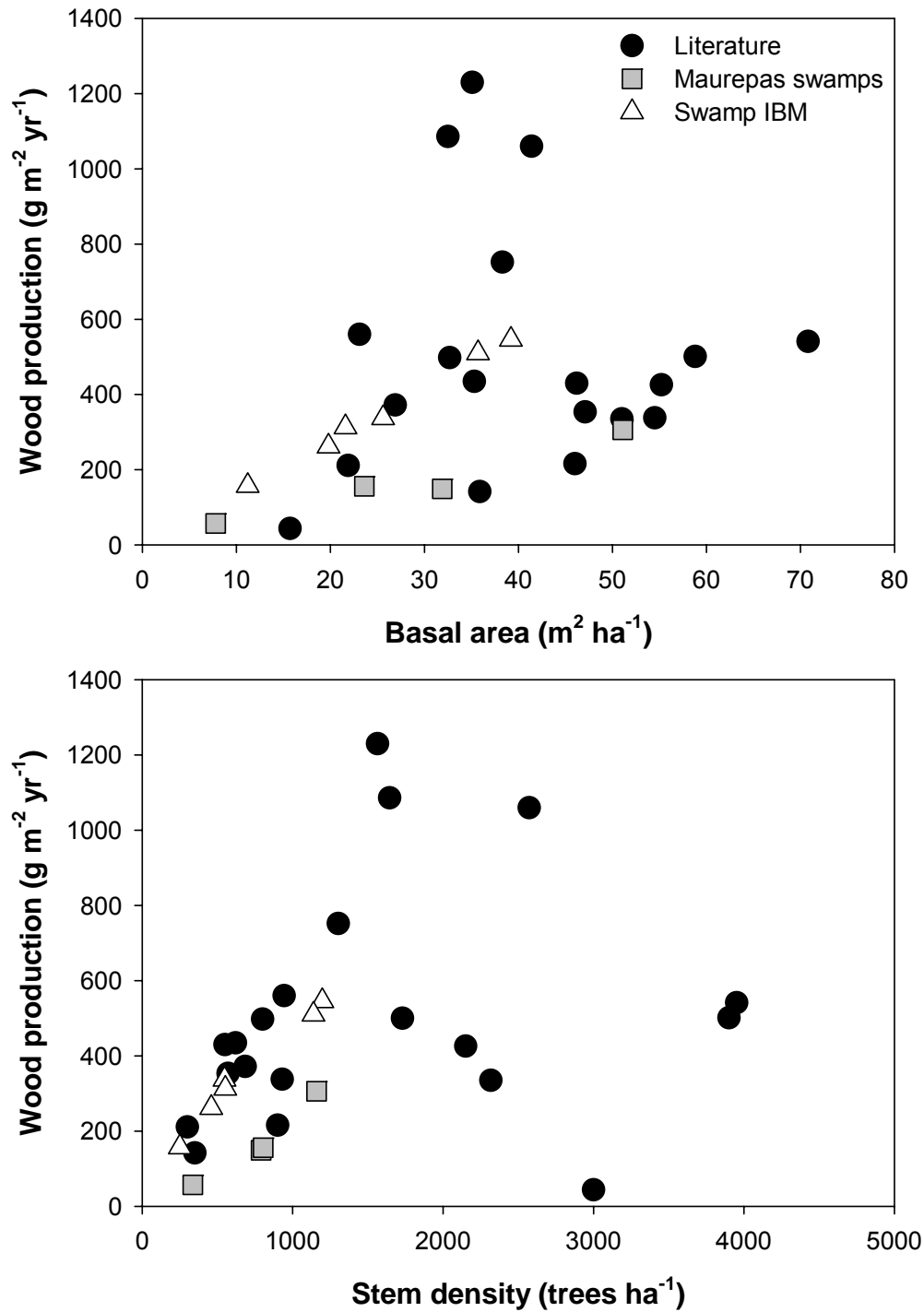


Figure 3.39 - Wood production in relation to basal area (top panel) and stem density (bottom panel) measured for the Maurepas swamp, simulated by the IBM, and reported for various field studies of cypress- or cypress-tupelo dominated swamps. Literature sources: Conner and Day (1976), Brown (1981), Conner et al. (1981), Dicke and Toliver (1990), Mitsch et al. (1991), Magonigal et al. (1997).

non-representative elevations in the corroboration, nutrient limitation, and leaf defoliation treatment. As the swamp IBM is very sensitive to mean elevation, it is possible that the model scenarios chosen to represent the Interior-West and Interior-East habitat types in the model corroboration were not very suitable matches, and that the true elevations at those sites are lower than the ones modeled. Another possibility is that the model's representation of growth and mortality processes results in too few trees that produce too much wood. Also, it is likely that there are other major limiting environmental or biological conditions in the Maurepas swamps that are impacting tree growth differentially throughout the swamp, and which are not included in the model. Among the model output variables examined, annual wood production is very sensitive to inter-annual variation in environmental and biological factors. A water quality analysis by Lane et al. (2003) of surface water collected in rivers and channels throughout the Maurepas swamps showed that nitrate concentrations in large areas of the swamp were less than 1% of those found in Mississippi River water, and were, in combination with low phosphate levels found, symptomatic of nutrient limitation throughout the swamp. Furthermore, both Effler et al. (2006) and Fox (2006) noted evidence of regular and wide-spread insect defoliation of both canopy tree species, *T. distichum* and *N. aquatica*, by the baldcypress leafroller (*Archips goyerana*) and the forest tent caterpillar (*Malacosoma disstria*) in the Maurepas swamps in recent years. Large-scale defoliation of canopy trees would force the affected trees to grow a second crop of leaves, which could result in reduced wood growth during those years.

Another important model to data mismatch besides overestimation of wood production was that the model tended to overestimate the dominance of *T. distichum* over *N. aquatica* in the corroboration simulations (Table 3.6). According to how the

equations in the model were specified, *N. aquatica* adult trees should have a growth advantage over *T. distichum* under flooding conditions exceeding five consecutive weeks of flooding, and a seedling survival advantage after twelve to seventeen weeks of consecutive flooding. Yet, even under the most flooded conditions simulated in the model (i.e., low mean elevation), *N. aquatica* never outperformed *T. distichum* in the model. As sizeable areas of the Maurepas swamp are heavily dominated by *N. aquatica* (i.e., Interior-West sites, Chapter 2), there are environmental conditions that have occurred in the Maurepas swamp that have promoted *N. aquatica* growth more than *T. distichum*.

One likely candidate among the species-specific tolerances that might make a difference in species advantages is shade tolerance, which was assumed equal for the two tree species in the model. Based on the 4-level categorical grouping of trees into classes of shade-tolerance by Burns and Honakala (1990), *T. distichum* would be classified as intermediate shade-tolerant, while *N. aquatica* would be classified as shade intolerant, which, at least at a coarse level, is not consistent with *N. aquatica* having an advantage over *T. distichum*.

Another possibility for the model underestimating a competitive advantage for *N. aquatica* could be the model glossing over how depth of flooding can affect the species differentially. *N. aquatica* has been reported to grow best in deep, periodic flooding, whereas *T. distichum* growth has been reported to be greater in shallow, permanent flooding (Keeland and Sharitz, 1995). Thus, it is possible that not only flood duration is important to these two species, but that flooding periodicity (i.e., return frequency) and depth of flooding also may be important to their differential selection. The swamp IBM is presently only checking flooding duration as a limiting factor, and not water depth or

periodicity. In addition, the data upon which the flooding tolerances of both species were based were sparse, and further modeling efforts are needed to investigate how slight changes in their relative flooding tolerances might shift species dominance patterns.

Differential grazing by mammalian herbivores also could cause the field data to show *N. aquatica* outperforming *T. distichum* while the model simulations do not. Differences in the spatial distribution of mammalian herbivores such as nutria (*Myocastor coypus*), a tree seedling predator responsible for destroying thousands of planted seedlings in the Maurepas swamps (Myers et al., 1995; Beville, 2002), also could contribute to species shifts in the field data that would not be reflected in model simulations.

The swamp IBM used cyclic records of environmental conditions and thus did not simulate any directional changes in environmental conditions, such as saltwater intrusion (Thomson et al., 2002) and continued relative sea-level rise (Penland and Ramsey, 1990). The swamp IBM used 49 years of stage data, correlated with all available salinity data, to provide an estimate of the effect of current climate variability on swamp survival and wood production. I chose repeating the 49-year time series of environmental conditions to allow each simulated swamp to reach a state of equilibrium with these environmental conditions, which facilitates the comparison of different flooding and salinity “treatments” in the model. Moreover, the swamp IBM in its present form does not model feedback interactions between biomass production and elevation, which have been shown to impact the rate of relative subsidence (Rybczyk et al., 1998). With the current formulation of the model, a scenario that includes sea-level rise will eventually lead to permanent flooding and a gradual decline and disappearance of the



swamp forest. Application of the model for examining the effects of sea-level rise should consider how sea level rise would affect the changes in the elevations of the model grid due to accretion through new sediment deposition and root growth.

At present, the swamp IBM uses seed dispersal and overstory shading as the only two positive tree interactions, both of which benefit tree regeneration. The increased seed supply near productive adults is modeled by using normal probability distributions for seed dispersal, which keep a large proportion of dispersing seeds in relatively close vicinity of their parent trees. Increased seedling survival under conditions of partial shading (Figure 3.16) is another mechanism by which the proximity of a limited number of larger trees facilitates regeneration by creating more favorable light conditions for seedling survival.

Bertness and Callaway (1994) hypothesized that facilitation between plant species, or among individuals of the same plant species, may become more important in community dynamics as abiotic stress or consumer pressure increase, a hypothesis that has been supported by numerous field observations (Callaway and Walker, 1997). For instance, McKee (1993) suggested that the aerial root systems of adult mangrove may improve soil redox conditions for mangrove seedlings. Similar effects of adult trees improving local soil conditions, and thus facilitating seedling survival, are also possible in swamp forests. Huenneke and Sharitz (1986) showed that seedling establishment in a South Carolina cypress-tupelo swamp predominantly occurred on protected stable microsites near existing trees and knees, which provide protection from falling and floating debris and higher elevations. Dead wood sites, by contrast, appeared to be of transitory importance to seedling establishment and are unlikely to provide long-term establishment benefits. Leaf litter presence and thickness may have species-specific

positive or negative effects on tree seedling establishment and have been shown to cause reversals in seedling establishment success ranking among some tropical tree species (Molofsky and Augspurger, 1992). Elevation increases through litter deposition and increased potential for nutrient recycling may provide positive factors impacting seedling survival, while the physical barrier of thick leaf layers may prevent seedlings from rooting and could contain or attract pathogens or leaf predators. As more information becomes available, these additional facilitation effects between species and among individuals can be included in the IBM.

#### 3.6.4. Comparison to Existing Models, Field Studies, and Experiments

The swamp IBM developed in this chapter shows good agreement with general swamp habitat change predictions in response to flooding and salinity made by numerous field researchers and other simulation models, and offers several advances for coastal swamp modeling. Modeling efforts by Conner and Brody (1989) showed that, even though mature *T. distichum* and *N. aquatica* are flood-tolerant, the total basal area of *T. distichum* and *N. aquatica* declines when water levels continued to rise, and no new trees are anticipated to be able to enter the understory under conditions of rising water levels (Toner and Keddy, 1997). Field and other modeling studies of swamps indicate that continual flooding, though not immediately detrimental to mature cypress-tupelo swamps, will lead to their gradual death over time (Harms et al., 1980; Mitsch and Rust, 1984; Conner and Day, 1988; Conner and Brody, 1989; Conner and Day, 1992; Xiao et al., 2002).

Model predicted responses to salinity are also in agreement with reported responses from other studies, although some caution is needed about the responses of mature trees. Greenhouse studies of *T. distichum* and *N. aquatica* seedlings grown in

pots under saline conditions (Pezeshki, 1987; Pezeshki et al., 1989; Allen et al., 1997; Conner et al., 1997; Effler and Goyer, 2006) indicate that *N. aquatica* is affected adversely by salinity levels as low as 2-3 ppt, while the response of *T. distichum* is more variable, which is likely due to genotypic variation (Allen et al., 1994; Krauss et al., 2000). Seedlings of both species died within 2 weeks when grown at 10 psu salinity in the greenhouse (Conner et al., 1997). While these greenhouse observations with seedlings are consistent with model predicted responses, other studies involving mature trees have shown more complicated responses to raised salinity. Field observations of tree survival in a swamp in South Carolina following hurricane Hugo (Conner and Inabinette, 2003) showed that *T. distichum* trees experienced high mortality following the hurricane-associated saline flooding, while *N. aquatica* did not, and cautioned that seedling tolerances may not necessarily be reflective of the tolerances of mature trees. In contrast, in the Maurepas swamps, *N. aquatica* were generally absent from swamp sites that experienced elevated salinity levels whereas *T. distichum* trees continued to grow (Chapter 2). Further field data needs to be collected to delineate the relative salinity tolerances of mature trees of both species more clearly.

Four existing models that simulate forested wetlands are SWAMP (Phipps, 1979), FORFLO (Pearlstone et al., 1985), FORMAN (Chen and Twilley, 1998), and SISM (Xiao et al., 2002). All of these models are either descendants of the JABOWA (Botkin et al., 1972) and FORET (Shugart et al., 1973) lineage of forest models, or follow a very similar modeling structure. SWAMP and FORFLO model bottomland hardwood forests with twenty-six tree species (Phipps, 1979; Pearlstone et al., 1985), SISM models a pure *T. distichum* swamp (Xiao et al., 2002), and FORMAN simulates a three-species mangrove swamp (Chen and Twilley, 1998). In these models, optimal

tree growth is constrained by life-history traits (e.g., maximum diameter, maximum height, maximum age), while realized growth is limited by stress (e.g., flooding), resource availability (e.g., space, light, water, soil type), and temperature. Trees are killed probabilistically when tree ring growth rates are low. Recruitment is capped by specifying a maximum number of new saplings that can be added per species per year, and is further limited by shade tolerance, which prevent recruitment completely under high stocking density and flooding. Growth and mortality occurs on annual time steps.

Typical plots sizes are 1/12 ha in FORFLO, 20x20 m in SWAMP and SISM, and 500 m<sup>2</sup> in FORMAN. FORFLO, SWAMP, and FORMAN simulate plots that are assumed to be well-mixed (i.e., location of individual trees within the plot is not defined), with environmental conditions assumed to be applied to all trees in the plot. SISM is a direct descendent from the SWAMP model and uses very similar equations and a single well-mixed plot for adult trees. SISM modified how seeds and seedlings were modeled in SWAMP by adding a finer spatial grid within the plot (2x2m cells) to simulate the spatially-explicit seed dispersal and seedling growth.

The IBM developed in this chapter can be considered the next generation version in the long lineage of forest succession modeling. The IBM uses similar equations for growth and mortality of individual trees, including species-specific tolerances and preferences and shading effects. The IBM does this, however, allowing for the simultaneous effects of salinity and flooding, and with greater spatial and temporal resolution and extent than these previous models. This increased resolution permits more realistic seed dispersal, and allows for localized effects of salinity, flooding, and competition for light (shading).

To my knowledge, the swamp IBM presented in this chapter is the first forested wetland model that combines the detrimental effects of both flooding and salinity simultaneously. Chen and Twilley (1998) added salinity and nutrients as growth-limiting factors to their gap dynamic mangrove model, but used flooding only as an environmental filter for seedling recruitment.

The swamp IBM developed in this chapter also goes beyond existing models in using a finer time step, simulating a larger domain, and representing the explicit locations of trees within the plot. In contrast to the annual dynamics simulated in FORFLO, SWAMP, FORMAN, and SISM (for adult trees), the swamp IBM simulates growth and mortality of all trees and seedlings at weekly time increments and for a 1-km<sup>2</sup> plot. Furthermore, the IBM divides the plot into 10x10m cells that have their own elevations and therefore water depths and salinities that vary spatially and temporally within the plot. The IBM then tracks the explicit tree locations of each tree on the plot. The SISM developed by Xiao et al. (2002) was a step towards this increased resolution used in the IBM. In SISM, a 2x2m grid was superimposed on the plot and seed germination and seedling growth was followed monthly; upon reaching 5-years old, individuals in SISM were considered adults and followed annually on the well-mixed plot like the other swamp forest models. The weekly time step and detailed spatial location used in the swamp IBM enables both seedlings and adult trees to experience differentially severe growth and mortality effects depending on where and when unfavorable environmental conditions occur within the plot. The higher resolution also allows for more realistic seed dispersal than the commonly global dispersal used in the previous models. SISM, with its finer grid and time step for seeds and seedlings, allowed for seed dispersal via hydrochory. The IBM accounted for both water transport

of seeds via flooding (hydrochory) and the proximity to the parent tree. Time and additional model testing will determine if the inclusion of salinity and flooding effects, and the finer resolution spatial and temporal scales used in the IBM, results in more realistic and accurate predictions of swamp forest dynamics than the previous generation of coarser models.

The swamp IBM developed in this chapter is readily transferable to other basins and locations that are dominated by cypress-tupelo swamp. Many parameters used in the model were taken from the results of greenhouse studies or from field experiments not located in the Maurepas Basin. The model was, furthermore, calibrated to basal areas, stem densities, and wood production values reported for numerous swamps throughout the southeastern United States, and corroborated to data from the Maurepas Basin. Applying the model to other locations requires site-specific knowledge of water-level and salinity fluctuations at a 1-km<sup>2</sup> scale and elevation differences at a 100-m<sup>2</sup> scale. Whether there are sufficient site-specific data for other locations for model application depends on the questions of interest.

#### 3.6.5. Future Directions

I see five particularly interesting directions for the further development of the swamp IBM: (a) resolution of why wood production was higher than observed in the corroboration simulations, (b) further specification of species differences in tolerances to salinity and flooding, (c) inclusion of nutrient effects in the model, (d) inclusion of a feedback interaction of swamp growth on elevation, and (e) refinement of the seed germination and dispersal processes. The first three directions will require additional experimental and field data collection. Field data from additional places within and outside of the Maurepas Basin would help to resolve the levels of wood production

expected under a variety of conditions, and provide additional information about model accuracy and robustness. The environmental conditions of further sampling efforts could be simulated in the model, and model-predicted basal areas, stem densities, and wood production could then be compared to the field data. Experimental approaches are most likely needed to improve estimates of species differences in tolerances to salinity, flooding, and other environmental variables.

The inclusion of nutrient effects and nutrient turnover in the model may improve model predictions of wood production in the nutrient-limited Maurepas swamp, and would make the model better suited to predict future ecosystem changes arising from planned restoration efforts (Chapter 2). Extensive field research has shown that the Maurepas swamps are substantially nutrient limited (Lane et al., 2003), and that experimental nutrient augmentations in the Maurepas swamps greatly enhance aboveground biomass production of the herbaceous vegetation (Parsons, 2002) and *T. distichum* (Greene, 1994; Myers et al., 1995; Boshart, 1997; Effler et al., 2006). One simple way to add nutrients into the swamp IBM would be to make the annual maximum growth rate also a function of nutrients, so that maximum annual growth is greater under conditions of high nutrient availability and reduced under nutrient poor conditions. It may also be necessary to include some evaluation of nutrient turnover in the model, as, at least in many tropical forests, nutrient efficiency and nutrient turnover have been shown to affect tree growth more strongly than ambient nutrient conditions (Vitousek and Sanford, 1986).

The fourth direction for model improvement is relating the biological productivity to the elevation in the cells, which would then influence the hydraulics. Forested wetlands can contribute to accretion through root growth and the addition of

decomposing organic matter such as leaves (Rybczyk et al., 2002). Using a combination of field research and simulation modeling, Rybczyk et al. (1998) showed that the forest growth contributions to increases in elevation could, in turn, result in reduced flooding and would further increase productivity. The productivity-driven increases in elevation could also mitigate the effects of relative sea-level rise, even though these processes alone are unlikely to offset projected rates of eustatic sea-level rise (Gornitz, 1995).

The fifth and final direction for model improvement is to refine the seed dispersal and germination dynamics. I addressed seed dispersal through hydrochory (Middleton, 2000) in the model by the rough approximation of calculating the time a cohort of seeds would be floating or submerged with flood water from the time of seed fall to the time of germination. I converted this potential floating time to a proportion of the maximum possible floating time any seed could float before the end of the germination time, and used this proportion as a multiplier to a fixed maximum dispersal distance. One limitation in this approach is that new trees in my model could actually be assigned locations in model cells that remain permanently flooded throughout the germination season and which could, therefore, not actually support seed germination. A more detailed seed tracking approach would be necessary to track seed drift throughout the grid and to limit seed dispersal and germination only to plots that are suitably dry. While not specifically tracking seed cohorts through a modeled swamp, Xiao et al. (2002) partially addressed this issue by forcing all seeds to germinate only within plots that dried up during the germination period.

The model presented in this chapter offers promise as a useful tool for better understanding how multiple environmental factors (e.g., flooding, salinity) interact with



competition among trees to determine productivity over time in a swamp forest. The model was developed with the philosophy that fine spatial scale interactions of environmental variables on trees and among individual trees can lead to improved forecasts of how changes in environmental conditions can affect long-term forest dynamics. With some additional improvements, the model should prove to be a valuable tool for restoration planning by allowing the quantification of the long-term forest responses to changes in elevation, flooding, and salinity.

### 3.7 References

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## **CHAPTER 4. TO SEE THE FOREST FOR THE TREES: COMPARING THE SIMULATION RESULTS OF AN INDIVIDUAL-BASED SWAMP MODEL TO A LANDSCAPE MODEL**

### **4.1 Introduction**

Both landscape spatial models (Costanza et al., 1990; Martin et al., 2000; Reyes et al., 2004) and individual-based forest succession models (Phipps, 1979; Pearlstine et al., 1985; Chen and Twilley, 1997; Xiao et al., 2002) have been used successfully to model wetland habitat change. Landscape and individual-based models fundamentally differ in how they represent spatial variation in environmental conditions and how this variation affects the biological predictions. Existing coastal landscape models generally focus on predicting the dynamics of flooding, salinity, and sediment supply over broad landscapes, and using these broad predictions of environmental conditions to simulate the responses of highly generalized habitat types. Habitat types that have been represented in landscape models include fresh marsh, intermediate marsh, brackish marsh, salt marsh, and swamps. In contrast, individual-based forest succession models focus on predicting the responses of individual trees and tree species composition to fine-scale, local environmental gradients. Individual-based model often operate on a finer spatial scale than landscape models.

Landscape spatial models have been developed over the last two decades to describe and predict wetland habitat change in coastal Louisiana under various restoration and climate change scenarios (Costanza et al., 1990; Martin et al., 2000; Reyes et al., 2000; Martin et al., 2002). The Coastal Ecological Landscape Spatial Simulation (CELSS) model was the first landscape spatial model for coastal Louisiana, and was originally developed for the Western Terrebonne basin (Costanza et al., 1990). The CELSS model contained land-building (i.e., sediment build-up to form new marsh



surface), biological production (i.e., marsh and swamp primary production), and habitat switching (e.g., marsh to open water) algorithms, and was capable of simulating future habitat change scenarios for 50 years (Martin et al., 2002). A recent descendant of the CELSS model is the Mississippi Delta Model (Martin et al., 2000; Martin et al., 2002; Reyes et al., 2004). This next generation of the coastal Louisiana landscape models revised the original CELSS model to extend the spatial scale to cover more than 8,500 km<sup>2</sup>, to use variable time-steps ranging from 20-1,200 seconds in the hydrodynamics module of the model, to increase the temporal resolution of ecological processes from a weekly time-step to a daily time-step, and to allow for predictions of 100 years. This version of the landscape model continues to be modified and used, most recently as part of a coast-wide restoration planning effort for Louisiana (Twilley, 2003).

There are several features that make landscape models an attractive choice for modeling coastal habitat change. Landscape models are capable of modeling habitat change over large areas of diverse habitats, and they are designed to be easily transferable to different coastal basins. Due to general nature of habitat types being represented, relatively few habitat-specific parameters are needed and these parameters are readily available from the literature. Landscape spatial models incorporate location-specific algorithms that allow feedback between the local processes (e.g., sediment deposition, flooding, plant growth, decomposition) and landscape dynamics (e.g., sea-level rise, sediment supply, wind), so that both the landscape (i.e., habitat types, elevations, bathymetry) and the intensity of the processes affecting it (e.g., flooding, plant growth) change through time (Boumans and Sklar, 1990). There are also several aspects of landscape models that can limit their applicability for evaluating coastal habitat change, especially when forecasts are

needed for forested habitats. One current limitation of the landscape modeling approach is the aggregation of plant species and communities into generic habitat types with generalized tolerances to common environmental stressors. Determining at what level organisms need to be represented in models (e.g., every species versus total biomass) in order to obtain acceptable accuracy in model predictions remains a major challenge in ecological modeling. Trees exhibit a wide range in their tolerances among species. While accurate and precise predictions of the exact species composition of a swamp may be overkill, the species mix can greatly affect how the community responds to changes in salinity and flooding. Furthermore, the landscape modeling approach generally represents environmental conditions on relatively coarse spatial scales (km's). Some would argue that it is the interaction among individual trees and the interaction of trees with their environmental conditions on the scale of meters that is critical to accurately predicting responses to changed conditions (e.g., saltwater intrusion, relative sea-level rise).

Individual-based wetland forest succession models can address these two potential shortcomings of landscape models, but at the expense of greater data demands, focus on one habitat type, and difficulties in being applied to very board spatial areas. IBMs often simulate thousands of individuals and keep track of their individual characteristics (e.g., size, age, location, species, growth) through time. Each individual's growth, survival, and reproduction are defined through functions that depend on the condition of the individual, on the presence and condition of neighboring individuals, and on local environmental conditions. As a result, IBMs model detailed individual and species level responses, and the accumulation of these become population and community responses, such as size class distributions, age distributions,

and species composition. The cost of this greater detail is that IBMs can have enormous data demands to specify fine-scale variation in environmental conditions and species-specific differences in biology and tolerances. IBMs are generally applied at much smaller spatial scales than landscape models, ranging from replicated 20-m<sup>2</sup> plots (Phipps, 1979) to 1-km<sup>2</sup> areas (see Chapter 3), and they model species within the single habitat type of forest. Thus, relating IBM results to the coast-wide scale is difficult.

In this chapter, I compare the predictions between the Mississippi Delta Model landscape model (Reyes et al., 2000) that was adapted to the Maurepas basin, and a detailed swamp forest IBM (Chapter 3). I use the environmental conditions (salinity and flooding) simulated by the landscape model as input to the IBM, and then compare the landscape and IBM predictions of swamp forest change over 100 years. Based on the results using identical environmental conditions, I then repeated the IBM simulations using modified salinity and flooding to understand the similarity and differences between the predictions from the two models further. Finally, I discuss how the two different modeling approaches can be used to inform each other to improve our forecasting ability for how swamp forests respond to changes in environmental conditions in coastal landscapes.

## **4.2. Methods**

### **4.2.1. A Brief Description of the Swamp IBM**

The swamp IBM simulates the weekly germination, growth, and survival of two tree species, *Taxodium distichum* (baldcypress) and *Nyssa aquatica* (water tupelo). The IBM is described in detail in Chapter 3. The spatial extent of the swamp IBM is 1 km<sup>2</sup>, and tree locations are modeled in continuous space within the 1 km<sup>2</sup>. Environmental conditions (i.e., salinity and flooding) are modeled at a spatial resolution

of 10m by 10m (100 m<sup>2</sup>) cells on the 1 km<sup>2</sup> grid. Each 100 m<sup>2</sup> cell in the grid has a fixed elevation, and stage and salinity for the entire map are read in weekly. The weekly flooding status of each cell is determined by comparing the cell's elevation to stage each week. If flooded, the swamp IBM keeps track of the flooding duration by advancing the cell's weeks-of-flooding counter and the cell's salinity is updated with the current water salinity. Once a cell dries up, the flooding counter is reset to zero, and it retains the salinity it experienced the previous week until it gets flooded again.

For each living individual tree, the swamp IBM keeps track of its species, location, age, diameter, size class, basal area, and diameter growth. Seedlings and saplings up to 4 years old are modeled as cohorts associated with their parent tree. At 4-years of age, surviving saplings are converted to individual trees. Each tree individual is followed until its eventual death or the end of the simulation.

Tree growth for individual trees is modeled as a set of species-specific functions based on salinity, weeks of continuous flooding, time of the year, and shading from neighboring trees within a 10-m radius. Tree mortality due to slow growth and a random source is modeled annually. Both annual mortality components are applied equally to adult trees of both species at the end of the growing season each year. Salinity in each cell causes weekly mortality of seedling cohorts and individual adult trees in that cell. Spatial interactions in the model occur through shading and recruitment, which include the potential for density-dependent effects on survival.

Individual trees become capable of producing seeds when they reach 10 years of age, and seed viability and seedling survival are tracked in parent-specific cohorts each week during the growing season. Reproduction (i.e., seed release) occurs once a year in November. The number of seeds released is determined from species-specific

maximum numbers of seeds per tree, which are modified based on tree size and annual growth. Seeds can germinate in a period from in early March until the end of June, but only under non-flooded conditions. Up to the time that a 100 m<sup>2</sup> cell dries up during the germination period, seed numbers are decremented weekly to represent the loss of seed viability during winter dormancy and under flooded conditions. Following germination, seedling mortality is represented by a set of species-specific multiplicative functions of survival based on flood duration, salinity, and shading, which are evaluated weekly during the growing season. Surviving seedlings are converted to individual trees in their 4<sup>th</sup> year of age, at which time they are assigned their continuous location within the grid. The location of new trees is calculated by determining random directions in the north-south and east-west directions and by determining the maximum dispersal distance based on the proportion of time between seed fall and germination that a tree's seed cohort remained floating (i.e., in a flooded cell).

#### 4.2.2. A Brief Description of the Landscape Model

Reyes and colleagues developed a landscape regional model for the Maurepas wetlands based on previous landscape modeling efforts to detect coastal habitat change in the Mississippi River Deltaic Plain (Reyes et al., 2000; Martin et al., 2002). The landscape model consists of four major modules (Figure 4.1) that govern the interaction of environment and generalized wetland plant communities over a model extent of 3,251 km<sup>2</sup> and at a spatial resolution of 1 km<sup>2</sup>. The four modules of the landscape model are a: (1) hydrodynamic module; (2) soil building module; (3) biomass production module; and (4) habitat switching module. The wetland habitat types included in the model are swamp, fresh marsh, intermediate marsh, brackish marsh, and salt marsh.

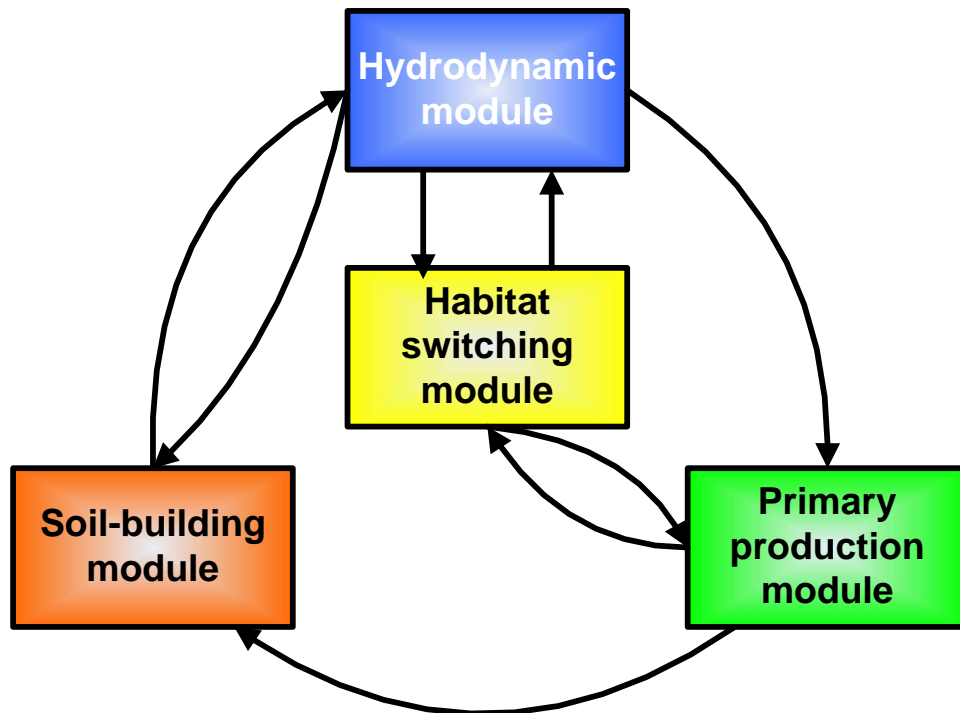


Figure 4.1 - Overview of the four modules of the landscape model that govern the interactions among hydrodynamics, primary production, soil-building, and habitat switching.

The hydrodynamic module governs the two-dimensional movement of water, salinity, and sediments among the 1 km<sup>2</sup> model cells in the grid. The model reads in historic time-series records of rainfall, wind velocity and direction, river discharge, tidal input through Pass Manchac, salinity, and sediment concentration. Relative sea-level rise (RSLR) is included in the landscape model at a rate of 1.31 cm yr<sup>-1</sup> for the period from 1955 through 1974, and a rate of 1.19 cm yr<sup>-1</sup> thereafter. Horizontal surface flows are calculated based on relative water height (i.e., hydrologic head), relative land elevation (i.e., slope), wind velocity and direction, and Manning's coefficients. Surface water leaves or enters cells through horizontal flow from or to its four neighboring cells, infiltration into sediment/soil pore space, evaporation, and precipitation. Salinity moves as a conservative tracer in the surface water through diffusion and mixing. Suspended

sediments, detritus, and litterfall also move with surface water flows, but they are non-conservative. The non-conservative suspended materials can get deposited in cells at low flow velocities, and deposited sediment can be re-suspended by high flow velocities. The water depth in each 1 km<sup>2</sup> cell is determined as the difference between water height and surface elevation in a time-step in hourly or shorter time steps. Flooding and salinity values are averaged to obtain daily values for use in the biomass production module.

The biomass production module determines the plant biomass that is produced aboveground and belowground in each generalized habitat type on a daily basis. The biomass production module uses daily flooding and salinity values from the hydrodynamic module, and sends production information to the soil building and habitat switching modules (Figure 4.1). Each wetland habitat type is assigned an initial biomass, a biomass production rate, a respiration rate, a range of salinity tolerated, and a range of flooding tolerated based on the dominant plant species that represents this habitat in the Louisiana coastal zone. Plant biomass production is modeled separately in aboveground and belowground components, which are limited by salinity, flooding, and air temperature modifiers, and take into account translocation of aboveground to belowground biomass, mortality, and respiration.

The soil building module keeps track of deposited organic matter and inorganic sediments, suspended sediments, and belowground biomass production in each cell, and determines their potential contributions to surface elevation changes. The soil building module uses production inputs from the biomass production module and feeds elevation change data into the hydrodynamic module (Figure 4.1). Both inorganic sediment and the combination of dead organic matter and belowground live organic

matter contribute to surface elevation, but whereas inorganic sediment is conserved, organic matter is lost at constant rates through decomposition. Suspended inorganic sediments enter or leave the model as a function of the surface water inflow and runoff calculated in the hydrodynamic module.

The habitat switching module is invoked bi-annually to determine if or what kind of habitat changes take place. Each day, the habitat switching module compares each cell's daily salinity and flooding values from the hydrodynamic module and biomass production values from the biological production module to its habitat-specific tolerance ranges or maxima and minima. If the cell falls within its assigned habitat's defining range, a counter for the same habitat type is advanced. If the cell's conditions fall within the range of a different habitat type, the counter of the different habitat type is advanced. In the landscape model, swamp salinity tolerance is set between 0 and 2 psu, while swamp habitat flooding tolerance is assigned so that swamp habitats maintain 100% production even under permanent flooding on a daily basis. Biomass production rates are set at the minimum production rate of  $20.3 \text{ g m}^{-2} \text{ day}^{-1}$  for a habitat to remain swamp. After two model years, the habitat switching module determines the highest habitat-type counter of each cell and, if it differs from the current habitat type in the cell, changes the habitat type to the habitat with the highest counter.

#### 4.2.3. Comparison of Landscape and Individual-based Models

Landscape model values of weekly salinity and water depth were read into the swamp IBM, and the IBM's prediction of basal area was compared to the landscape model's prediction of habitat type (swamp or marsh) over 100 years. This was done for eight cells in the landscape model, for which the landscape model predicted several different temporal patterns of habitat changes. The landscape model simulates four



possible major outcomes over its typical 100-year simulations: (1) swamp habitat persists over the 100 years; (2) swamp converts to marsh within the 100 years; (3) marsh converts to swamp within the 100 years; and (4) marsh habitat persists over the 100 years. The landscape model used repeating sequences of historical records of precipitation, air temperature, solar irradiance, wind speed and direction, water temperature, and river stage from 1956-1988 as environmental inputs, and the landscape model was initialized with the 1988 vegetation and habitat maps generated by the USGS National Wetlands Research Center for this region. Reyes (personal communication) identified cells within the landscape model that matched the habitat change or persistence outcomes (1), (2), and (4). There were no instances in the simulation of the landscape model that I used in which marsh converted to swamp (outcome (3) above). Reyes provided the 100-year time-series of mean weekly water depth (Figure 4.2) and salinity (Figure 4.3) for two landscape model cells that showed swamp persistence (i.e., scenarios 1a and 1b), for four landscape model cells that underwent habitat changes from swamp to marsh after 49-53 years (scenarios 2a-d), and for two landscape model cells that showed marsh persistence (scenarios 3a and 3b).

I used the water depth and salinity time-series provided by the landscape model (Figures 4.2 and 4.3) as inputs to the swamp IBM, so that I could make model comparisons using the same salinity and flooding conditions. The water depth provided by the landscape model was converted into stage data for use in the swamp IBM by adding the mean elevation of each landscape cell to water depth. The steady increase in stage resulted in increases in flooding duration in each scenario (Figure 4.4), so that

each scenario remained flooded for 80% to 100% of the growing season each year after maximum stage was reached in or near year 50.

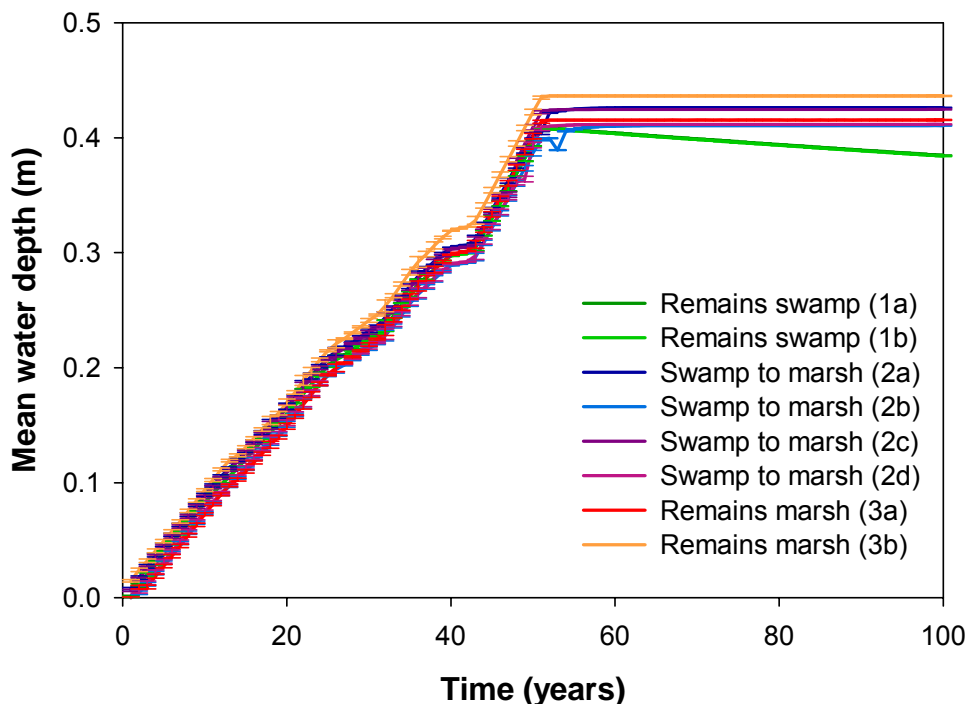


Figure 4.2 - Mean ( $\pm$  SD) water depth above the mean elevation during the swamp IBM growing season for 100 years in each of the eight landscape model scenarios.

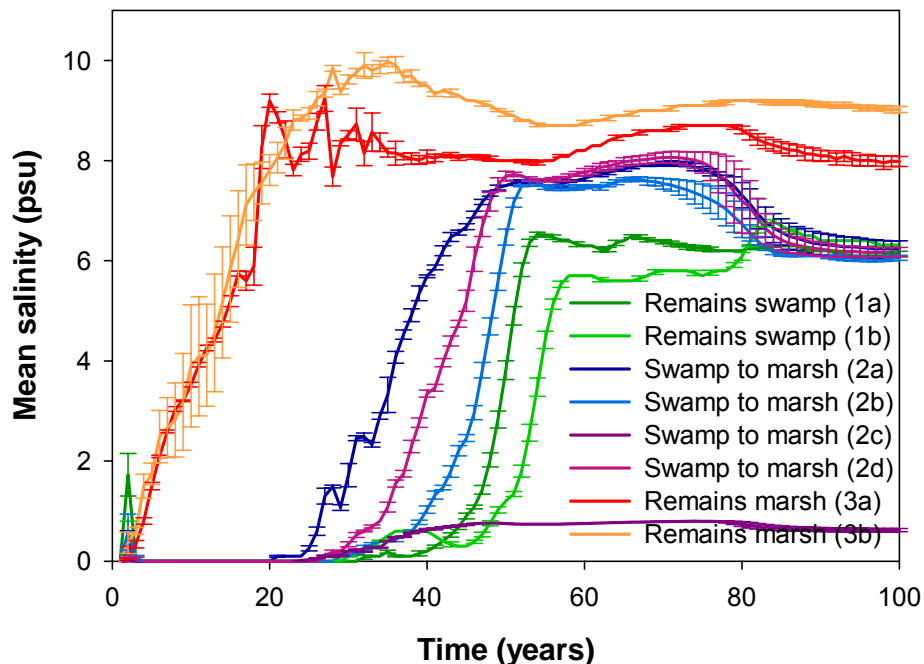


Figure 4.3 - Mean ( $\pm$  SD) growing season salinity for 100 years in each of the eight landscape model scenarios.

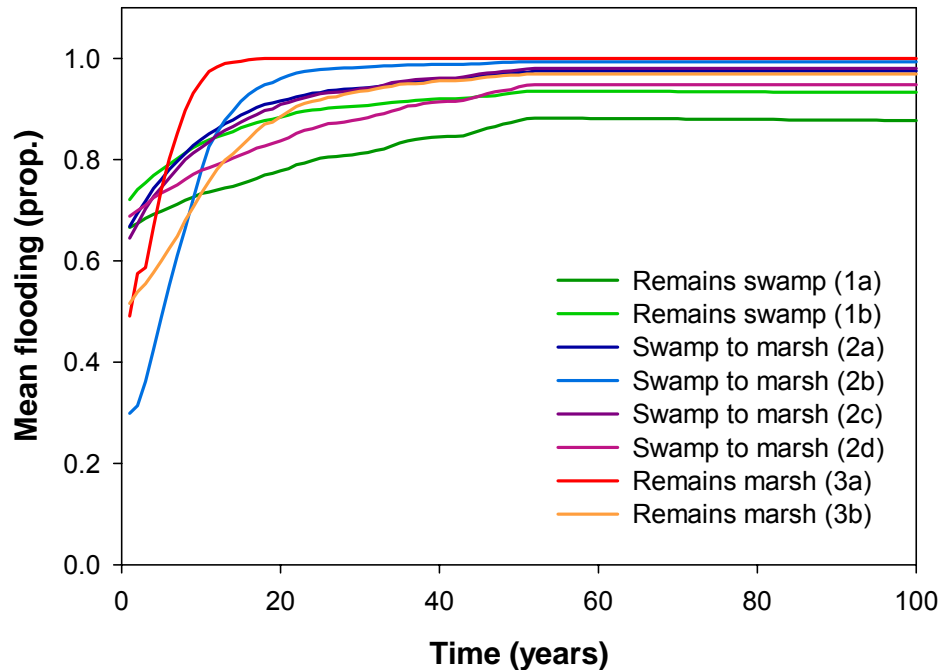


Figure 4.4 - Proportion of the growing season that is flooded each year over 100 years in each of the eight landscape model scenarios. The proportion was determined by calculating for how many weeks in each growing season each cell was flooded and then averaging over all cells in the grid.

The location of each of the eight landscape model cells was used to locate the matching landscape scene in the finer-resolution elevation map needed by the swamp IBM (Figure 4.5). The 1-km<sup>2</sup> resolution elevation data used by the landscape model and the 100-m<sup>2</sup> resolution elevation data used by the swamp IBM were both based on the same 5-m resolution LIDAR map for the land-portions of the modeled landscape, and the same 15-m resolution bathymetry map for the water bodies in the landscape (see Chapter 3). The mean elevations of the 100 m<sup>2</sup> cells for each scene used in the swamp IBM were adjusted to have the same overall mean elevation as the elevation of the associated 1 km<sup>2</sup> cell. This was done to minimize any differences in elevation of the 100 m<sup>2</sup> cells from the 1 km<sup>2</sup> cell that could arise by slight inaccuracies during aligning the larger cells of the landscape model with the finer cells of the elevation map. The

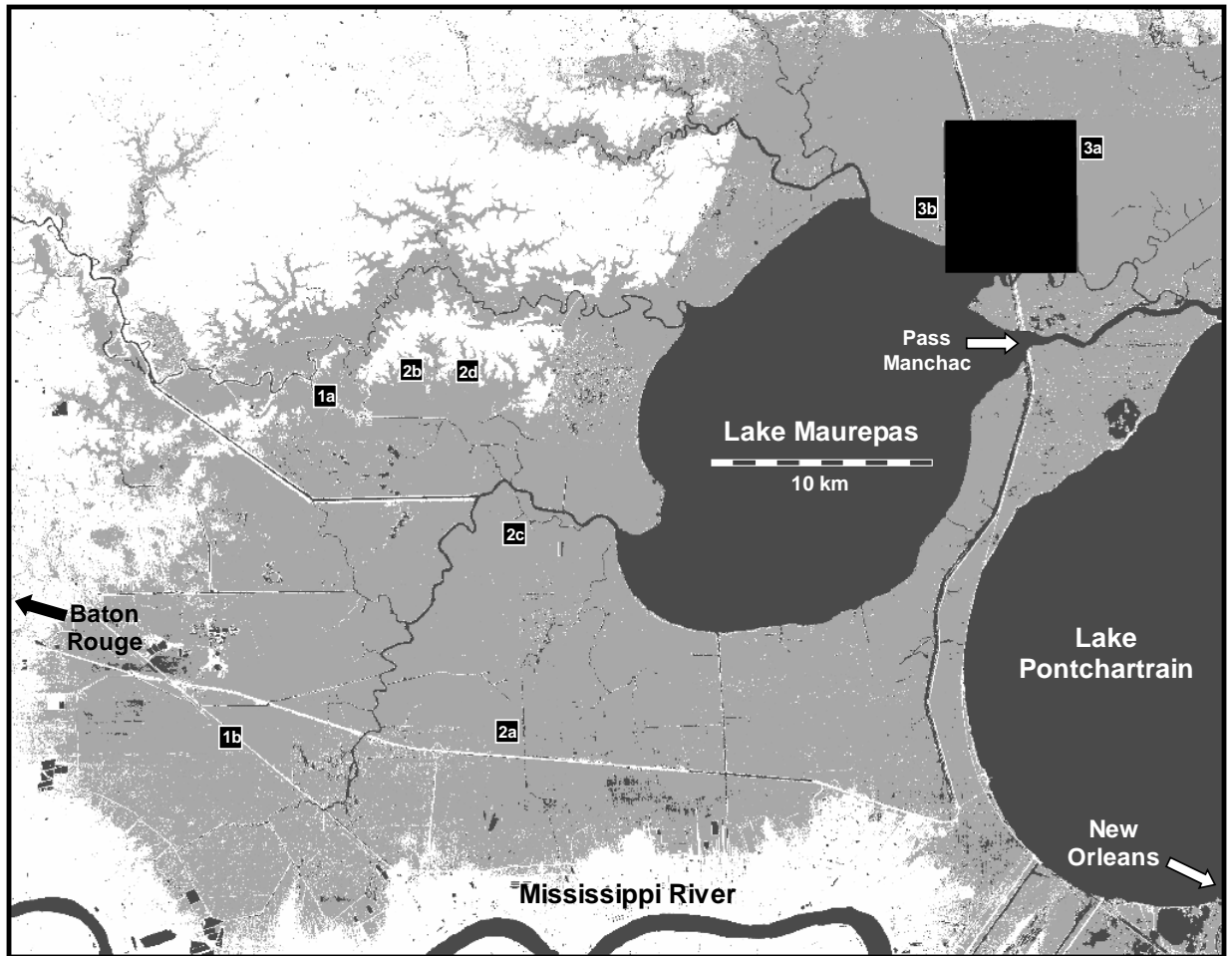


Figure 4.5 - Map of the Maurepas swamps and the locations of the eight landscape model cells used in the model comparison. The cells are indicated by the small black boxes inscribed with numbers matching their scenario identification number. Open water is shown in dark grey, wetlands in light grey, and uplands in white. The black box shades an area of missing elevation data.

elevation characteristics of the eight landscape scenes used in the model comparison are summarized in Table 4.1, and shown in Figure 4.6 for the four cells that the landscape model predicted marsh persistence and in Figure 4.7 for the four cells that the landscape model predicted a switch from swamp to marsh.

The swamp IBM was run for 100 years using the salinity and water depth conditions recorded at each of the eight landscape model cells. Annual basal area (summed over the two species) was used as the IBM output variable. The six

Table 4.1 - Elevation characteristics of the eight landscape scenes corresponding to the eight scenarios used in the model comparison. Summary data is based on the elevations in the 10x10 m cells within each of the 1-km<sup>2</sup> scenes.

Landscape scene	Mean $\pm$ SD (m)	Median (m)
Remains swamp – Scenario 1a	0.360 $\pm$ 0.523	0.218
Remains swamp – Scenario 1b	0.310 $\pm$ 0.289	0.223
Swamp to Marsh – Scenario 2a	0.181 $\pm$ 0.229	0.141
Swamp to Marsh – Scenario 2b	0.530 $\pm$ 0.098	0.530
Swamp to Marsh – Scenario 2c	0.220 $\pm$ 0.161	0.186
Swamp to Marsh – Scenario 2d	0.500 $\pm$ 0.205	0.431
Remains Marsh – Scenario 3a	0.400 $\pm$ 0.043	0.401
Remains Marsh – Scenario 3b	-0.029 $\pm$ 0.435	0.007

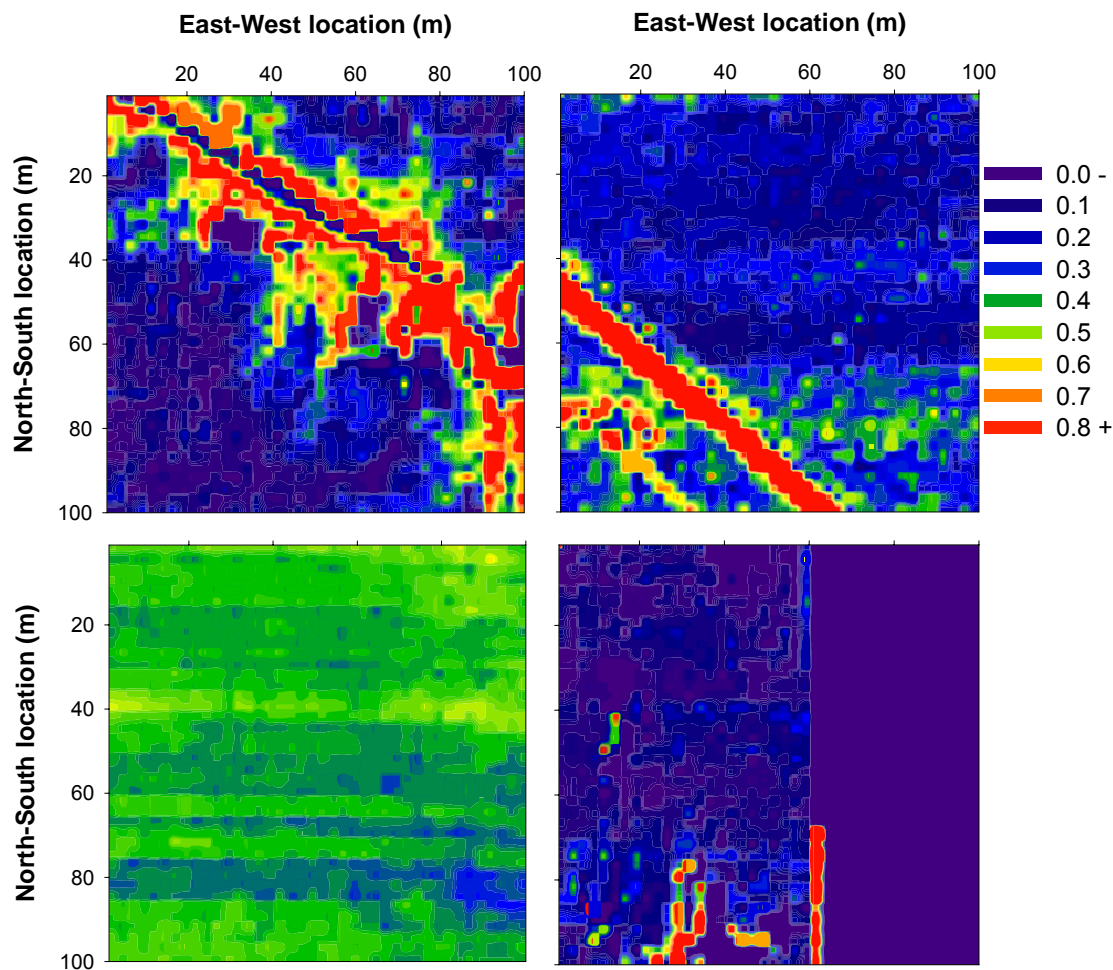


Figure 4.6 - Elevation (in m, relative to mean sea-level) maps of four of the eight 1-km<sup>2</sup> landscape scenes used in the model comparison. Swamp persistence scenarios 1a and 1b are shown in the top row. Marsh persistence scenarios 3a and 3b are shown in the bottom row. Note that elevations less than 0.0 m and elevations greater than 0.8 m were binned into the smallest and largest elevation categories shown in the legend.

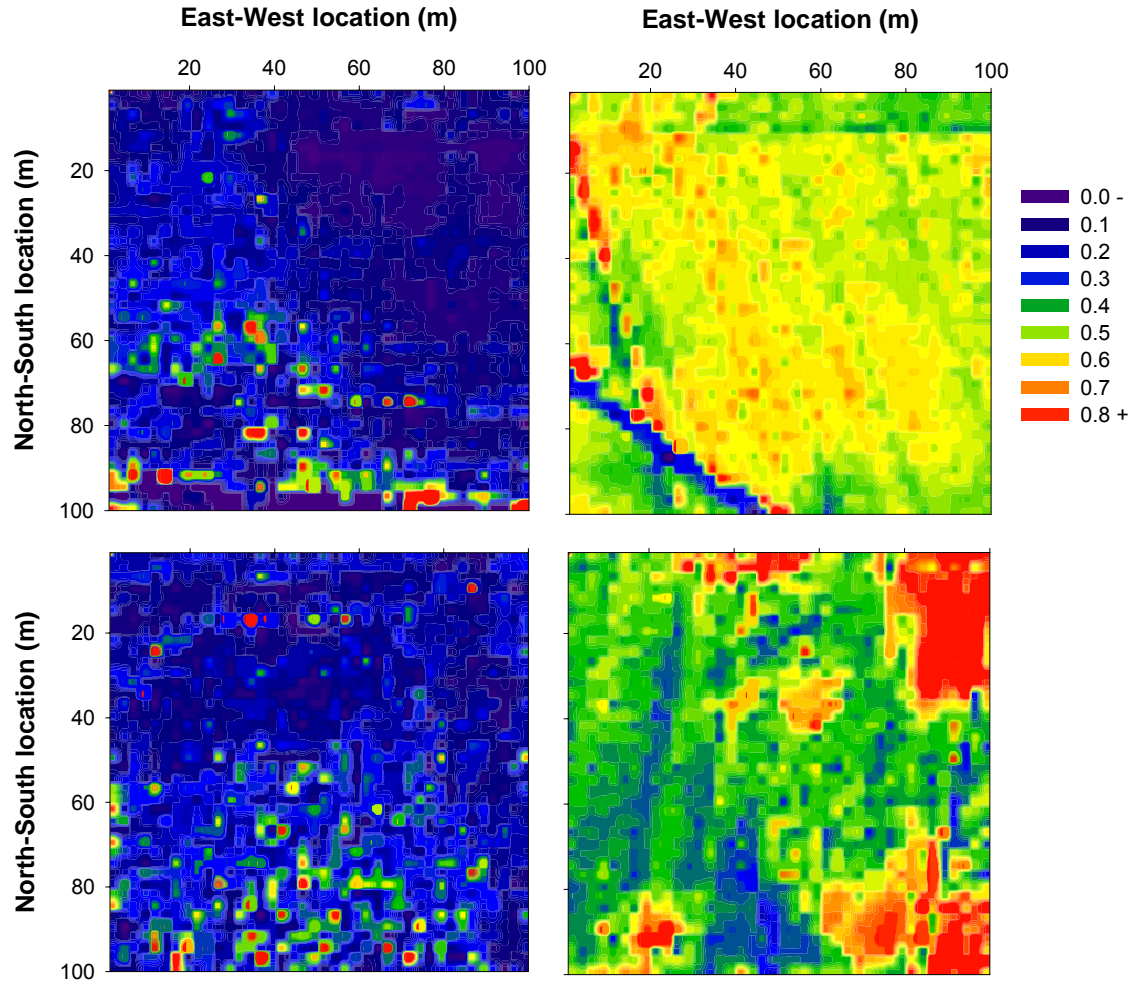


Figure 4.7 - Elevation (in m, relative to mean sea-level) maps of four of the eight 1-km<sup>2</sup> landscape scenes used in the model comparison that exhibited habitat change from swamp to marsh within 100 years in the landscape model (scenarios 2a-d, from left to right, top to bottom). Note that elevations less than 0.0 m and elevations greater than 0.8 m were binned into the smallest and largest elevation categories shown in the legend.

landscape model cells that started out as swamp (scenarios 1 and 2) used high initial basal areas representative of an intact swamp, and the two landscape model cells that started out as marsh (scenario 3) used low-biomass initial conditions representative of a planted swamp (Chapter 3). A basal area of 40-50 m<sup>2</sup> ha<sup>-1</sup> generally indicates an intact, dense forest (Chapter 2), while 0 m<sup>2</sup> ha<sup>-1</sup> can be either marsh or open water. I defined the threshold of the functional transition from swamp to marsh to be at 10 m<sup>2</sup> ha<sup>-1</sup>, and I used this threshold to determine if and when a habitat change from swamp to marsh

had occurred in the swamp IBM simulations of basal area. Additional IBM output variables were used to help interpret the results of the IBM. The additional explanatory variables included: mean salinity and mean degree of flooding during the growing season, mean number of tree deaths from salinity per year, and the number of recruits (age-4 saplings) per year.

Based on the results that used the original salinity and water depths from the landscape model, I performed two additional sets of eight simulations of the IBM with modified salinity values and flooding. In the first follow-up simulation experiment, I reduced the salinities predicted by the landscape model to one-third of their original values (Figure 4.8). In the second follow-up experiment, I retained the reduced salinity levels of the first follow-up modeling experiment and added frequent “droughts” to the water-depth time-series predicted by the landscape model. The “droughts” were

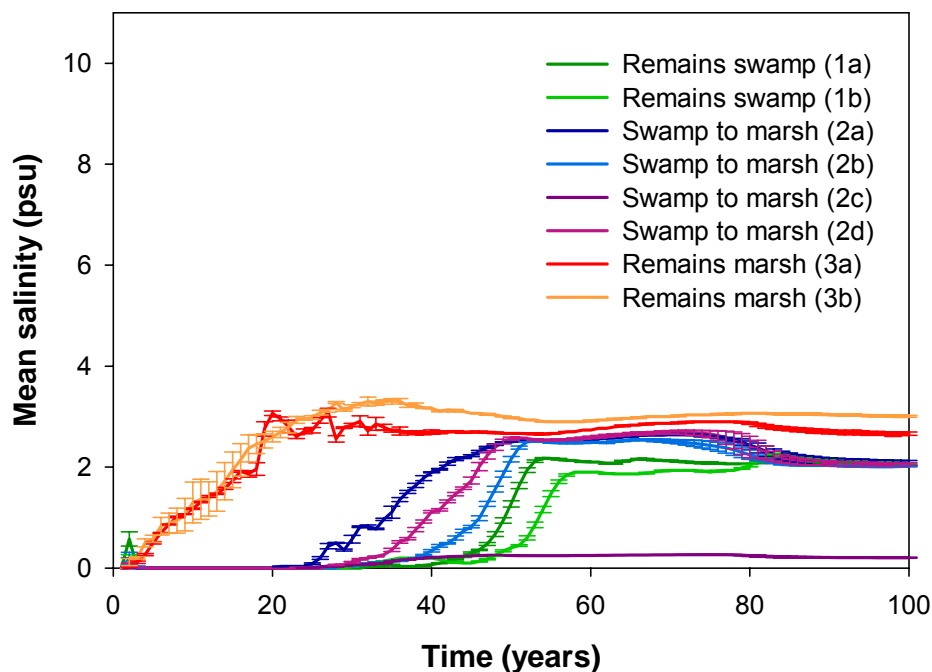


Figure 4.8 - Reduced mean ( $\pm$  SD) salinity during the swamp IBM growing season for 100 years in each of the eight landscape scenarios. Salinity was reduced to one-third of its original values shown in Figure 4.3.

created by setting stage to -0.2 m throughout the entire growing season during two consecutive years every five years, resulting in a repeating flooding pattern of 2 drought years followed by 3 years of flooding. Mean salinity under reduced salinity with droughts showed a similar pattern as the reduced salinity without droughts imposed (Figure 4.9). The same IBM output variables used in the first simulation experiment (e.g., basal area, salinity, flooding, recruitment) were also used for the second and third simulation experiments.

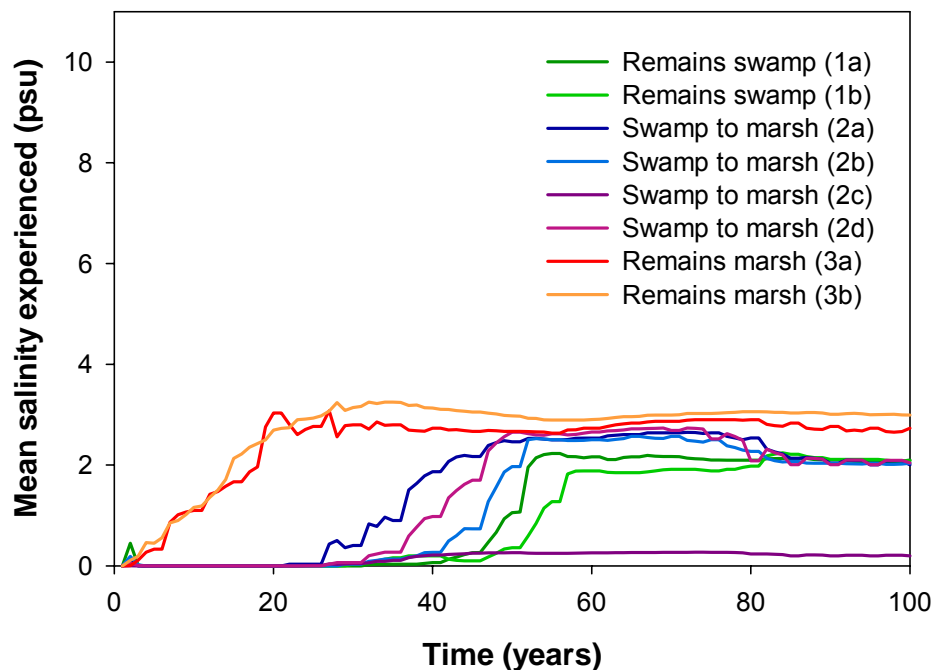


Figure 4.9 - Mean salinity actually experienced throughout the 1-km<sup>2</sup> model grid of the swamp IBM for 100 years in each of the eight landscape model scenarios under reduced salinity and periodic droughts. The salinity experienced is a result of the combined effects of reducing the original salinity to one-third its value and reducing the stage to -0.2 m every 5<sup>th</sup> and 6<sup>th</sup> year.

## 4.3. Results

### 4.3.1. Experiment 1: IBM Simulations with Original Salinity and Water Depths

The landscape model and the swamp IBM generally agreed in their predictions of marsh habitat persistence and in most of their predictions of habitat switches from



swamp to marsh near year 50, but they disagreed in their predictions of swamp persistence (Figure 4.10). In the swamp IBM simulations, all swamp scenarios but one were predicted to convert to marsh within 40-60 years, and both scenarios that started out as planted swamp remained marsh throughout the 100 years. The order in which the scenarios converted from swamp to marsh in the swamp IBM corresponded to the order in which the scenarios were subjected to dramatic increases in salinity (Figure 4.3), which resulted in high salinity induced mortality (Figure 4.11). The only scenario that did not convert to marsh in the swamp IBM predictions was scenario 2c, a swamp that was predicted to convert to marsh in year 50 in the landscape model. Mean salinity in scenario 2c never exceeded 2 psu (Figure 4.3), and thus salinity mortality was low in the IBM for this scenario.

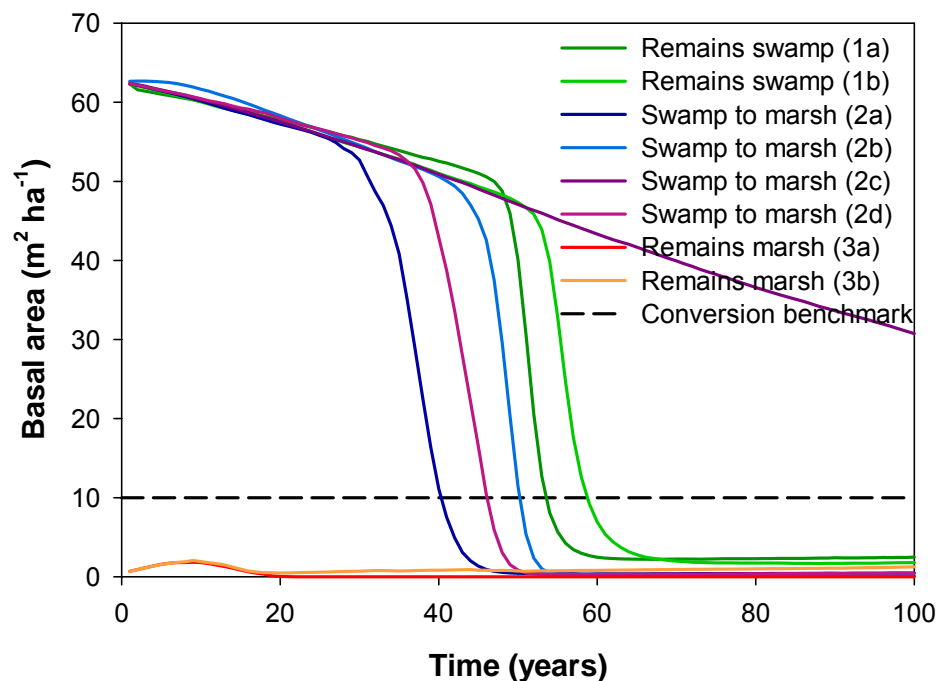


Figure 4.10 - Mean basal area over 100 years predicted by the IBM for the eight landscape model scenarios. The IBM used the same environmental conditions in each scenario as the landscape model.

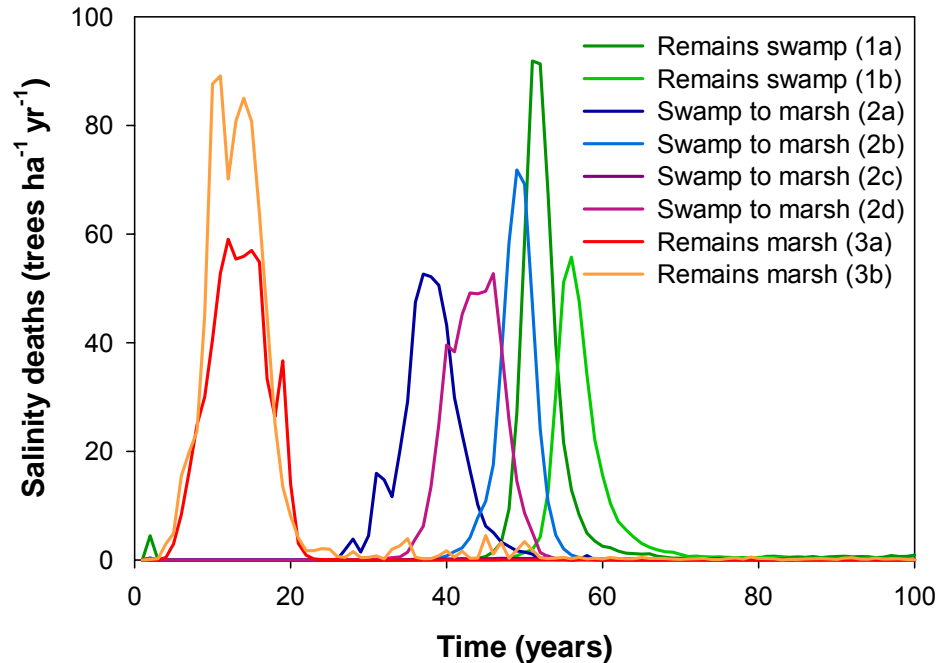


Figure 4.11 - Mean number of tree deaths caused by salinity in each year in the IBM simulations of the eight landscape model scenarios. Most deaths caused by salinity occur around year 50 in non-marsh scenarios, when salinities increase in all landscape scenarios.

Recruitment (number of 4<sup>th</sup> year seedlings) in the IBM was generally low for all scenarios (Figure 4.12), and decreased through time as mean water depths increased (Figure 4.2). Due to how germination is formulated in the IBM, seeds cannot germinate under flooded conditions. The average amount of flooding during the growing season experienced throughout the model grid was lowest in landscape scenes that had high elevation features, such as scenarios 1a, 1b, and 2d (Figures 4.6 and 4.7). Scenarios that experienced less flooding locally in the grid had a slightly higher number of recruits than scenarios that were flooded more evenly. In each simulation there are initial spikes in recruitment during the first five to ten years (Figure 4.12), when flooding had not yet increased greatly. Subsequently, increasing flooding limited recruitment to such a degree that it could no longer keep up with random and slow-growth mortality culling

of individual trees, and stem densities started to decline. Even in scenario 2c, in which salinity levels remained too low to cause swamp degradation, basal area and stem density continually declined throughout the 100 years because of a lack of recruitment due to the near-permanent flooding.

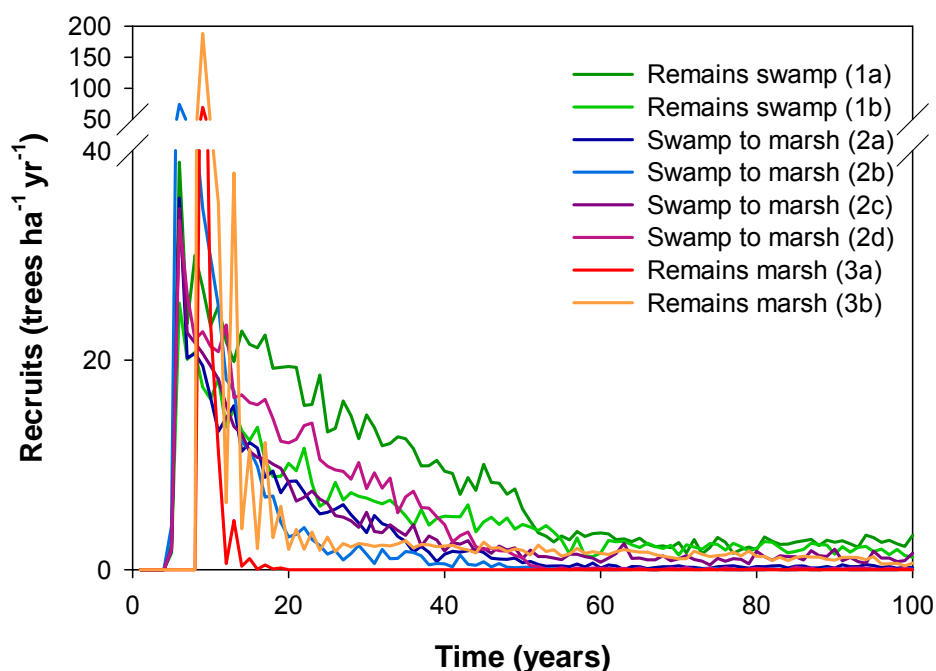


Figure 4.12 - Mean number of new 4-year old recruits predicted by the IBM for 100 years in each of the eight landscape model scenarios. Scenarios 1a-2d used an intact swamp as initial conditions, while scenarios 3a and 3b used a planted swamp as initial conditions.

#### 4.3.2. Experiment 2: IBM Simulations with Reduced Salinity

Reduced salinity delayed the decline in basal area in scenarios involving landscape model cells that stayed swamp and in cells that converted to marsh (scenarios 1 and 2), and resulted in higher basal area for the scenario 3 of the marsh remaining marsh (Figure 4.13). Under conditions of reduced salinity (Figure 4.8), the swamp IBM predicted almost all of the swamp habitat changes that had been predicted by the landscape model, but habitat conversions from swamp to marsh were predicted much later in the 100 years. Even after a reduction in salinity to roughly 2-3 psu, the

salinity effect remained strong enough in the swamp IBM to force all the existing swamp scenarios slowly towards marsh. The habitat change scenarios 2a, b, and d reached the habitat conversion benchmark of basal area of less than  $10\text{m}^2\text{ ha}^{-1}$  after 85-100 years. Annual numbers of deaths due to salinity were reduced by roughly four-fold in each scenario between the original salinity and reduced salinity simulations (Figure 4.14 versus Figure 4.11), resulting in a slower decline in basal areas between the original and reduced salinity conditions. However, due to the lack of sufficient recruitment (Figure 4.15), even the scenarios that were predicted to remain swamp by the swamp IBM had very low basal areas by the end of the simulations (Figure 4.13) and were nearing the benchmark value for swamp conversion to marsh.

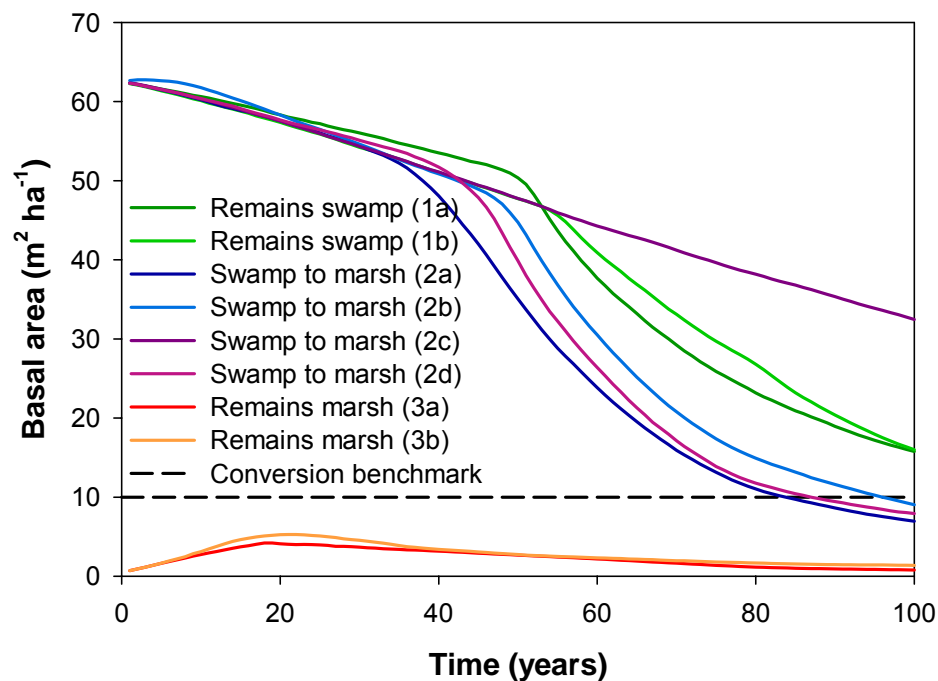


Figure 4.13 - Mean basal area over 100 years predicted by the IBM for the eight landscape model scenarios under reduced salinity.

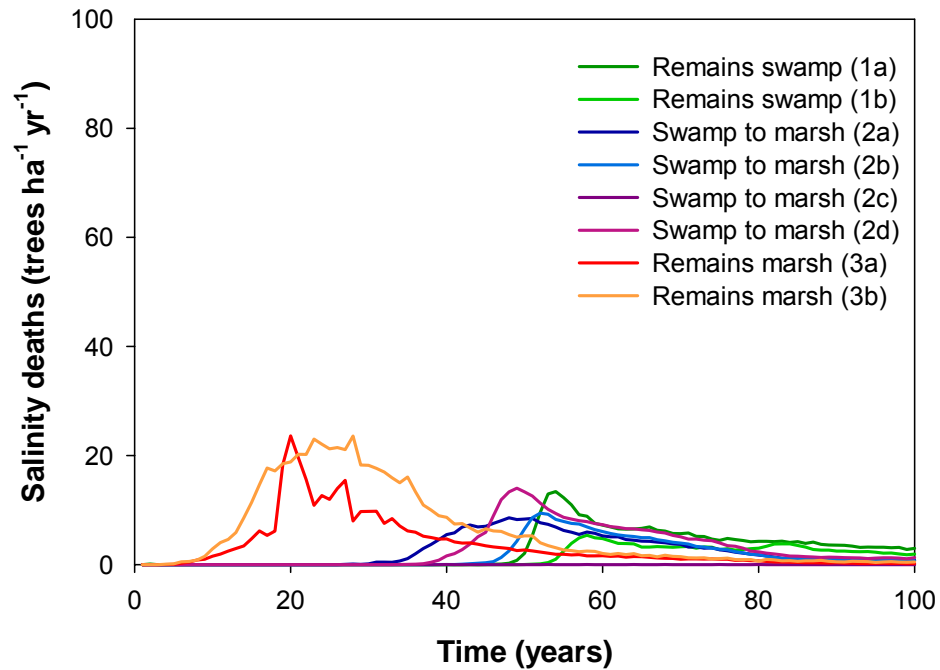


Figure 4.14 - Mean number of tree deaths caused by salinity in each year in the IBM simulations of the eight landscape model scenarios under reduced salinity.

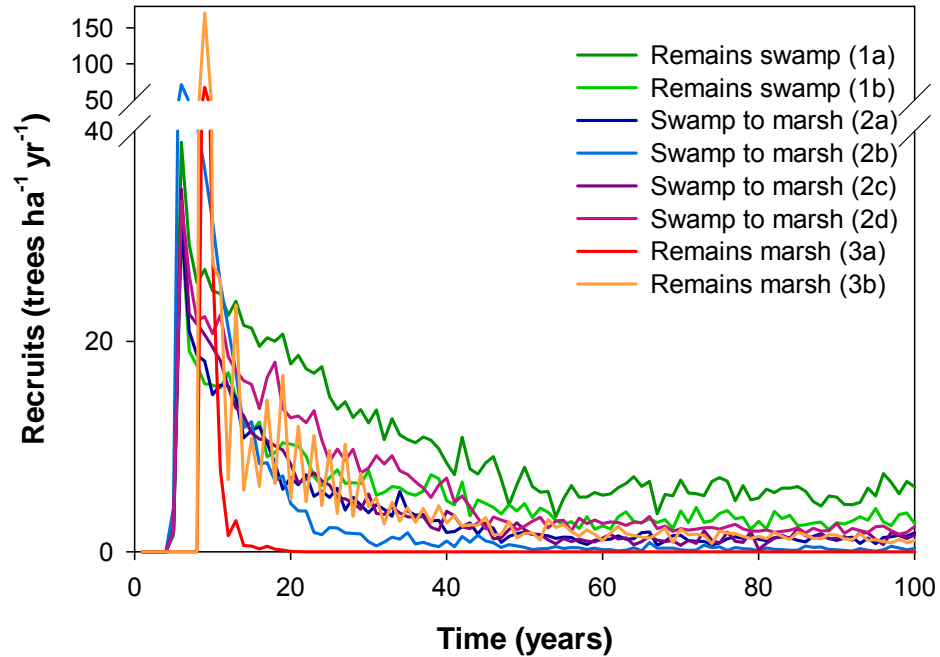


Figure 4.15 - Mean number of new 4-year old recruits predicted by the IBM for 100 years in each of the eight landscape model scenarios under reduced salinity.

#### 4.3.3. Experiment 3: IBM Simulations with Reduced Salinity and Droughts

Combining reduced salinity with frequent occurrences of droughts further delayed the decline in basal area for the landscape model cells that showed persistent swamp and swamp to marsh conversions, and the IBM still predicted scenario 3 as marsh that stayed marsh (Figure 4.16). In the swamp IBM, the mean salinity experienced by trees in dry 100 m<sup>2</sup> cells of the 1 km<sup>2</sup> landscape scene remains the same as the salinity the cell experienced when it was last flooded. Thus, the mean salinity experienced by trees with reduced salinity and droughts (Figure 4.9) was roughly equal to the salinity they experienced in the reduced salinity experiment without droughts (Figure 4.8). The number of salinity deaths per year with droughts (Figure 4.16) was actually higher than in the reduced salinity simulations without droughts (Figure 4.14) because there were more trees present on the grid, and was quite close to the number of salinity deaths

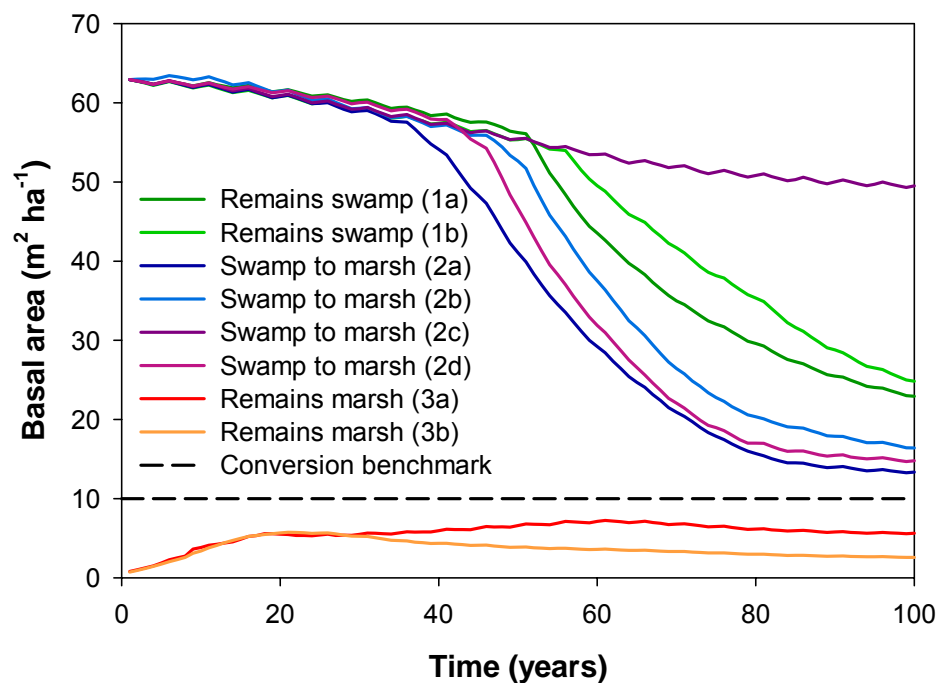


Figure 4.16 - Mean basal area over 100 years predicted by the IBM for the eight landscape model scenarios under reduced salinity and periodic droughts.

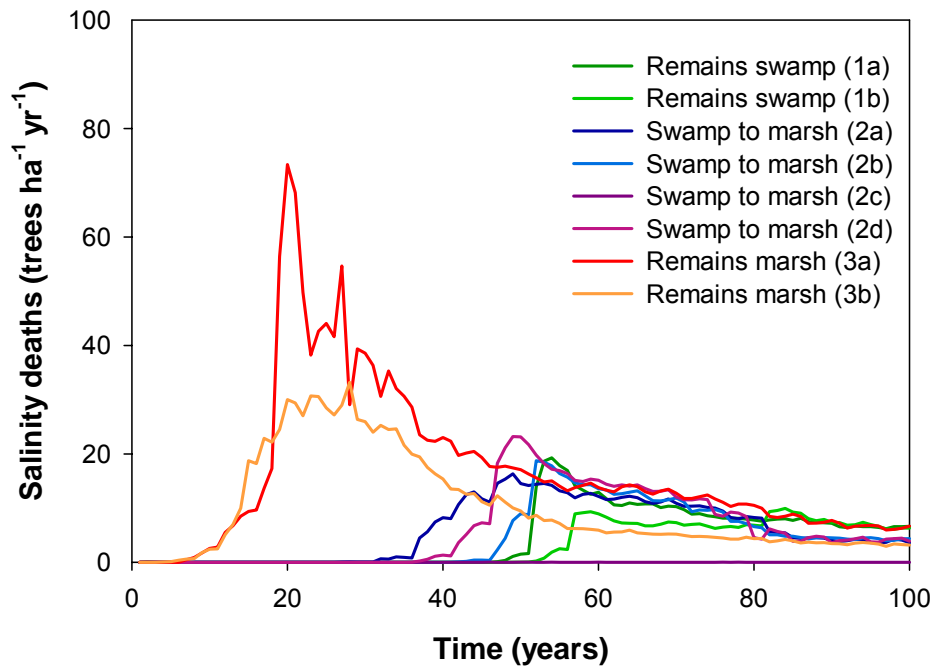


Figure 4.17 - Mean number of tree deaths caused by salinity in each year in the IBM simulations of the eight landscape model scenarios under reduced salinity and periodic droughts.

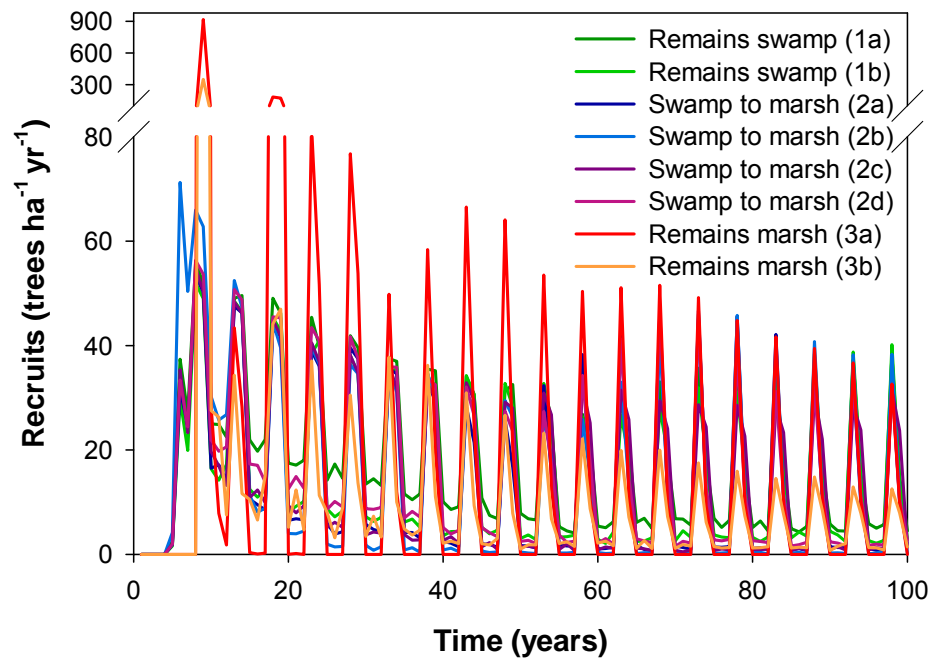


Figure 4.18 - Mean number of new 4-year old recruits predicted by the IBM for 100 years in each of the eight landscape model scenarios under reduced salinity and periodic droughts.

predicted under the original salinity conditions for scenario 3 (Figure 4.11).

While not reducing the negative effect of salinity (Figure 4.17), the addition of droughts still benefited swamp survival in the IBM by increasing recruitment during the reduced flooding years (Figure 4.18). Recruitment showed high values during the drought years, which allowed the populations to persist longer.

#### **4.4 Discussion**

The challenge of formulating an integrated and comprehensive ecosystem restoration plan for the entirety of the rapidly deteriorating Louisiana coastal zone (Twilley, 2003), presents a problem that relies on modeling and ultimately goes to the fundamental issue of scaling. The problem of scaling is deciding upon the most appropriate temporal, spatial, and biological scales for an analysis or model (Levin, 1992). Should a habitat model use simple rules for determining the habitat type in an area, or should the model simulate the detailed interactions among individuals to determine the habitat type? How small should the spatial cells be in order to represent the important effects of spatial heterogeneity in elevation and flooding on habitat type switching realistically? What is the appropriate temporal resolution needed for estimating the effects of flooding and salinity on vegetation (e.g., tree) dynamics on a spatial grid where hydrodynamics are solved in time-steps of seconds? There is no simple, single answer or formula for determining the best temporal, spatial, and biological scales for a model. Yet, each researcher introduces, often unknown, biases into his or her predictions by choosing the specific scales of their model. Simply including more and more detail is not optimal, and trying to represent very disparate scales in one model creates conceptual and computational problems (Urban et al., 1999).



How then, in a practical sense, do we deal with the problem of scaling when trying to develop models for forecasting? First, we recognize that we cannot *a priori* identify a single correct set of temporal, spatial, and biological scales to use. Second, we need to choose scales (albeit not unique) that appear, based on current knowledge, to be appropriate to our questions, while remaining cognizant of how patterns at the selected scales are affected by patterns and processes occurring on other scales (Levin, 1992). We may be able to achieve an integration of disparate scales by investigating what information is critical to capture because it is transmitted across scales, which fine-scale details only contribute to “noise” on larger scales and can be effectively ignored, and which broad scale processes are important as drivers of fine-scale dynamics (O'Neill et al., 1986).

One practical approach for assessing how the scales of a model affect its predictions is to compare models that include overlapping prediction variables but that operate on different scales (e.g., Rose et al., 1991). The comparison among multiple models can be used to quantify uncertainty, to inform all models in the comparison, and, ultimately, to formulate a single integrated model that has increased overall accuracy and precision. Use of multiple models with their alternative formulations is the approach employed by the Intergovernmental Panel on Climate Change to forecast global climate change (Randall et al., 2007). Successful linkage of the wide range of temporal scales (e.g., seconds for flow velocities, centuries for geological change) and spatial scales (e.g., microbial activity at microscopic scales, Mississippi River watershed drainage area) is a necessary step and an invaluable tool in the planning of coast-wide restoration efforts. Deciding on the spatial, temporal, and biological detail needed in

ecological models to achieve a desired accuracy in forecasting remain part of the “art of modeling.”

In systems where direct observation of processes at the scale of interest are not available or feasible (e.g., forest development under regimes of decadal fire disturbance, global warming, ocean acidification), more detailed, smaller-scale models are often used to “parameterize” or test larger scale, more general models. In population ecology, for example, comparisons of IBMs and more general population models have been employed to explore the concept of self-organization (Fahse et al., 1998), refine generalized predator-prey interaction models (Wilson, 1998), and to parameterize, evaluate, and compare meta-population models (Hilker et al., 2006). Examples in forest and herbaceous vegetation modeling include using physiological models of individual trees (TREGRO) to scale to the level of forest stands (Siegel et al., 1995), combining biome distribution models with detailed ecosystem physiology models to obtain an integrated terrestrial vegetation climate change model (VEMAP) (Kittel et al., 1995), and combining individual-based forest gap models (Hybrid v.3.0 and ED) with vegetation layers to extrapolate plant and ecosystem responses to biosphere scales (Friend et al., 1997; Moorcroft et al., 2001).

In this chapter, I compared the habitat switching predictions during 100-year simulations from a broad-scale landscape model commonly used in the evaluation of coastal habitat change throughout the Louisiana Coastal Zone (Costanza et al., 1990; Martin et al., 2002; Reyes et al., 2004) with the predictions of a much more spatially, temporally, and biologically detailed IBM. A single spatial cell in the landscape model (1-km<sup>2</sup>) was the entire spatial domain of the 10,000 100-m<sup>2</sup> cells of the IBM, and very coarse habitat switching algorithms of the landscape model were contrasted with the

IBM that follows thousands of individual trees that were affected by local conditions on the scale of meters.

Both the landscape model and the IBM were used to simulate habitat dynamics over 100 years using identical environmental conditions. The weekly salinity and water depth at eight specific cells in the landscape model were read into the IBM, which used a finer scale elevation map for each of the same locations. Landscape model predictions of whether the cell was swamp or marsh were compared to annual basal areas computed by summing the basal areas of the individual trees in the IBM. Both models show relatively good agreement in predicting marsh persistence and the timing of swamp conversion to marsh (Figure 4.10). However, the models disagreed on the persistence of swamp (scenario 1), as the landscape model predicted swamp for the entire 100 years for two of the cells while the IBM predicted their conversion to marsh within 100 years. The models also disagreed on one of the cells for which the landscape model predicted a switch from swamp to marsh (scenario 2c), whereas the IBM allowed the persistence of the swamp.

The agreement between the landscape model and the IBM for scenarios that involved swamp becoming marsh (scenario 2) is encouraging, but it is not a rigorous comparison of the models because of the relatively high salinities used in the simulations. The comparison of the models using the original salinity values was based on high enough salinity values (about 6 psu, Figure 4.3) to cause major mortality. Thus, the IBM predicting the switch from swamp to marsh at about year 50 when salinities got high is not a difficult challenge for the models. Swamp forests simply cannot tolerate salinity values of 6 psu and higher. The general salinity tolerance of *T. distichum* has been reported to range from 2 psu (Chabreck, 1972) to 8.9 psu (Penfound and

Hathaway, 1938). Field observations in the Maurepas swamps indicated that chronic exposure to salinity levels ranging from 1 to 4.5 psu caused 10-80% mortality of all prevalent swamp tree species over 5 years (Chapter 2). The swamp IBM may be overly sensitive to low levels of salinity, as the swamp IBM used seedling mortality data as the basis for its evaluation of both seedling and adult tree mortality. In a review of the waterlogging tolerance of woody species, Gill (1970) noted that waterlogging tolerance increases with increasing size and age of trees.

The easy challenge provided by the swamp to marsh scenario makes the disagreement between the landscape model and IBM for scenario 1 (swamp persisting as swamp in Figure 4.10) of particular concern. Simply reducing salinity did not enable the IBM to predict the range of responses predicted by the landscape model. Additional simulations of the IBM with reduced salinity and with reduced salinity and periodic, imposed drought conditions resulted in slowed decline in basal areas, but for all of the scenarios (Figures 4.13 and 4.16); thus, if salinity was reduced to allow swamp to persist in the IBM (agree with scenario 1), then the swamp to marsh scenarios were also affected and they were predicted to remain swamp much longer. Furthermore, despite reducing salinity by about 70% from its original value (Figure 4.8 and 4.9 versus Figure 4.3), which successfully reduced salinity mortality (Figure 4.14 and 4.17 versus Figure 4.11), and imposing droughts, which increased recruitment (Figure 4.18), basal area was still predicted to decline in the IBM for all scenarios that started with an intact swamp.

Closer examination of the swamp IBM predictions suggests that a smaller spatial scale than used by the landscape model (on the order of 100 m<sup>2</sup> like the IBM) may be necessary to model swamp persistence. For example, at the 1 km<sup>2</sup> scale, the

landscape model predicted that scenario 1a, at a mean elevation of 0.36 m above sea-level, would remain swamp throughout a 100-year simulation (Figure 4.13). However, the finer scale variation in elevation within this 1-km<sup>2</sup> used by the IBM (location labeled 1a in Figure 4.5, amplified in Figure 4.6) showed that most of the cell is at very low elevation with a high elevation ridge running through the center. The finer scale of the IBM resulted in no tree regeneration occurring in the low areas that dominate the map, with all new successful trees occurring only on the high elevation ridge. This was clear in a spatial map of tree ages after the 100 years of IBM simulation under scenario 1a that shows only old trees remaining in the low elevation places (i.e., no young trees growing) and the swamp converting to marsh (Figure 4.19). At an average elevation exceeding 0.8 m above sea-level, even the ridge may not allow swamp to persist and could become rarely flooded bottomland hardwood forest or upland. Thus, while the “average” elevation of a 1 km<sup>2</sup> cell used by the landscape model may be suitable for

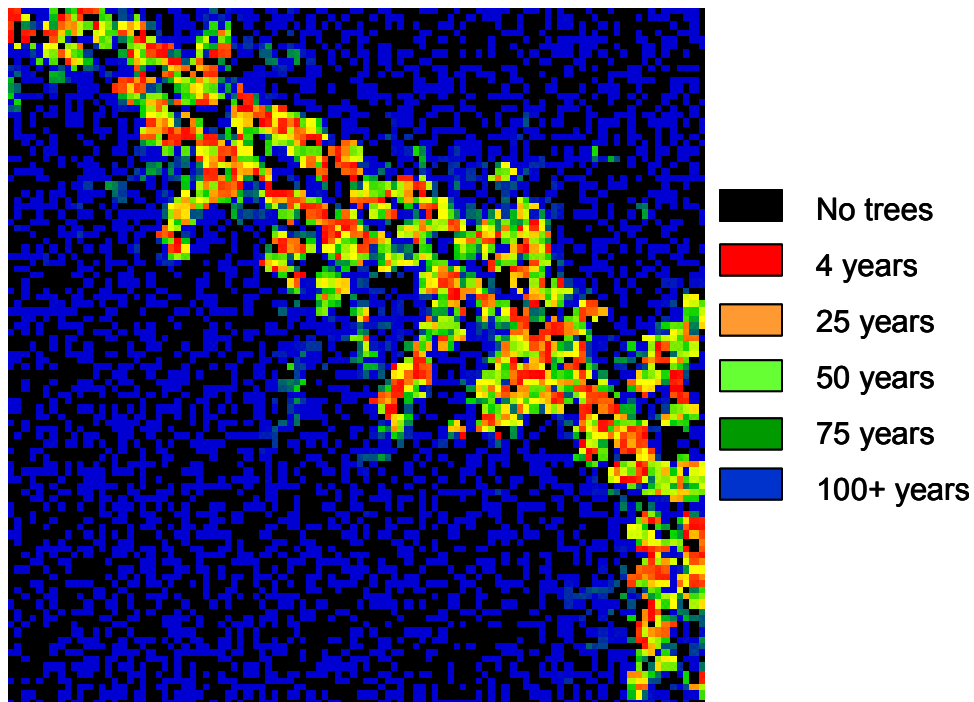


Figure 4.19 - Mean age of trees per 10x10 m plot in scene 1a after 500 years.

swamp persistence, the finer scale elevation features of the map used by the swamp IBM suggest that the non-random variation in elevation could lead to faster swamp decline than expected from the mean elevation.

Another issue raised by comparing the landscape model and IBM is the role of flooding in seedling survival. The swamps in the landscape model are capable of withstanding permanent flooding without any apparent consequence to recruitment or survival. By contrast, near-permanent flooding has substantial negative effects on tree recruitment in the swamp IBM (Chapter 3). It has been hypothesized that some swamp forests in the Louisiana coastal zone may have established completely during isolated draw-down events (i.e., droughts) in the past, as these swamps show little to no regeneration under current flooding regimes (Conner and Day, 1976). Thus, the inhibitory effect of permanent or near-permanent flooding on seed and young tree survival is a potentially important factor that should be revisited in the landscape model.

My model comparison approach shows great promise as a means for identifying critical aspects of both the IBM and landscape models that need to be tested and the key data that needs to be collected for improving both models. Based on the relatively simple comparison performed here, two important issues (salinity and flooding sensitivity) should be further examined. Interestingly, in both cases, the IBM showed higher sensitivity to changes in these environmental variables than the landscape model. Long-term datasets that include habitat type and information on potential driving forces (e.g., salinity, flooding) are not currently available, and thus the habitat switching algorithms in the landscape model are necessarily based on short-term information about the effects of salinity and inundation regimes on the persistence of each of the habitat types. In a review of the landscape model's habitat change algorithms

undertaken as part of a broader review of habitat modeling for restoration planning for the Louisiana coast (Twilley, 2003), the rigor of the habitat switching module was classified as low. Thus, analyses, such as the analysis presented in this chapter, that provide a comparative test of the habitat switching algorithms (albeit versus other models), are very valuable for improving the rigor of the habitat models, which are critical for coastal restoration planning.

My results suggest that how salinity and flooding effects are represented in both models should be scrutinized and additional comparisons using results from other cells in the landscape model and other simulations of the landscape model with lower salinity values should be performed. Further sensitivity analysis of the swamp IBM would provide useful additional information about which aspects of the IBM should be investigated further. The swamp IBM is currently limited in its expression of a dynamic environment by its use of historic time-series data for salinity and stage as inputs. While simple manipulations of the time-series data of salinity and stage flooding are possible, the swamp IBM still lacks a feedback interaction with its environment by which swamp growth can alter such expressions of environmental forcing as flooding through elevation change. The landscape model offers a simpler biological approach but with fairly sophisticated hydrodynamics, while the IBM offers a spatially-detailed and biologically-detailed approach with simplified hydrodynamics. A critical next question for inter-model comparison is whether the landscape model underestimates swamp responses to changed environmental conditions, or that the IBM overestimates the responses. A set of model comparisons using contrasting environmental conditions and outcomes, coupled with close inspection of the details of both models and their

predicted sensitivities to change in environmental conditions relative to field and greenhouse studies, can enable resolution of the biases of both models.

Ultimately, what we learn about both models from their inter-comparison should lead us to an improved integrated model. Two feasible methods for linking the landscape model and IBM are either through a statistical approach or through a computational approach. In a statistical approach, the finer-scale swamp IBM could be used to estimate better habitat switching rules based on a series of simulations of the IBM with different intensities and durations of salinity and flooding, alone and in combination. A computational linkage between the landscape model and the swamp IBM would be to embed the swamp IBM into the landscape model, so that the landscape model actually runs all the biological process routines in the swamp IBM for all landscape cells that are swamps within the landscape model's domain. Future model development should focus on linking the landscape approach and the individual-based approach for the next generation of swamp models that are needed for better understanding the rapidly disappearing coastal swamp forests and for evaluating alternative restoration actions.

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## CHAPTER 5: GENERAL CONCLUSIONS

The majority of the Maurepas swamp is stressed and seems to be on a trajectory of slow degradation. The swamps have been cut off from the sustaining spring floods of the Mississippi River for over a century, and flood control levees, abandoned raised railroad tracks, and spoil banks from oil canal dredging have further disrupted the natural hydrology in large areas. The lack of freshwater and sediment input and throughput are indicated by low bulk densities, and very low nutrient concentrations in the surface water throughout the swamp (Lane et al., 2003). Similar to other low-elevation swamps in the southeastern United States, the Maurepas swamps are dominated by *T. distichum* and *N. aquatica* in the canopy, and by *A. rubrum* var. *drummondii* and *F. pennsylvanica* in the midstory (Conner and Day, 1976; Harms et al., 1980; White, 1983; Visser and Sasser, 1995; Rheinhardt et al., 1998).

The field data collected and analyzed in Chapter 2 showed that, with the exception of a few areas in the swamp interior south-west of Lake Maurepas, aboveground biomass production, stem densities, and basal areas throughout most of the Maurepas swamps were low and in the range of that reported for nutrient-poor, stagnantly flooded swamps (Schlesinger, 1978; Taylor, 1985; Mitsch et al., 1991; Conner and Day, 1992). Near-continuous flooding appears to be the largest stressor in the swamp interior, and nutrient limitation throughout the swamp is very likely. The combination of saltwater intrusion and flooding stress is killing large proportions of the trees located along the eastern shore of Lake Maurepas near Pass Manchac, and most of these areas are likely to convert to marsh or open water within a few decades (Barras et al., 1994). Swamp areas on the western margin of Lake Maurepas were not as

severely impacted by the salt-water intrusion as swamp areas near Pass Manchac, and returned to low ambient salinity levels more quickly after the drought.

The two-species IBM I developed (Chapter 3) offers promise as a useful tool for better understanding how multiple environmental factors (e.g., flooding, salinity) interact with competition among trees to determine productivity over time in a swamp forest. The swamp IBM appears quite robust in its predictions and showed good agreement during model corroboration between model predictions and field observations of basal areas and stem densities in the Maurepas swamp. The model predicted large negative responses to changes in elevation (i.e., flooding duration) and to increases in salinity. Simulations used a broad range of mean elevations, including the 90<sup>th</sup> and 10<sup>th</sup> percentiles of wetland elevations found in the Maurepas Basin. Increases in flooding via lowered mean elevations led to reductions in predicted basal areas, stem densities, and annual wood production. In response to low levels of salinity (~ 1-3 psu), the swamp IBM predicted greatly decreased basal areas similar to those observed along the eastern lakeshore of Lake Maurepas. In an additional simulation, higher salinity (~2-6 psu) resulted in a swift degradation of the modeled forest, quickly eliminating *N. aquatica*, and leading to the disappearance of *T. distichum* within 50 years. Taken together, the results of the corroboration and of the mean elevation and salinity simulations indicate that the swamp IBM is capable, with a fair degree of reliability, of modeling the basal area and stem density under a wide range of environmental conditions found in the Maurepas Basin.

While the swamp IBM appears to simulate total stem density and basal area quite well, some caution is needed in interpreting annual wood production and in interpreting all three variables on a species-specific basis. The model showed a

consistent tendency to overestimate annual wood production as it was measured in the four distinct habitats that were monitored in the Maurepas swamp and that were used as corroboration benchmarks. Also as part of the corroboration, the model overestimated the dominance of *T. distichum* over *N. aquatica* compared to the field data. Two possible explanations for the model to data mismatches are that there are other local stressors affecting tree production measured in the field that were not included in the model, or that the model's representation of wood production and species-specific differences in tolerances need further refinement.

Four particularly interesting directions for the further development of the swamp IBM are a resolution of why wood production was higher than observed in the corroboration simulations, further specification of species differences in tolerances to salinity and flooding, the inclusion of a feedback interaction of swamp growth on elevation, and the refinement of the seed germination and dispersal processes. The first two directions, particularly, will require additional experimental and field data collection. The third direction for model improvement is relating the biological productivity to the elevation in the cells, which would then influence swamp hydrology, and may benefit from existing wetland relative elevation change models (e.g., Rybczyk et al., 1998). The fourth and final direction for model improvement is to refine the seed dispersal and germination dynamics and will require a more detailed seed tracking approach to monitor seed drift throughout the grid and to limit seed dispersal and germination only to plots that are suitably dry.

My comparison of the IBM with the landscape model (Chapter 4) shows great promise as a means for identifying critical aspects of both models and key data to be collected for improving both the landscape model and the swamp forest IBM.

Specifically, the comparison of the IBM to a broader-scaled landscape habitat change model revealed that both salinity and flooding sensitivity should be further examined in both models. The models showed relatively good agreement in predicting marsh persistence and the timing of swamp conversion to marsh, but disagreed on the scenarios that had swamp persisting as swamp. The salinity and stage used by the landscape model that permitted swamp to remain swamp over the 100 years consistently resulted in the IBM predicting declining basal area and thus swamp becoming marsh.

The comparison of habitat switching responses in both models was based on high enough salinity values (about 6 psu) to cause major mortality and was thus not a difficult challenge for the models. Field observations in the Maurepas swamps indicated that chronic exposure to salinity levels ranging from 1 to 4.5 psu caused 10-80% mortality of all prevalent swamp tree species over 5 years, and swamp forests simply cannot tolerate salinity values of 6 psu and higher on a long-term basis. Additional comparisons using results from simulations of the landscape model with lower salinity values should be performed to achieve a more rigorous comparison of the habitat change predictions in both models.

Another issue raised by comparing the landscape model and IBM (Chapter 4) is the role of flooding in seedling survival. The swamps in the landscape model are capable of withstanding permanent flooding without any apparent consequence to recruitment or survival. By contrast, near-permanent flooding has substantial negative effects on tree recruitment in the swamp IBM. As it has been shown that *T. distichum* and *N. aquatica* seeds cannot germinate under flooded conditions (DuBarry, 1963), the

inhibitory effect of permanent or near-permanent flooding on seed and young tree survival is a potentially important factor that should be revisited in the landscape model.

Overall, the IBM showed higher sensitivity to changes in both salinity and flooding than the landscape model. Whether this suggests that the coarser landscape model would underestimate responses to changed environmental conditions, or that the IBM would overestimate the responses, remains an open issue. The landscape model offers a simpler biological approach but with fairly sophisticated hydrodynamics, while the IBM offers a spatially-detailed and biologically-detailed approach with simplified hydrodynamics. Future model development should include how best to link the landscape approach and individual-based approach for the next generation of swamp models needed for better understanding the rapidly disappearing coastal swamp forests and for evaluating alternative restoration actions.

A Mississippi River diversion into the Maurepas swamp has already been approved as a restoration project under CWPPRA, and it is currently in Phase 1 (engineering and design) of its implementation. Re-establishing the natural hydrology of coastal swamps by reconnecting them even partially to their historic river sources is likely to benefit the persistence and productivity of these subsiding wetlands by restoring a natural flow of sediments, nutrients, and freshwater into these degrading swamps in order to slow, halt, or reverse the process of deterioration (Coleman et al., 1998; Day et al., 2000; Mitsch et al., 2001). Because of the baseline monitoring efforts and analyses conducted to date (including Chapter 2), this restoration effort will provide a unique opportunity to further study and model the dynamic ecosystem responses to changes in the current gradients of flooding stress, salinity stress, and nutrient limitation.

Considering the ecological, economic, cultural, and aesthetic importance of forested wetlands worldwide, a more detailed understanding of the processes of forested wetland loss and the potential for wetland preservation and restoration is required to ensure the future of these valuable ecosystems. Our uncertainty regarding the long-term effects of wetland restoration efforts is exacerbated in forested wetlands by the great longevity of the canopy trees in coastal swamps (Wilhite and Toliver, 1990), which makes long-term habitat change detection difficult. Using the baseline field data documented in Chapter 2, the individual-based model developed in Chapter 3, and the comparison of the individual-based forest succession model to the existing, commonly used landscape model in Chapter 4, the ingredients are available for the development of the next generation of quantitative tools to be used for forecasting swamp forest responses to changing environmental conditions and for evaluating the potential effects of restoration actions. The next generation of models for forecasting will likely be a combination of the individual-based and landscape models developed and evaluated in this dissertation.

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## VITA

Born in Freudenberg, Germany, Susanne Sigrid Hoeppner moved with her family to Massachusetts at the age of 17. After completing her high school education there, she went on to get a Bachelor of Arts degree in Biology from Suffolk University, Boston, Massachusetts, with an emphasis on marine studies. Following her college years, she worked as an intern with the National Oceanographic and Atmospheric Administration, NOAA, and as an environmental scientist for an environmental consulting company. During this time, she made new contacts and friends that sparked her interest in wetland ecology - particularly in swamps - which motivated her to continue her education in Louisiana. She completed her Master of Science in biological sciences at Southeastern Louisiana University with Gary P. Shaffer, while holding a sought-after EPA STAR fellowship and teaching introductory biology and statistics labs. While there, she delved deeper into wetland science and developed an avid interest in statistics, a fascination that led her to apply for a dual degree program at Louisiana State University. She entered the Department of Oceanography and Coastal Sciences at Louisiana State University as a graduate research assistant in August 2002, and joined the Department of Experimental Statistics one year later. En route to her Ph.D., Susanne completed her master's in applied statistics under the direction of Dr. James P. Geaghan with the topic: "Controversy resolved? Detecting changes in university counseling center trends over a 12-year period." Meanwhile, she started to work her way into the challenging field of simulation modeling under the expert guidance of Dr. Kenneth A. Rose. Focusing her research interest on swamp ecology and individual-based modeling, she will be receiving a Doctor of Philosophy degree in oceanography and coastal sciences in May 2008. Upon completing her degree, Susanne will return to New England and looks

forward to beginning work as a post-doctoral researcher with Dr. Jeffrey S. Dukes in the Department of Biology at the University of Massachusetts in Boston - still working with trees, but now looking at climate change. Susanne is an avid reader, and she enjoys music, movies, cooking, and walks with her dog.