

CREST 2006 – 2008 Final Report

RESTORATION ENHANCEMENT OF BLACK MANGROVE ESTABLISHMENT IN BARRIER ISLAND/HEADLAND PROJECT DESIGN: DETERMINATION OF DIFFERENTIAL TOLERANCE THRESHOLDS OF PROPAGULES AND SEEDLINGS

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Submitted by

**Mark W. Hester
Lauren K. Alleman
Jonathan M. Willis**

**Coastal Plant Ecology Laboratory
Department of Biology
University of Louisiana Lafayette
Lafayette, LA 70504**

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MANAGEMENT SUMMARY

Caminada-Moreau Black Mangrove Field Study

Populations of black mangroves in coastal salt marshes and barrier islands in Louisiana are subject to regular hurricane disturbances, the most recent of which were Hurricanes Katrina/Rita in 2005 and Hurricanes Gustav/Ike in 2008. The impacts of these hurricanes on population structure and reproductive output of the black mangrove trees on the Caminada-Moreau coast were monitored from 2005 through 2008, which encompassed both high and low hurricane disturbance years. Our objectives were to determine autogenic capacity for recovery, as well as propagule production rates (either for self regeneration of a damaged parental population, or in the context of evaluating the potential for human-dispersal of propagules from one population to a restoration site).

To accomplish these objectives, we monitored propagule production rates, tree height, and canopy area of 50 black mangrove trees in a population at the Caminada-Moreau coast near Port Fourchon, Louisiana. Annual measurements were taken +/- 3 ordinal calendar days from October 15, which is typically when propagules are approaching their peak maturity on their parent trees in Louisiana prior to being abscised and dispersed. Propagule production was at a minimum following Hurricane Katrina in 2005. Average propagule production after Hurricane Katrina (2005) was 131 propagules per square meter of mangrove canopy compared to 252 propagules per square meter of mangrove canopy in 2006. Average propagule production per square meter of mangrove canopy was slightly less in 2007, due to the observed relatively greater investment in growth. Average height and canopy area of trees were greatest in 2007 in comparison to the previous years. Trade-offs in vegetative growth and reproduction were evident, with years of high reproductive output (2006) being followed by years of relatively greater vegetative growth (2007). Interestingly, individual trees appear to alternate years of high propagule production with years of low propagule production, rather than display a consistent population-level response. Rates of propagule production are encouraging in the context of both self-sustainability and expansion of this Caminada-Moreau population, as well as the potential for this population to serve as a renewable propagule source for human-dispersal of propagules to targeted restoration areas.

Controlled Greenhouse Studies

There continues to be a need for improved techniques for enhancing successful establishment of appropriate and high value plant species on barrier islands and coastal salt marshes during rehabilitation efforts. The black mangrove (*Avicennia germinans*), which is unique in the southern Louisiana coast as a flood- and salt-tolerant tree, is one such species that has become recognized as a critical component of barrier island salt marsh restoration efforts. Our ongoing efforts to develop a black mangrove restoration template is envisioned to result in better-informed restoration plans by elucidating important physiological constraints of seedlings of different age classes to environmental stressors that are common to barrier islands. It is generally acknowledged that seedlings become more tolerant of stressors as they mature, but selecting the youngest seedlings possible that are able to withstand the conditions of a backbarrier or coastal salt marsh restoration site may save both time and financial resources. Our findings indicate that young seedlings (under the age of 6 months) and older seedlings (12 to 24-months old) have similar physiological tolerances to stressors, including elevated salinity levels,

sand burial, and fluctuating water table (soil moisture availability), although some age-class differences in tolerance were evident as discussed below.

Elevated Salinity

This study tested the effect of substrate interstitial (porewater) salinity level (0, 24, 48, 72, and 96 ppt) on the survival, growth, and biomass allocation of two age classes of black mangrove seedlings (12- and 24-month olds). The lethal salinity level for both age classes of seedlings tested in this study was 96 ppt. There were sublethal salinity effects that were evident at 72 ppt, including leaf loss and negligible growth rates. The older age cohort of seedlings (24-months old) had the greatest total biomass at 48 ppt, but the younger age cohort (12-months old) had the greatest biomass at 24 ppt. Importantly, the 12-month old seedlings were able to alleviate the initial size advantage of the 24-month olds when grown under the 24 ppt salinity level, where both age classes produced equivalent amounts of above- and belowground biomass. As such, we suggest that high elevation sites that are only very infrequently flooded (and which may become hypersaline) should generally be avoided in the design elevation template for black mangroves.

Sand burial

In this study, we tested the effect of sand burial (0 cm, 5 cm, 10 cm, 15 cm, and 20 cm) on two age classes of seedlings (6- and 18-month olds). The transportation of sand, as may occur via aeolian processes due to the high winds often present on the coast, or especially as major sand re-distribution events (including overwash of dune environments) during the landfall of tropical storms and hurricanes, can be an important modulating variable on the survival of coastal vegetation, particularly recently transplanted vegetation at restoration sites.

We determined that sand burial depths greater than the height of the mangrove seedling resulted in 100% mortality, regardless of the age of the seedling. In this context, 18-month old seedlings are able to tolerate approximately 5 cm more burial than the 6-months olds based solely on age/height relationships. Interestingly, moderate depths of sand burial (5 cm and 10 cm) stimulated the growth of 6-month old seedlings in the first 4 weeks post-burial, but did not stimulate the growth of 18-month old seedlings. Overall, seedlings of both age classes are very tolerant of sand deposition, making them well suited for planting in backbarrier marshes.

Fluctuating Water Table

We assessed the effect of hydrologic regime (biweekly fluctuations, bimonthly fluctuations, or static) and water-table depth (0 cm, -15 cm, -30 cm, -45 cm, and -60 cm) on the growth, biomass allocation, and photosynthetic response of two age classes of black mangrove seedlings (6- and 18-month olds). Substrate elevation is important in determining the soil moisture, as well as influencing the pH, nutrient availability, and redox potential of the site, which may have significant impacts on the growth and vigor of the vegetation.

Our results indicate that a water-table depth of -30 cm under a substrate composed of fine sand is ideally suited for 6-month old seedlings. These conditions result in soil moistures that range from 10-20%. Similarly, optimal water-table depth for 18-month old seedlings is between -15 and -30 cm, where soil moisture ranges from 17-24% and 10-20%, respectively. Therefore, black mangrove seedlings between 6 months and 18 months of age will both perform well at an average water-table depth of -30 cm under Louisiana conditions of fine sand and microtidal hydrologic regime.

FIELD MONITORING: TRADEOFFS BETWEEN GROWTH AND REPRODUCTION FOLLOWING DISTURBANCE IN A SOUTHERN LOUISIANA BLACK MANGROVE POPULATION

Abstract

Coastal vegetation in Louisiana is subject to frequent and often severe disturbances. The strong tropical storms and hurricanes that impact the Louisiana coast are predicted to increase in intensity and frequency with global climate change. Hurricanes immediately alter hydrology during their passage and can cause extensive physical damage to the coastal habitat. They can further modify coastal habitats through sedimentation processes, with large-scale redistribution of sediments often occurring. A key species of southern Louisiana's coastal salt marshes and barrier islands is the black mangrove, *Avicennia germinans*. This woody species provides critical habitat, structure, and complexity to the marsh in addition to stabilizing sediment and slowing erosion. To assess the effect of major hurricane impact on the population dynamics of the Louisiana black mangrove, we began monitoring the growth and reproductive patterns of a population at the Caminada-Moreau headland following Hurricane Katrina, a Category 3 storm that made landfall on August 29, 2005. In mid October of 2005, 2006, and 2007, at the peak of propagule maturity, we measured the reproductive output (propagule production), as well as height and canopy diameter of 50 black mangroves of varying age/size classes, with the goal of providing managers with a reliable estimate of average propagule production per area of mangrove habitat. Our census of this population spanned years of high hurricane disturbance and years with little or no hurricane activity, thereby providing us with an ideal natural laboratory in which to assess how disturbance may modulate energy allocation to sexual reproduction (propagule production) versus allocation to growth or maintenance/repair costs in the aftermath of severe disturbance. The year of lowest total propagule production was in 2005, approximately 45 days after the landfall of Hurricane Katrina. Propagule production increased significantly in 2006 but not in 2007. The average height and area of the mangrove leaf canopy increased slightly in 2006, but the relative magnitude of increase was greater in 2007 than in the previous years. These trends illustrate that, at the population level there is interannual variation and tradeoffs in growth, maintenance, and reproduction following hurricane disturbance. Regression estimates of propagule production per square meter of mangrove canopy range from 252 propagules m⁻² during relatively mild years (2006) to 131 propagules m⁻² in years of high hurricane disturbance (2005).

Introduction

Hurricane Disturbance in Louisiana Coastal Salt Marshes

Coastal Louisiana plant communities experience major disturbances in the form of tropical storms and hurricanes on a regular basis due in part to Louisiana's geographic position at the northern edge of the Gulf of Mexico. Hurricane season in Louisiana extends from June 1 to November 30, with 95% of all intense hurricane activity from August through October when surface water temperatures in the Gulf of Mexico are in excess of 28° C (Landsea 1993). As levels of greenhouse gasses increase in the atmosphere, thereby trapping more long-wave radiation, an overall warming trend may lead to an increase in the average surface temperature of the Gulf of Mexico (Webster et al. 2005). Warm surface water feeds tropical depressions and storms, leading to stronger and more intense storms. Given that the frequency and intensity of tropical storms and hurricanes may increase in the future, implications for the adaptation of coastal plant communities to disturbances are uncertain.

The co-dominant species of the salt marsh and backbarrier marsh plant communities of the southeastern Louisiana coast are smooth cordgrass, *Spartina alterniflora*, and black mangrove, *Avicennia germinans*. Salt marsh plant communities have historically kept pace with rising and falling sea levels by a self-regulatory process of balancing optimal growth and marsh surface elevation increase with decomposition under changing scenarios of sea level and hydrologic regime (Nyman et al. 1993; Morris et al. 2002; McKee et al. 2007b). In this sense they are resilient to gradual, cumulative environmental changes. However, the community response to acute, rapid environmental changes such as sediment translocation, storm surge inundation, and wind damage may be slow and unpredictable, due to the heterogeneity of the landscape and the disturbance (Carlton and Bazzaz 1998). Though the nature of community disturbance varies, the way in which species respond to disturbance in terms of adjustments in the relative allocation of energy to growth, reproduction, and maintenance may be universal (Diaz et al. 2004).

Black Mangrove Botany

In Louisiana, black mangroves are of particular interest in the context of restoring the structure and function of the degraded coastal salt marshes and barrier islands. The complex root system of the black mangrove is comprised by cable roots and negatively gravitropic pneumatophores that extend out of the sediment (Tomlinson 1986). Pneumatophores have specialized structures known as lenticels that serve to provide the root system with additional oxygen needed for respiration and are an adaptation to anoxic soil conditions. The density of pneumatophores is positively correlated with the rate of sediment accretion; thus, black mangroves can be considered "ecosystem engineers" (Furukawa and Wolanski 1996; Wright and Jones 2004.) An ecosystem engineer is a species capable of modifying the local habitat and driving the secondary succession of the community. Mangrove roots produce an oxidized rhizosphere in which the aeration of sediment around the roots raises the redox potential and lowers sulfide concentration of the soil (McKee et al. 1988; Patterson and Mendelsohn 1991). In addition to driving sediment dynamics and edaphic characteristics, black mangroves provide critical habitat for myriad avian and invertebrate fauna (Robertson and Duke 1987; Caudill 2005). The woody

structure is favored by brown pelicans for building nests because the nests are elevated above high tide inundation (Visser et al. 2005).

Unlike black mangroves in the tropics that can reach heights of 30 meters (Tomlinson 1986), Louisiana black mangroves are shorter in stature and rarely grow taller than 2 meters due to freeze-intolerance (McMillan and Sherrod 1986; Patterson et al. 1997). Due to this temperature constraint, Louisiana's southernmost islands and coastal salt marshes represent the current northernmost latitudinal extent of their range. Black mangroves have been documented in Louisiana since the 1930's (Penfound and Hathaway 1938). As this ecotype is at the northern limit of its range, these black mangroves may be more cold-tolerant than other tropical ecotypes (McMillan and Sherrod 1986). Although extreme, prolonged cold events resulted in mortality of aboveground black mangrove tissue they have the ability to resprout (coppice) from the base of the tree (Patterson and Mendelssohn 1991).

Black mangroves have a unique life history strategy that facilitates rapid establishment. Specifically, following pollination and fertilization, black mangroves produce propagules that germinate on the parent tree. This strategy is different from the seeds that most plants produce that have an obligate dormant period (Farnsworth 2000). Live germination in the black mangrove is technically referred to as cryptovivipary since these propagules have a thin, protective layer enclosing them (pericarp), which differentiates them from truly viviparous species like the red mangrove, *Rhizophora mangle* (Tomlinson 1986; Saenger 2002). When the propagules are abscised from the parent tree in mid to late October, the peak of propagule maturation in Louisiana, they may be transported by tides to a suitable substrate where they may strand and establish. Propagules can remain buoyant for extended periods of time, resulting in the potential for significant dispersal distances (Rabinowitz 1978a).

Growth, Reproduction, and Maintenance

The reproductive effort of a plant can be explained in terms of the amount of energy allocated to reproductive structures and seeds, or propagules in the case of *Avicennia germinans* (Reekie and Bazzaz 1987a). Photosynthetic yield can be partitioned to the major processes of a plant's life cycle, which are growth, reproduction, and maintenance. A substantial investment in reproduction results in a comparatively lesser level of investment in growth or maintenance. The converse is also true for the other processes; a plant may undergo vegetative growth at the expense of reproductive effort (Reekie and Bazzaz 1987a and 1987b; Diaz et al. 2004). Tradeoffs such as this can occur in different ways, such as in stress-tolerating plants that typically have slow growth rates because they must allocate energy to the production of chemical compounds to ameliorate internal water potential (Grime 1977). Following a major disturbance where plants sustain physical damage, such as defoliation, photosynthate will be allocated to the repair or maintenance of vegetative tissue at the expense of reproductive structures (Anten et al. 2003).

Our goals were to assess the relative energy allocation to growth, reproduction and maintenance, in addition to quantifying the reproductive output per square meter of mangrove canopy. Estimates of annual propagule production that span years of either high or low hurricane disturbance may provide managers with useful estimates of reproductive potential that may be utilized in estimates of potential population sustainability and expansion, or in regards to the

potential for harvesting propagules as a renewable resource from a well-established population for human-dispersal to restoration areas, such as coastal and backbarrier salt marshes.

Site Description and Methods

Site Description

Our study site was located in the Caminada-Moreau headland, where a persistent population of black mangroves is associated with *Spartina alterniflora* salt marsh on the southeastern Louisiana coast at 29°6'22''N, 90°10'59''W (Patterson and Mendelssohn 1991; Patterson et al. 1997). The Caminada-Moreau headland is part of the Lafourche delta complex, an ancestral Mississippi delta lobe that was abandoned by the Mississippi River approximately 400 years ago (Boyd and Penland 1988). This headland is a source of sediment nourishment for the Isles Dernieres, the flanking barrier islands of this delta complex (Coleman et al. 1998). The Lafourche delta lobe is experiencing some of the highest rates of erosion of the Louisiana coast with the beach and backbarrier marsh reported to be eroding at a rate of 33 meters per year, making it one of the most vulnerable places on the Louisiana coast to land loss and the effects of sea-level rise (McBride and Byrnes 1997; Day et al. 2005).

The vegetation in this region is typical of the southeastern Louisiana coast (Hester et al. 2005) and includes coastal plant species such as beach tea (*Croton punctatum*), beach morning glory (*Ipomoea pes-caprae*), and seashore paspalum (*Paspalum vaginatum*) in the beach and dunes, and marshhay cordgrass (*Spartina patens*), seaside golden rod (*Solidago sempervirens*) in the rear dune and swale. The high marsh is approximately 200 meters inland from the beach; it is interspersed with halophytes (*Salicornia* spp.), black mangroves (*Avicennia germinans*), and saltgrass (*Distichlis spicata*), which then grades into a black mangrove/smooth cordgrass (*Spartina alterniflora*) association, followed by mostly monospecific stands of smooth cordgrass in the low marsh. Bay Champagne forms the eastern border of the population. The most recent prolonged cold-weather event occurred in 1989, where the temperature recorded a weather station on Grand Isle, Louisiana recorded temperatures below 0° for 72 consecutive hours (Station GDIL1, NOAA National Data Buoy Center 2007).

Methods

We identified and tagged 50 trees in this population that were randomly selected from a pool of representative trees in a manner that adequately represented the range of sizes and ages of mangroves present, spanning from young seedlings to larger, more mature mangroves. The initial tree sample selection took place in mid October, 2005, following the landfalls of both Hurricane Katrina and Hurricane Rita.

We measured the maximum height of each tree from the base of the trunk to the top of the tallest branch. The average diameter of the canopy was measured by measuring the widest chord of the canopy crown (approximately the middle of the canopy) and then taking another diameter measurement perpendicular to the first.

A complete census of each tree's propagule production was conducted, regardless of the size or apparent maturity of the propagule. Propagules that had already been abscised from the parent tree and were lying on the ground were not counted. A subset of propagules (10% of total propagule count) was randomly collected from each tree to ascertain length, width, weight, and percent moisture of the propagules. Maximum propagule length and width were measured with digital calipers to the nearest millimeter after being transported back to the lab. Propagule dry mass was determined after propagules had been dried at 65° C to a constant weight.

At each tree sampled, we also surveyed the elevation of the sediment surface near the base of the trunk (relative to a permanent benchmark) and collected soil samples to a depth of 15 cm to determine pH, salinity and percent organic matter (LOI).

A repeated-measures ANOVA was conducted to test for significant differences among years in height, area, and propagule production. To meet the assumptions of parametric analysis, data points greater than 2 standard deviations from the mean were eliminated from the dataset as outliers.

Results

Total average propagule production per black mangrove tree was significantly lower in the first census post-Katrina (October 2005) than in all subsequent years ($F = 11.901$, $p = 0.001$), (Figure 1.1). Further, the mangroves in 2005 were significantly shorter in height and smaller in area than in subsequent years of 2006 and 2007 ($F = 16.3$, $p < 0.001$; $F = 23.093$, $p < 0.001$, respectively). Because our first sampling (2005) was in the aftermath of Hurricane Katrina and represents a post-disturbance baseline assessment, we cannot directly assess the magnitude of damage directly inflicted to the trees from the hurricane. Nonetheless, based on subsequent years' data (as discussed, see below), it appears that high wind velocities associated with Hurricane Katrina caused damage to the crowns of the trees and any propagules that were maturing at the time of the hurricane.

Propagule production more than doubled in the following year (2006 census; Figure 1.1). Both tree height and canopy area also increased relative to the 2005 census; in the case of canopy area, this increase was significant ($F = 7.639$, $p = 0.008$; Figures 1.2 and 1.3). In the 2007 census, propagule production did not significantly increase, but both mangrove height and canopy area were significantly greater than both the previous years ($F = 10.649$, $p = 0.002$; $F = 23.093$, $p < 0.001$, respectively).

The average size of propagules varied interannually from 2005 to 2007, although not significantly. Propagules were smallest in 2005 (both length and width were smallest recorded), whereas propagules tended to be longer in 2006 and wider in 2007 (Figure 1.4). Mean propagule dry mass was greatest in 2006 ($0.949 \text{ g} \pm 0.055$). Soil edaphic factors (pH, salinity, and percent organic matter) and elevation were not significantly different between these years.

Propagule production per tree varied interannually overall, as well as by individual tree over time. Importantly, the highest production trees were different each year (Table 1.1); trees that displayed high reproductive output one year generally displayed a much weaker reproductive output the following year. Similarly, there were only two trees that consistently did not produce

any propagules in consecutive years. This indicates that trees balance years of high reproductive output with years of lower reproductive output (Figure 1.5).

Propagule production per tree remained highly correlated with individual tree canopy area across years with larger tree canopy areas producing greater numbers of propagules (Figure 1.6). At the level of the population, propagule production expressed per area of mangrove canopy was greatest in 2006 (mean of 214 propagules m^{-2} of mangrove canopy) compared to 2005 (mean of 147 propagules m^{-2}) and 2007 (mean of 163 propagules m^{-2}).

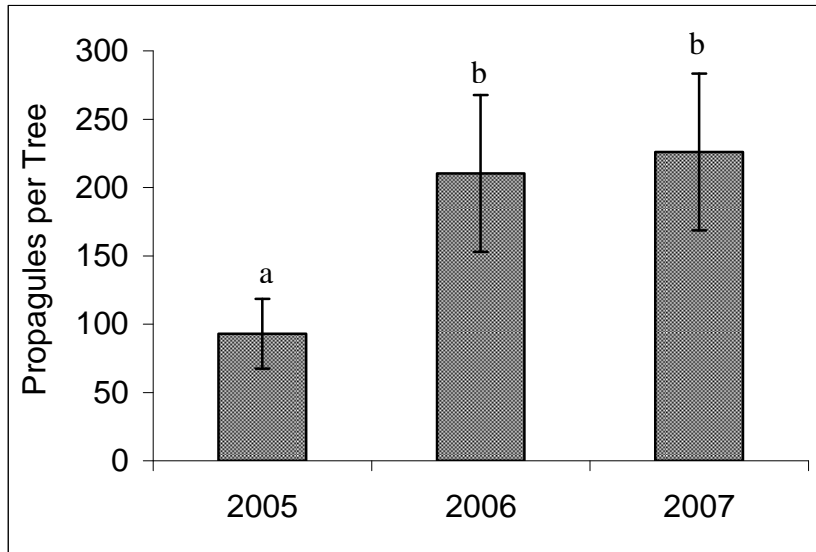


Figure 1.1. Propagule production per individual mangrove tree (mean \pm 1 SE). Means with the same letter are not significantly different.

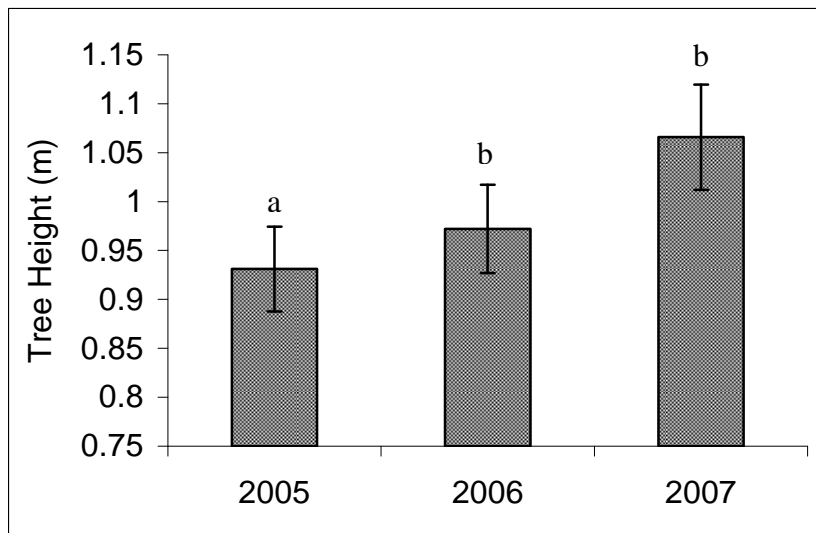


Figure 1.2. Mangrove tree height (mean \pm 1 SE). Note that the bottom of the y-axis is truncated to more clearly illustrate the change in height over the years. Means with the same letter are not significantly different.

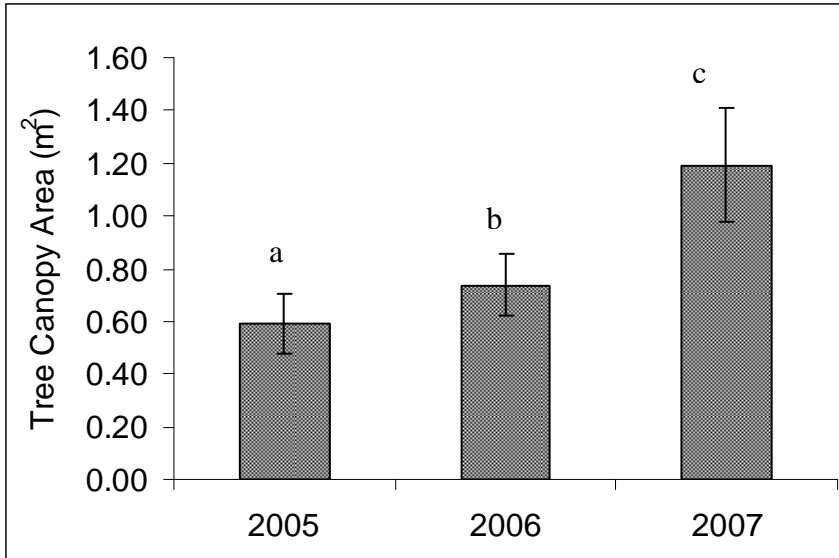


Figure 1.3. Area of individual mangrove tree canopies (mean \pm 1 SE) over time. Means with the same letter are not significantly different.

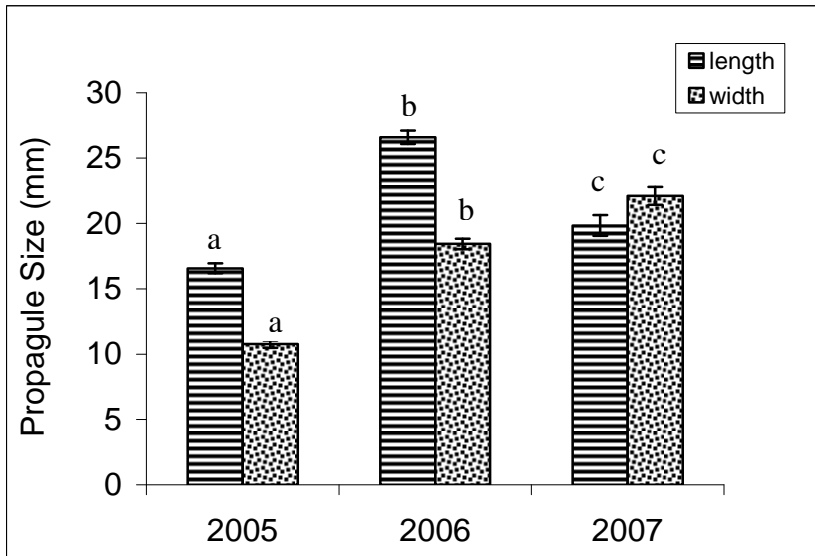


Figure 1.4. Length and width of propagules produced over time (mean \pm 1 SE). Means with the same letter (within a morphometric measure) are not significantly different.

Table 1.1. Annual maximum (top row) and minimum (0) propagule production rates per tree over time showing individual tree tag numbers associated with those values.

	2005	2006	2007
Tree # (propagules produced)	61 (1015)	26 (1968)	25 (1528)
Tree #s with no propagules	27, 33, 43, 48, 56	31, 51, 54, 55, 56, 63	44, 54, 66, 67

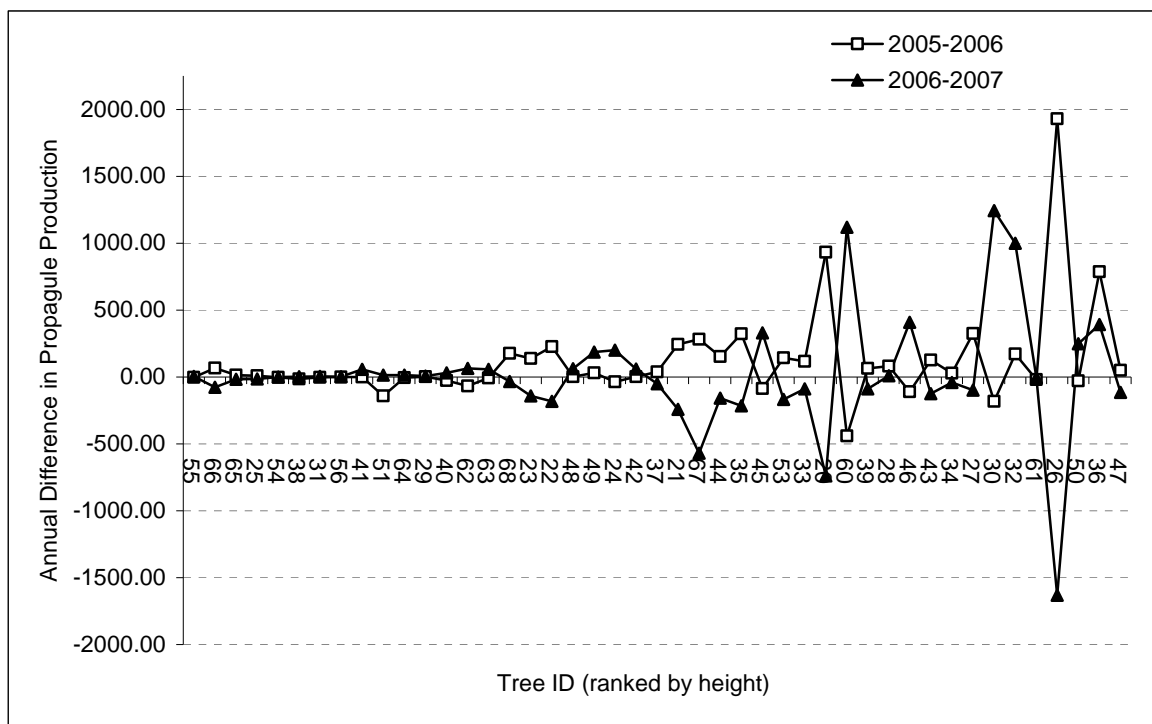


Figure 1.5. Change in magnitude of propagule production by individual tree, ranked from left to right by order of increasing height.

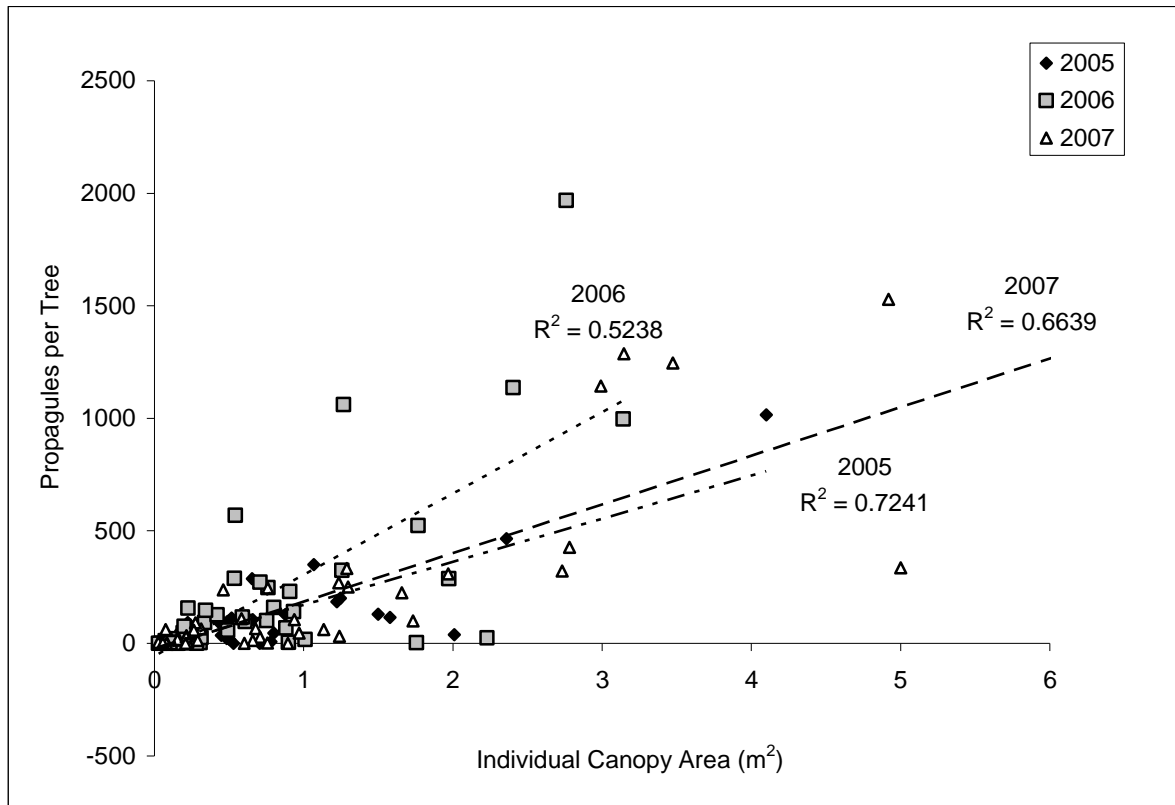


Figure 1.6. Propagule production per individual mangrove tree canopy area in 2005, 2006, and 2007 with correlation coefficients, where the number of propagules produced per square meter of mangrove canopy was estimated to be 131 in 2005, 252 in 2006, and 185 in 2007.

Discussion

The distribution and community structure of Louisiana black mangroves may be strongly influenced by the supply-side ecology, or the number of propagules able to arrive and establish at a site, with successful establishment and expansion being modulated by abiotic factors and biotic interactions (Lewin 1986; Sousa et al. 2007). Understanding the supply-side ecology of a species at its northernmost latitudinal limit in North America can provide valuable insight into the observed distribution of black mangrove. In northern Australian estuaries, surveys reveal that mangroves are more sparsely populated than space and environmental conditions would explain; the rationale for the observed distribution is due to insufficient propagule supply and dispersal constraints (Wells 1996; Bunt 1996; Ball 1998; Clarke et al. 2001). Based on our study of the population at the Caminada-Moreau headland, propagules do not appear to be limiting, although the long-distance dispersal of propagules is constrained to the extent that the tidal creeks, bays, and inlets traverse this region of salt marsh. Within these dispersal limitations, abiotic factors such as temperature and physical energy at the coast, constrain the areas of potential black mangrove recruitment and colonization. Nonetheless, the population at the Caminada-Moreau headland presently has been expanding, based on the number of young seedlings we observed over the years and the recent lack of prolonged cold-weather events.

Hurricane disturbance results in low reproductive output relative to years of normal disturbance. The implication of this is that decreased reproductive output can result in fewer new seedlings establishing that year. Such was the case in Florida in 2004, when Hurricane Charley caused a reduction in propagule production and new seedling recruitment in a population of red mangroves (Proffit et al. 2006). The impact of Hurricane Katrina in 2005 on the population at Caminada-Moreau resulted in many fewer mature and viable propagules that fall, but in the next year following the hurricane (2006), average propagule production per tree more than doubled. The range of estimates of propagule production on an individual level (per tree) and at the population level (per area mangrove canopy) may be useful for managers who wish to restore black mangroves and quantify the potential crop of propagules based on aerial photography. Restoration of mangrove forests around the world has historically been limited in scope and success by the prohibitive cost and effort of using containerized seedlings (Ablaza-Baluyut 1995; Sanyal 1998). The judicious use of propagules in place of, or in conjunction with, seedlings is a restoration technique that has not yet been optimized.

Propagule size was smallest following the 2005 hurricane disturbance. Generally speaking, larger propagules are more mature and are believed to be more viable than smaller propagules (Rabinowitz 1978a). Smaller propagules may not have as many carbohydrate reserves or may take longer to establish, expending more energy than is being acquired by photosynthesis (Rabinowitz 1978a), although this may not always be apparent, or a constraint, in a given year (Gary Fine, pers.com). Propagules with extended obligate stranding times may be at a disadvantage in a high-energy system because tidal action can dislodge propagules before they have had a time to take hold in the sediment (Farnsworth 2000; Clarke et al. 2001). Since the 2005 propagules were smaller in size and weighed less than propagules in 2006 and 2007, one inference is that viability may be lower in high-disturbance years, and as such, natural regeneration may be severely limited that year.

At the population level, trade-offs in the total energy allocation to growth, reproduction and maintenance are evident. Although we do not have pre-hurricane measurements to compare with the post-Katrina measurements, the 2005 propagule production appeared to be affected by the hurricane as evidenced by our data. It is likely that many propagules were physically dislodged from trees in late August 2005, and those that we did measure were either those that remained intact or the result of a post-Katrina reproductive effort. Regardless, the overall mangrove response to the disturbance in 2005 at the typical time of peak propagule maturation was to not produce a large number of propagules. In the following year (2006), propagule production doubled, and height and area of the mangroves increased only slightly relative to 2005. Based on the magnitude of increase in reproductive output relative to the increase in size, plants appeared to allocate considerably more resources to propagule production than to vegetative growth. In 2007, although propagule production was not significantly different than 2006, height and area both increased significantly, indicating that the relative energy allocation to vegetative growth was greater than that allocated to reproductive output. Patterns of energy allocation at the population level do, indeed, vary interannually and appear to reflect responses to the intensity and timing of acute disturbance superimposed upon a mosaic of moderately-dynamic abiotic fluctuations.

Interestingly, at the level of the individual, tradeoffs in the amount of energy allocated to reproduction by year were often evident as annual oscillations. In these cases, if an individual tree produced a large number of propagules one year, it produced a smaller number of propagules in the next year. The difference in magnitude of propagule production per individual tree varied (oscillated) in nearly equal and opposite directions; for example, the increase in propagule production in 2006 was essentially equivalent to the decrease in propagule production in 2007 and was most evident in the larger trees. It is important to note that this response is different than synchronized masting often reported at a regional level during relatively stable periods of resource supply and utilization (Ricklefs 1997). In this study, we have observed that responses of individual black mangrove trees display a propensity for alternating the amount energy allocation to reproduction between years, which may be further modulated by the amount of damage sustained during periods of intense disturbance. We anticipate that continued monitoring of this population over time will elucidate whether the trade-offs in energy allocation have a definite periodicity or are more driven by stochastic disturbance processes.

CONTROLLED GREENHOUSE EXPERIMENTS: EFFECTS OF ELEVATED SALINITY LEVEL, SAND BURIAL AND FLUCTUATING WATER TABLE ON YOUNG AGE CLASSES OF BLACK MANGROVE SEEDLINGS

Abstract

Louisiana's barrier islands provide myriad ecosystem services that include storm surge protection, wave attenuation, habitat complexity, biodiversity, and productive fisheries. Backbarrier marsh degradation and coastal erosion could greatly diminish these ecosystem services. To ameliorate these losses, vegetative stabilization is employed as a crucial component in barrier island restoration. Once successfully established, dune and backbarrier marsh plant species can act as autogenic ecosystem engineers, stimulating positive feedbacks in sediment accretion and land building. One native backbarrier and coastal salt marsh species of Louisiana's barrier islands is the black mangrove (*Avicennia germinans* (L.) L.). Restoring black mangrove plant communities can be costly and labor intensive when traditional containerized seedlings are utilized. We suggest that black mangrove propagules may be effectively utilized in conjunction with transplanted seedlings if potential differences in physiological tolerances between propagules and seedlings can be elucidated in regard to environmental stressors that may limit plant establishment, growth, and vigor on barrier island restoration projects. These stressors include elevated salinity levels, sand burial, and fluctuating water tables. We determined the effects of these stressors on the growth, photosynthetic response, and biomass allocation of in a series of manipulative greenhouse experiments in which two different age classes of black mangroves were evaluated. Depending on the experiment, either newly established propagules (6 months old) and 18-month old seedlings were compared or 12-month old and 24-month seedlings compared.

Twenty-four month old seedlings had a slightly higher salinity tolerance than 12-month old seedlings, evidenced by the greatest total biomass occurring at 48 ppt for the older age class, as compared to 24 ppt for the younger age class. Total biomass was not significantly different between 12- and 24-month old seedlings at 24 ppt; however, the 24-month old seedlings had significantly greater biomass than the 12-month olds in all other salinity levels (0, 48, 72, and 96 ppt). Mortality occurred at salinity levels of 96 parts per thousand (ppt) in both age classes of seedlings after two weeks. There were sub-lethal salinity effects on growth rate and leaf abscission that were evident at 72 ppt. A similarly high level of tolerance to sand burial occurred in both age classes. Moderate levels of burial (5 to 10 cm) stimulated growth in the initial 3 weeks post-burial. Mortality occurred only if sand burial depth completely covered a plant's photosynthetically active tissue, and because 12-month old seedlings were taller on average than 6-month old seedlings, they displayed greater survivorship. A fluctuating and static water table experiment was conducted to further elucidate the optimal hydrologic conditions for establishment of black mangrove seedlings. Mangrove seedlings planted at a water-table depth of -45 to -60 cm from the substrate surface had slower growth rates and lower total leaf area

than those seedlings planted either at a water-table depth of -30 cm, -15 cm, or 0 cm (i.e., water table at the substrate surface). Maximum root biomass production in the upper 15 cm of the soil profile was associated with a mean soil moisture of 15-17%, which occurred at water-table depths of -15 and -30 cm. Overall, our results indicate that relatively young seedlings (6-months to 18-months old) do not have ecologically significant differences in physiological tolerances to key environmental stressors on barrier islands, with the exception of response to sand burial where survival appears directly correlated with plant height. Therefore, seedlings of different age/size classes can be utilized effectively throughout a black mangrove restoration template design. However, if high marsh sites are in close proximity to unstabilized sediment, then larger seedlings may be better able to tolerate either wind-blown burial, or burial from overwash events.

Introduction

Land loss in Louisiana is a result of both natural and anthropogenic factors. Extensive manipulation of the floodplain via levees and canals combined with saline intrusion and an overall reduction in the sediment load and water quality of the Mississippi River are the contributing factors to the state of Louisiana's wetlands (Turner and Rabalais 1991; Day et al. 2005; Day et al. 2007; Swarzenski et al. 2008). Louisiana's barrier islands are, in essence, the first line of defense against storm surge and wave energy for the coastline and inland marshes (Lopez et al. 2007). Though small in total area, barrier islands have a disproportionately large influence in the development and protection of complex estuarine ecosystems. Barrier islands directly support Louisiana's productive fisheries and oil and gas industry that are valued at billions of dollars (Day et al. 2005). The role of these islands in dissipating wave and storm surge energy has been demonstrated by Stone et al. (2005). Models show a strong inverse correlation between intact barrier island land mass and the height and intensity of waves on back barrier marshes (Stone and McBride 1998). If there is no physical barrier to mitigate incoming storm wave energy from a storm, this force is redistributed farther inland to a greater area of marsh. Further, recent rates of coastal erosion (on the magnitude of 1 meter per year) can be partially attributed to increased tidal influence due to decreased barrier island land integrity (Watzke 2004). The total area of barrier islands is directly proportional to the amount of protection it provides; larger land masses offer greater protection from storms than smaller ones (Constanza et al. 2006).

Though total land mass of Louisiana's barrier islands is relatively small, the degree to which they influence habitat complexity along landward marshes is significant (Hester et al. 2005). Barrier islands buffer the force of wind and water to landward marshes, resulting in a gradient of wetland habitat types that are both highly productive and biodiverse (Hester et al. 2005). Dune vegetation on these islands trap and bind sand, thereby maintaining the dune features, which make storm overwash and island breaching less likely (Mendelssohn et al. 1991). Hester et al. (2005) described the positive relationship between the plant cover or biomass on a dune and the rate of sand accumulation in that system. Healthy dunes contribute to stable backbarrier marsh development through physical protection. Therefore, vegetative stabilization of both dune and marsh communities is important in barrier island restoration projects (Mendelssohn et al. 1991). Physically planting marsh species in areas devoid of vegetation increases the longevity of the marsh because successfully-established plants help accrete sediment, which maintains the marsh elevation above the mean sea level (Cahoon et al. 2005). Black mangroves are a highly desirable species for the vegetative stabilization of Louisiana's sediment-starved, ephemeral island system due to their capacity to accumulate organic matter and keep pace with sea level rise (McKee et al. 2007).

The dynamic environmental conditions present across barrier island habitat types exert strong influence on which species can establish. Barrier islands are a harsh environment with multiple stressors present along the gradient of ecotones present (Hester et al. 2005). These range from drought stress, sand burial, and wind abrasion and salt spray on the beach and dunes to elevated low soil organic matter, nutrient limitation, and elevated salinities in the swale and backbarrier marsh (Burdick and Mendelssohn 1987; Chen and Twilley 1998; Hester et al. 2005; Wang and Horwitz 2007). Successful plant species colonization requires dispersal to favorable sites (or microsites) that are within the physiological tolerances of the species (van der Valk 1981; Rand

2000). Although dispersal is a prerequisite for the establishment and spread of a new population, these founders must establish and persist at a critical density for the population to be self-sustaining (Sousa et al. 2007). Establishing and restoring black mangroves on barrier islands in Louisiana has the potential to increase the longevity and sustainability of the islands via sediment trapping and contributing organic matter to soil building processes; once black mangroves are well-established, they have the potential to produce, and trap propagules and continue to expand (Lewis 2005). The root system of the black mangrove is a combination of lateral adventitious roots and belowground cable roots from which aboveground pneumatophores extend. Rates of sediment accretion increase in proportion to the density of this aerial adventitious root system (Young and Harvey 1996).

Life history stage can have a profound effect on physiological tolerance of plants. Generally, young seedlings have a narrower range of tolerances than do mature plants (Lambers et al. 1998). Most mangrove species are viviparous; that is, they produce seeds that bypass obligate dormancy and germinate while still attached to the parent tree (Farnsworth 2000). Black mangroves are cryptoviviparous as their cotyledons and hypocotyl are enclosed in a protective layer called a pericarp, which is in contrast to truly viviparous species such as the red mangrove, *Rhizophora mangle*. Black mangrove propagules in Louisiana typically mature from early October through November when they are abscised from the parent tree, after which they may be dispersed by tidal action. The postulated advantage to this mode of reproduction is that the propagule, once abscised from the parent tree, does not have the additional stage of breaking dormancy after stranding on suitable substrate (Rabinowitz 1978a; Farnsworth 2000).

Typically, restoration is performed with containerized seedlings that can be costly and labor-intensive to deploy. We suggest that restoration success may best be enhanced through the synergistic approach of planting seedlings in the more stressful areas, followed by human dispersal of propagules throughout areas where they may strand at high tide. In Louisiana, we suggest that establishing *Spartina alterniflora* in association with *Avicennia germinans* will greatly assist in propagule stranding and retention within the restoration template. An additional benefit of this type of establishment approach for a species at the northern limit of its range is that the probability of loss of vegetated habitat due to weather extremes may be at least partially offset by reduced costs of establishment.

Black mangroves are facultative halophytes, and based on their natural zonation apparently have an intermediate flood tolerance (Mitsch and Gosselink 2000). Typical neotropical mangrove zonation begins at the land-sea interface with red mangrove, *Rhizophora mangle*, followed by black mangrove, *Avicennia germinans*, and finally and farthest upland, white mangrove, *Laguncularia racemosa*. However, black mangroves are the most cold tolerant of the neotropical mangroves and they are the only species present in Louisiana at this time. Extreme cold events defined as temperatures below freezing for more than 24 hours will result in mortality, though black mangroves have the ability to resprout from the base of their stems (McMillan and Sherrod 1986; Patterson and Mendelsohn 1991).

Another key environmental stressor on backbarrier marshes is salinity. Elevated salinity levels can occur in salt pans on barrier islands due to infrequent overwash events or astronomical tides (Mitsch and Gosselink 2000). In these hypersaline areas, only halophytic plant species can exist,

such as *Salicornia spp.* (Bertness 1991). Salt glands on black mangrove leaves extrude any salt that is not actively excluded by the roots, making them the most salt tolerant of the new world mangroves (Patterson and Mendelssohn 1991; Saenger 2002). Although this information is useful in interpreting patterns of zonation, the effect of elevated salinity levels on propagule establishment in previously unvegetated areas is unknown.

The geomorphology of the barrier islands is in constant flux because they receive the full force of wave and storm energy. Barrier islands are typically positioned in relatively high-energy environments, where waves constantly rework sediment and storm events can translocate sediment by scouring and redeposition of material. The effect that sediment deposition has on a plant depends on both the type of material (i.e., particle grain size and organic matter) and the rate at which it is deposited. Sand burial is conceivably less smothering than other types of burial because the large particle size allows for some degree of aeration. Burial by silts and clays as from river overbank flooding is potentially more devastating to plants (Millar et al. 1965; Maun 1998; Ellison 1998). Ecologically speaking, sediment deposition is a normal process in healthy wetlands and is associated with positive effects on plant growth and maintaining marsh surface elevation, whereas rapid burial, as may happen during a severe disturbance event, is completely different. Several studies of rapid sedimentation in mangrove forests around the world found that sediment burial is lethal for mangroves if the depth of burial exceeds the height of the specialized adventitious root structures, or pneumatophores (Gordon 1988; Ramcharan 1997; Waisel 1997). The lethal burial depth for young seedlings is less clear, but because they may have a lower tolerance to stressors early in their ontogeny (Lambers et al. 1998), they may be less stress tolerant in general and not have the carbohydrate reserves that are required to survive a burial event.

The hydrology of a particular site, which has strong influence on soil salinity, moisture, redox potential, and nutrient dynamics, is intimately tied to site elevations. Crewz and Lewis (1991) discovered that the most important determinant of tidal marsh restoration was the use of tidal datums to determine the elevation at which to construct tidal platforms for revegetation with mangroves and sea grasses. Mangroves often cannot establish in lower intertidal areas because of high wave energies (Nettel and Dodd 2007), whereas the highest suitable elevations at which they can establish is influenced by site-specific characteristics, particularly edaphic characteristics such as soil texture and grain size, and soil salinity levels. Thus, elevation gradients are an important consideration in restoration design because of their influence on the hydrologic regime (Lewis 2005). The effect of water table depth or extended periods of high or low water levels due to meteorological events on the growth and vigor of black mangroves has not been investigated.

The overall objectives of the suite of experiments presented herein is to determine black mangrove growth, photosynthetic, and biomass allocation responses of young age classes of seedlings to environmental stressors often encountered in Louisiana backbarrier marsh restorations. These stressors include elevated salinity levels, sand burial, water table depth, and water-table fluctuations as may be influenced by meteorological events. We determined the effects of these stressors via manipulative greenhouse experiments.

Materials and Methods

To elucidate potential differences in the physiological tolerances of different age classes of young black mangrove seedlings to environmental stressors, we designed a series of controlled greenhouse experiments. These experiments were conducted at the Center for Ecology and Environmental Technology (CEET) in Lafayette, Louisiana from September 2007 – August 2008. The black mangroves used in the experiment were collected from a population at the Caminada-Moreau headland along the southeastern Louisiana coast (the same population monitored in the field study; see first research chapter) and raised in the greenhouse.

Three studies were conducted over a 12-month period. The first study was designed to test the salinity tolerance of 12-month old seedlings and 24-month old seedlings, and was conducted during the fall of 2007. The second study, designed to test the response of 6-month old and 18-month old seedlings to sand burial, and was conducted during spring of 2008. The final greenhouse study, designed to test the effect of fluctuating and static water tables on 6-month old and 18-month old seedlings, began in April 2008 and continued through the end of August 2008.

All seedlings utilized in these studies were reared from propagules collected from the black mangrove population located on the Caminada-Moreau headland, near Port Fourchon, Louisiana. Collection of propagules occurred in late fall of both 2006 and 2007. Propagules were established at the CEET research center and grown to the desired age classes under greenhouse conditions.

Elevated Salinity Levels

The goal of this study was to test the effect of elevated salinity levels on 12-month and 24-month old seedling growth and survival. Target salinity level treatments were: 0 ppt (control), 24 ppt, 48 ppt, 72 ppt, and 96 ppt and were obtained using a synthetic sea salt (Instant Ocean). This experiment was established as a randomized block factorial design as follows: 2 age classes x 5 salinity levels with 5 blocks (i.e., replicates), yielding 50 experimental units. Each seedling was planted in a four-liter horticultural pot filled with fine sand and placed in a 15-liter reservoir filled with water (at a given salinity level) that remained at a constant level of 10 centimeters below the surface of the soil.

Since seedlings had been grown under non-saline conditions, step-wise increases in salinity levels were necessary to reach the targeted salinity levels (except for the 0 ppt controls). Salinity levels were increased in weekly increments of 12 ppt until the specified target salinity levels were reached. When increasing salinity levels, the new salt solution was flushed through the sand in the pots several times, and then flushed with a 10% Hoagland's nutrient solution at the target salinity level, which was also used to fill the reservoir. In this way, the salinity effects we observed were due to chronic, increasing exposure to salt concentrations. Due to this method of increasing salinity, seedlings at 24 ppt remained at a constant salinity level for the duration of the experiment (8 weeks), seedlings at 48 ppt were at this salinity for 6 weeks, seedlings at 72 ppt treatment were at this salinity for 4 weeks, and seedlings at 96 ppt treatment were at this salinity for 3 weeks (note that the 96 ppt treatment was achieved as a single 24 ppt increment from the 72 ppt treatment).

The salinity of each pot was checked biweekly with a salinity/conductivity meter and salinity adjusted accordingly. Height, diameter, and leaf number were recorded weekly. The experiment continued until each unit was at its target salinity, and was terminated when seven of the ten plants at the highest salinity level (96 ppt) died. At this time, we harvested above- and belowground biomass, with aboveground biomass partitioned into live and dead components. The effects of age and salinity level were analyzed with a RBD ANOVA, whereas differences in growth rates were analyzed with a repeated measures RBD ANOVA. All data analyses were performed using SYSTAT 11.0 (SPSS, Inc. 2000).

Sand Burial

This study assessed the tolerance of 6-month old and 18-month old seedlings to sand burial of various depths. The treatment levels were: 0 cm (control), +5 cm, +10 cm, +15 cm, and +20 cm of sand burial. This experiment was established as a randomized block factorial design as follows: 2 age classes x 5 burial depths with 5 blocks (i.e., replicates), yielding 50 experimental units. The plants were planted in Atchafalaya River sand (97.33% fine sand), which is similar in composition to Caminada-Moreau sand (97.80% fine sand). PVC pipe (15-cm diameter) was cut to a height of 60 cm, fitted with a PVC drain grate with silt screen to allow water exchange, and filled with Atchafalaya river sand. The PVC mesocosms were placed inside 18-L buckets filled with fresh water that was maintained at a water table of -20 cm below the surface of the sand. Twenty-five 6-month old and twenty-five 18-month old seedlings were transplanted into the PVC mesocosms and allowed to recover from potential transplant shock for two weeks. PVC couplings, which served as extensions, were placed on the 15-cm diameter PVC to allow for the sand addition. These couplings were cut to match the various burial depth treatments, such that the total burial depth ranged from 0 to 20 cm of sand that was rapidly deposited on the sand surface of the mesocosms, each with a water table positioned at -20 cm relative to the pre-burial sand surface.

Weekly measurements of black mangrove height and number of leaves were monitored. For treatments in which sand deposition completely buried the plants, time to re-emergence was also recorded. After two months, the experiment was terminated with the harvesting of above- and belowground biomass. Biomass data was analyzed with a MANOVA and growth rates were analyzed with a repeated-measures RBD ANOVA to test for significant differences between the effects of age and sand burial and their interaction using SYSTAT 11.0 (SPSS, Inc. 2000).

Fluctuating Water Table

In this study, we determined the effect of various water-table depths and hydrologic regimes on growth and survival of 6-month and 18-month old seedlings. The hydrologic regimes were the following: static, fluctuating biweekly, and fluctuating bimonthly. The water-table depths were 0 cm, -15 cm, -30 cm, -45 cm, and -60 cm from the substrate surface. This experiment was a randomized block factorial design as follows: 2 age classes x 3 hydrologic regimes x 5 heights above the water table, with 5 blocks (i.e., replicates), yielding 150 experimental units. The planting mesocosms were constructed of PVC pipes, all of 15-cm diameter, but of different total heights to achieve the desired water-table depth treatments. If an experimental unit was assigned to a fluctuating hydrologic regime, the mesocosm was raised and lowered -15 cm below and +15 cm on either a biweekly or bimonthly basis such that its substrate surface moved these distances

from its assigned water-table depth treatment. In either case of fluctuating hydrologic regime, mesocosms moved a total range of 30 cm; movement always in the order of down 15 cm, then to the midpoint, then up 15 cm.

Plants were watered twice a week at a rate equivalent to the average natural precipitation at the Caminada-Moreau headland, which is approximately 1600 mm/year (Mendelsohn and Hester 1988). Cumulative stem height (primary stem height plus any additional branch lengths) and leaf number were measured every other week. Minimum, average, and maximum soil moisture in the upper 0-15 cm of the soil profile was determined throughout the study. In June and August 2008 we measured photosynthetic response (net CO₂ assimilation and stomatal conductance) using a LICOR-6400 photosystem (LICOR, Lincoln, NE). At harvest, we measured total leaf area using WinRhizo image analysis software (Regent Instruments, Inc. 2005). To harvest belowground biomass, the PVC mesocosms were cut longitudinally down the length of the container and soil and root samples were collected in 15-cm increments. Root biomass and mid-point soil moisture were determined at each depth increment. All biomass was sorted into various partitions and dried at 65° C to a constant mass and weighed. Data were analyzed with a repeated-measures MANOVA with contrasts using SYSTAT 11.0 (SPSS, Inc. 2000).

Results

Elevated Salinity Levels

Both aboveground biomass (stem and attached leaves at the time of harvest) and belowground biomass were consistently greater in the 24-month old seedlings than the 12-month old seedlings across all salinity levels except at the 24 ppt level, in which the biomass response of the two age classes were equivalent. The greatest aboveground biomass produced by the 12-month old seedlings occurred at this 24 ppt salinity level, whereas the 24-month old seedlings displayed their greatest aboveground biomass production at the 48 ppt salinity level (Figure 2.1). Belowground biomass production followed the same patterns for the two age classes (Figure 2.2). An important difference to note between age classes is that the 12-month old seedlings biomass maximum at 24 ppt was followed by a significant decline in production at higher salinity levels, whereas the biomass of 24-month old seedlings peaked at 48 ppt and then did not significantly decline at higher salinity levels. Total biomass (sum of above- and belowground biomass) was also significantly greater in 24-month than 12-month old seedlings across salinity levels except at 24 ppt, where differences in aboveground and belowground biomass were not statistically significant ($F = 0.01$, $p = 0.9394$ and $F = 0.30$, $p = 0.863$, respectively). Differences in aboveground and belowground biomass between 12- and 24-month old seedlings were marginally significant at 0 ppt ($F = 3.34$, $p = 0.0751$) and significantly different at 48 ppt ($F = 5.63$, $p = 0.0221$). Therefore, although 24-month old seedlings entered the experiment with inherently greater biomass than the 12-month olds, the 12-month old seedlings were able to 'catch up' and produce equivalent amounts of above- and belowground biomass when grown at the 24 ppt salinity level. The greatest cumulative change in height for both 12- and 24-month old seedlings occurred in the control (0 ppt) and lowest salinity level (24 ppt) treatments (Figure 2.3). The cumulative change in 12-month old seedling height was greatest at 24 ppt salinity level (Figure 2.3).

Root-to-shoot ratios were generally greater in the 24-month old seedlings, with greatest root-to-shoot ratios occurring at lower salinity levels in 24-month old seedlings than in 12-month old seedlings (Figure 2.4). Root-to-shoot ratios may increase in response to either a greater stress inhibition effect on the production of aboveground tissue relative to belowground tissue, and/or an actual decrease in aboveground biomass by leaf abscission to minimize the potential for transpirational water loss.

Our results indicate that both age classes of black mangrove seedlings assessed (12- and 24-month old seedlings) have the ability to tolerate salinity levels up to 72 ppt. However, both age classes of seedlings displayed substantial mortality within 3 weeks when exposed to the 96 ppt salinity level. Thus, prolonged substrate salinity of 96 ppt appears lethal to black mangrove seedlings regardless of age class. Sublethal effects of elevated salinity levels were apparent in the 72 and 96 ppt treatments, and included leaf browning, desiccation, and abscission. Total number of leaves per seedling at the end of the study was greatest at 24 ppt for both 12 and 24-month old seedlings. Salinity had a significant effect on total number of leaves abscised from the initiation to the end of the study ($F = 4.1$, $p = 0.007$), with higher salinity levels resulting in greater number of leaves abscised. This net change in leaf number of 12- and 24-month olds was significantly different, with 24-month olds losing more leaves ($F = 4.194$, $p = 0.047$), (Figures 2.5 and 2.6). By October 25, the sublethal effects of salinity toxicity in plants at 72 ppt were apparent as evidenced by leaf loss in both 12- and 24-month old seedlings (Figures 2.5 and 2.6).

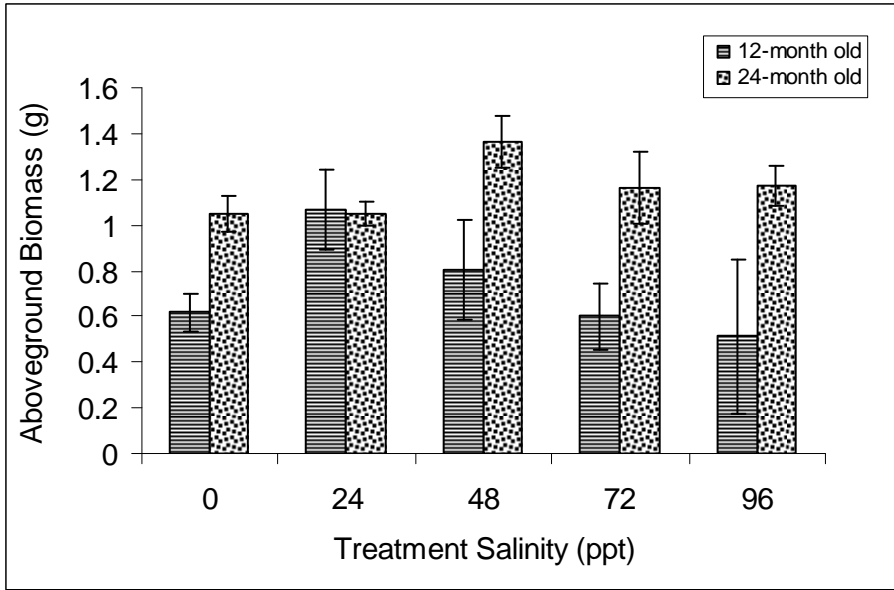


Figure 2.1. Aboveground biomass per mangrove seedling (mean \pm 1 SE).

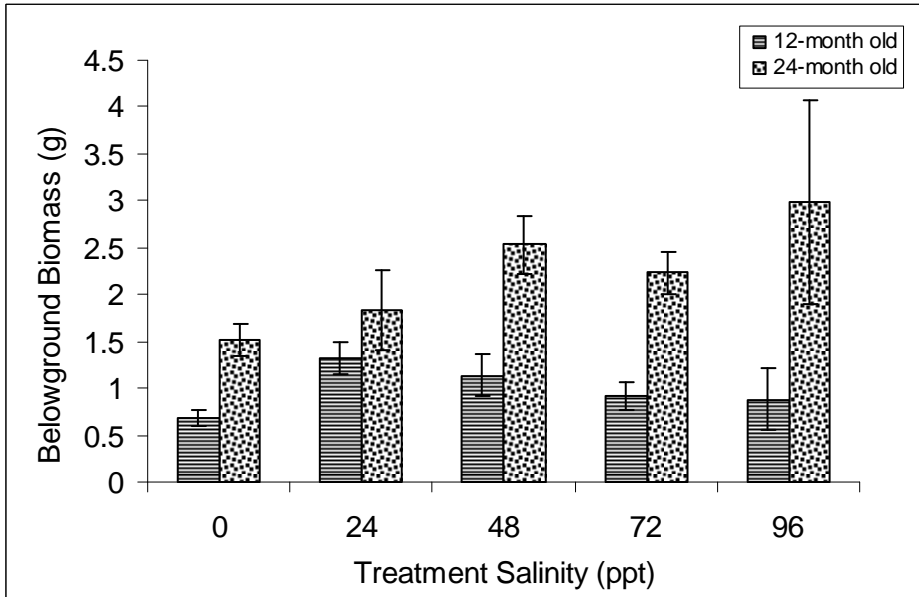


Figure 2.2. Belowground biomass per mangrove seedling (mean \pm 1 SE).

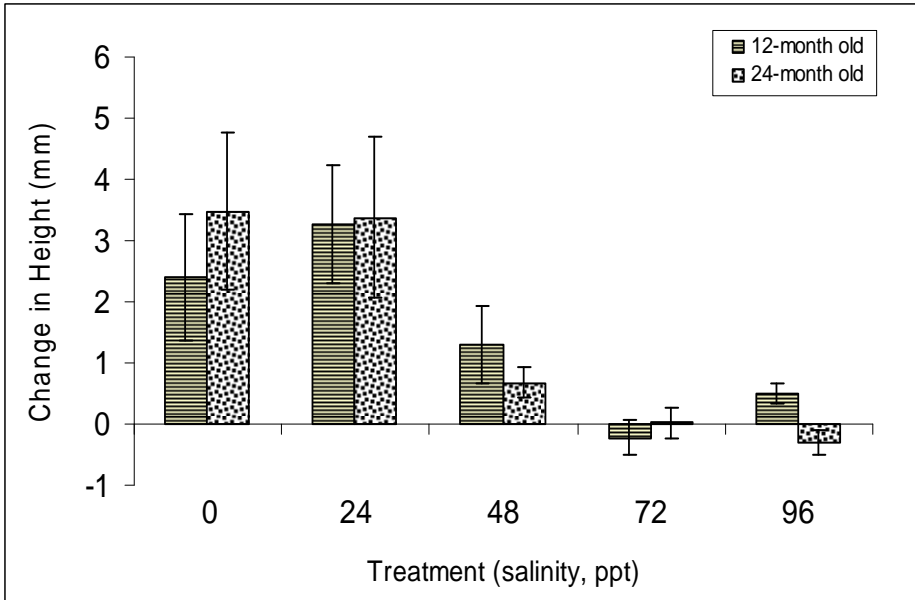


Figure 2.3. Cumulative change in height per mangrove seedling age class (mean \pm 1 SE).

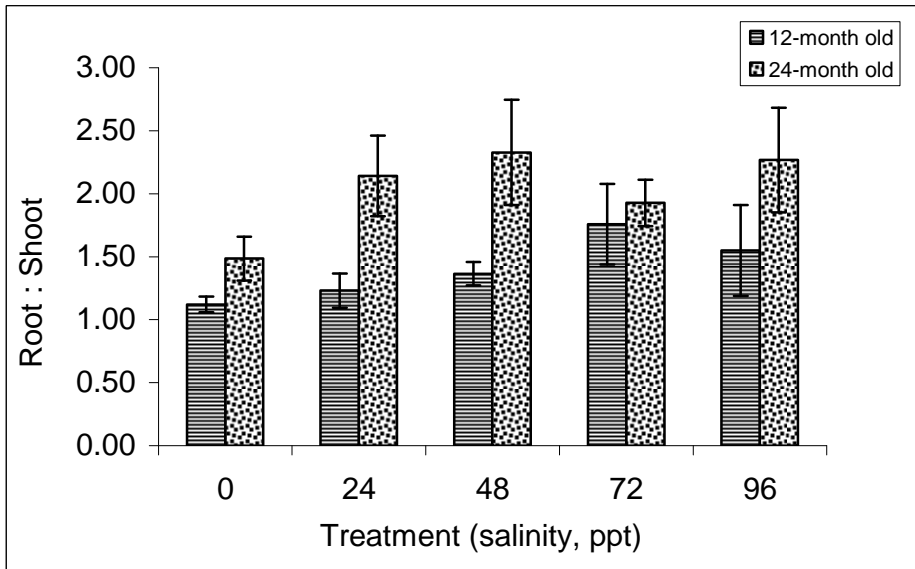


Figure 2.4. Biomass allocation ratio expressed as root-to-shoot per mangrove (mean \pm 1 SE).

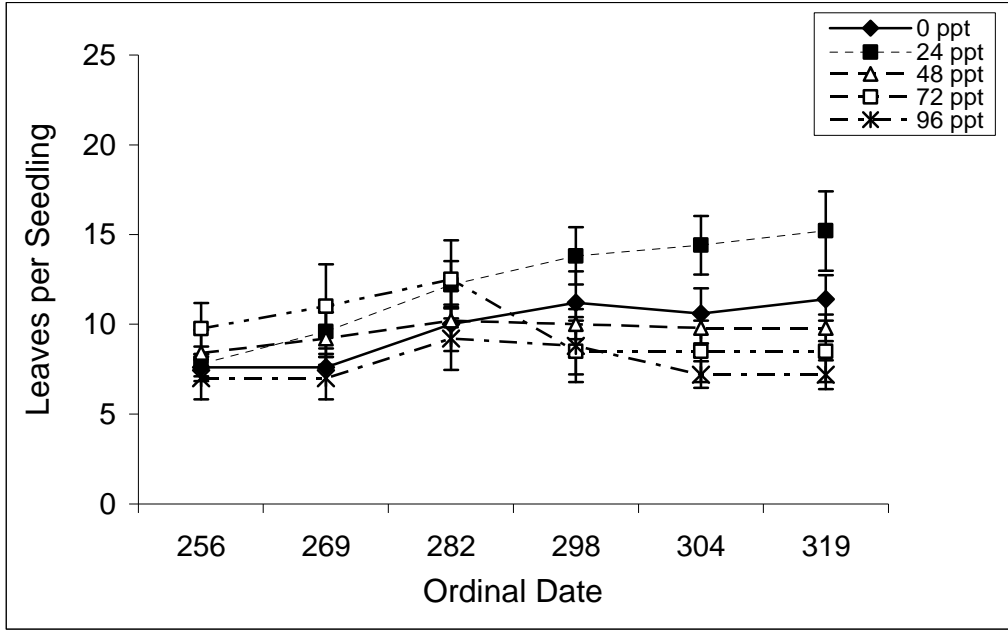


Figure 2.5. Net number of leaves per 12-month old mangrove seedling (mean \pm 1 SE). Net leaf loss peaked around ordinal date 298 (October 25, 2008) when salinity levels approached 72 ppt and increased to 96 ppt by ordinal date 304 (October 31, 2008).

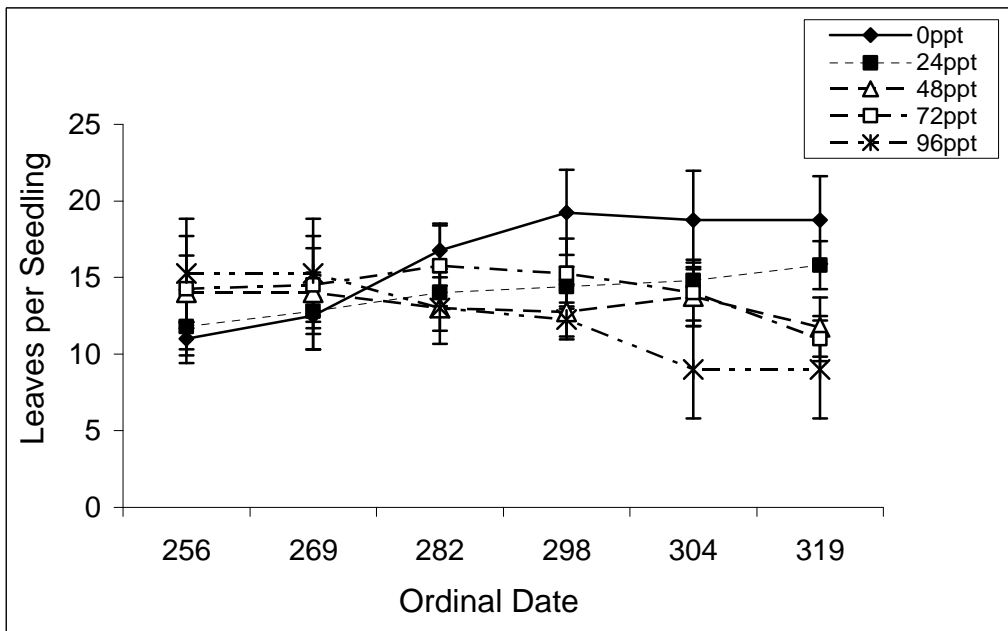


Figure 2.6. Net number of leaves per 24-month old mangrove seedling. Leaf loss peaked around ordinal date 298 (October 25, 2008) when salinity levels approached 72 ppt and increased to 96 ppt by ordinal date 304 (October 31, 2008).

Sand Burial

Many of the plants in the 15 and 20 cm sand burial treatments were completely covered by this depth of sand. When complete burial of all aerial tissue occurred, it proved to be lethal (Table 2.1). Thus, seedlings buried to a depth of sand exceeding their height demonstrated 100% mortality, whereas all seedlings that were not completely buried survived.

The effect of the sand burial on growth differed between the two age classes. Moderate sediment deposition appears to have a stimulatory effect on growth, though there is variation in the timing of this response between age classes (Figures 2.7 and 2.8). Eighteen-month old seedlings had significantly different growth rates than 6-month old seedlings over time ($F = 4.062$, $p = 0.013$), (Figures 2.7 and 2.8). The younger 6-month old seedlings in the control, +5 cm, +10 cm, and +15 cm treatments all had growth rates greater than or equal to 0.5 mm/day after one week of burial. In contrast, none of the 18-month old seedlings in any of the treatments had growth rates greater than 0.5 mm/day during the same period of time. Whereas 6-month old seedling growth rates were at the same rate from the time of burial (day 1, or ordinal date 62) to almost 4 weeks after burial (day 26, or ordinal date 87) and steadily decreased to a negligible growth rate by the end, the growth rates of the 18-month old seedlings increased slowly from a negligible rate and did not reach a maximum until 26 days into the study. The 18-month old seedling growth rates peaked around day 26, and then declined for the duration of the study (Figure 2.8). Overall, the growth rate around day 26 for both age classes was significantly greater than the growth rates of the rest of the study ($F = 2.407$, $p = 0.024$).

The effects of burial depth and age class were significant for total height, aboveground biomass, and belowground biomass. Significant differences in total height among treatments generally reflect the greater proportion of plant tissue buried by increasing burial depths. Minimal aboveground and belowground biomass for both age classes occurred at +15 and +20 cm burial depths (Figures 2.9 and 2.10). As expected due to the initial relative size differences of seedlings that are a year apart in age, there were significant differences in above- and belowground biomass between age classes. The total biomass of the 6-month old seedlings was affected at lesser burial depths than the 18-month old seedlings; 6-month olds tended to have lower biomass following any amount of sand burial (Figures 2.9 and 2.10), whereas the effects of burial on the 18-month olds were minimal until the maximum burial depth of +20 cm (Figures 2.9 and 2.10).

Table 2.1. Proportion of seedlings covered entirely by sand burial depth. Note that none of the seedlings in any of the lesser burial depths (+0, +5, +10 cm) were completely covered.

Burial Depth	6-month old seedlings buried	18-month old seedlings buried
+ 0 cm	0.00	0.00
+ 5 cm	0.00	0.00
+ 10 cm	0.00	0.00
+ 15 cm	0.60	0.00
+ 20 cm	1.00	0.60

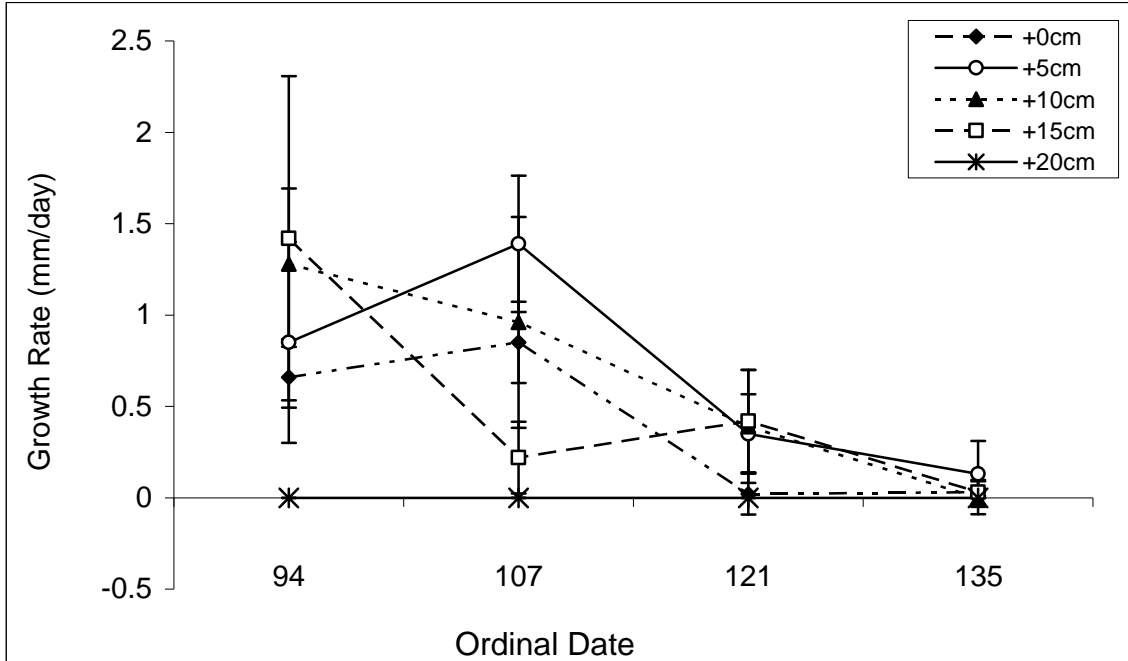


Figure 2.7. Growth rate per mangrove of 6-month old seedlings (mean \pm 1 SE).

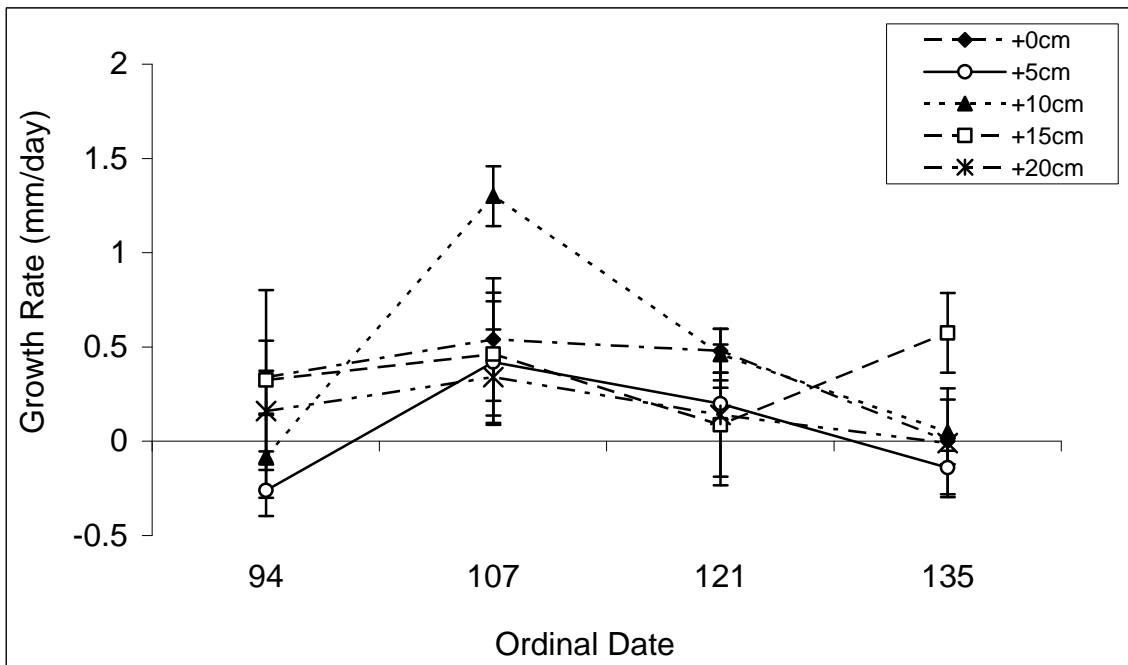


Figure 2.8. Growth rate per mangrove of 18-month old seedlings (mean \pm 1 SE).

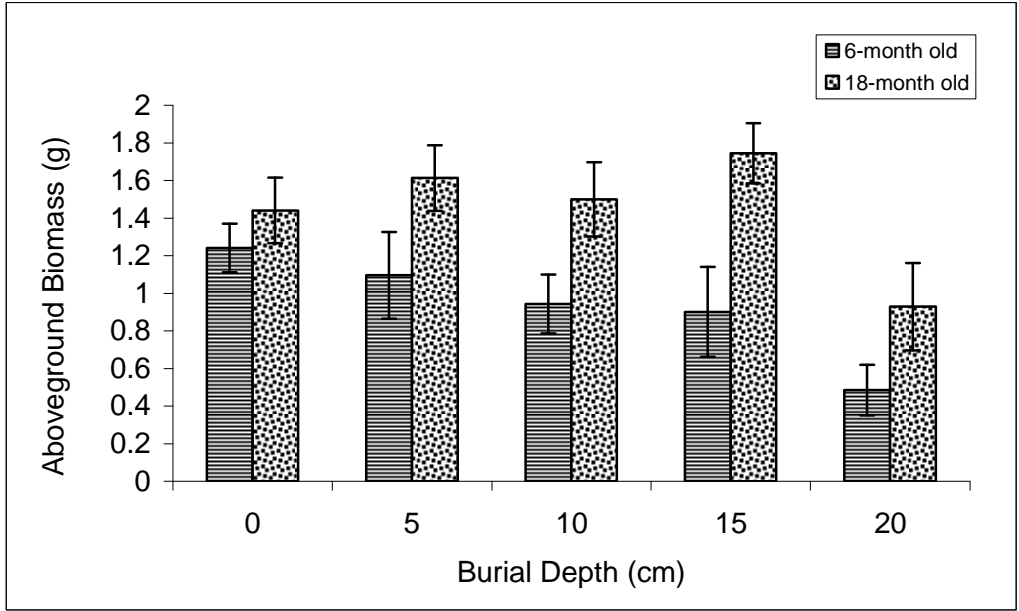


Figure 2.9. Aboveground biomass of 6-month old and 18-month old seedlings per mangrove (mean \pm 1 SE).

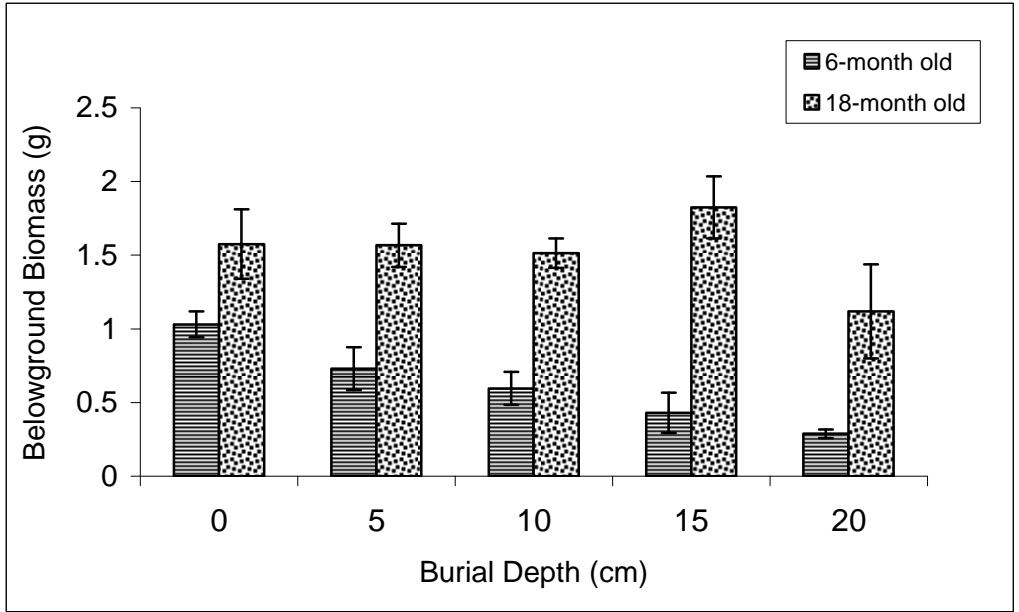


Figure 2.10. Belowground biomass of 6-month old and 18-month old seedlings per mangrove (mean \pm 1 SE).

Fluctuating Water Table

There were significant effects of water-table depth and age class on aboveground biomass, belowground biomass, final leaf count, and total leaf area (Table 2.2). Interestingly, there were no statistically significant effects of hydrologic regime (static, fluctuating biweekly, or fluctuating bimonthly regimes) on aboveground, belowground biomass (Figures 2.11, 2.12, 2.13, 2.14) or the net number of leaves. However, the differences in total leaf area between the three hydrologic regimes were marginally significant ($F = 2.958$, $p = 0.056$).

Leaf area ratio, defined as the total leaf area (cm^2) divided by the total seedling biomass (g) (Poorter and Remkes 1990, McKee 1995a), varied by seedling age, water-table depth, and hydrologic regime (Figure 2.15a, b, and c). Leaf-area ratio reflects the proportion of energy that is invested in light capture and photosynthesis (McKee 1995a). Six-month old seedlings had a greater average leaf area ratio with a smaller standard error around the mean (13.43 ± 0.53) than 18-month old seedlings (10.52 ± 3.55). There were significant differences among the various hydrologic regimes (Figure 2.15a, b, and c). Leaf area ratio was significantly greater in the bimonthly fluctuating regime ($F = 5.226$, $p = 0.024$), and significantly less in the biweekly fluctuating regime ($F = 8.196$, $p = 0.005$). Some interesting differences were observed in the leaf area ratio responses of 12-month old versus 6-month old seedlings (Figure 2.15). The 6-month old seedlings tended to produce greater leaf area ratios than 12-month old seedlings, except at the deepest (-60 cm) water-table depth. Further, this deepest water-table depth treatment (-60 cm) resulted in leaf area ratios that were significantly lower than the rest of the treatments ($F = 68.053$, $p < 0.001$, whereas water-table depths of -45 and -30 cm resulted in leaf area ratios that were significantly greater than all others ($F = 27.773$, $p < 0.001$ and $F = 21.680$, $p < 0.001$, respectively).

Physiological stress was quantified by measuring photosynthesis and stomatal conductance on two separate occasions at 4 and 6 months into the study. Water-use efficiency (WUE), defined as the moles of carbon fixed per moles of water lost via transpiration (Lambers et al. 1998), did not vary among water-table depths, hydrologic regimes, or age classes. However, time had a significant effect on water-use efficiency ($F = 3.514$, $p = 0.037$) and stomatal conductance ($F = 16.482$, $p = 0.000$). Table 2.3 summarizes the average rates of net CO_2 assimilation, stomatal conductance, and water-use efficiency.

Aboveground biomass includes stems and all attached leaves, both dead and alive, at the time of harvest. Average aboveground biomass for 6-month old seedlings was greatest at the -30 cm water table depth (Table 2.2), though the differences between hydrologic regimes were not significant. Average aboveground biomass for 18-month old seedlings was greatest at the three shallowest water-table depths regardless of hydrologic regime (Figure 2.12).

Total belowground biomass was greatest for both age classes at the -30 cm water-table depth, regardless of hydrologic regime (Tables 2.2 and 2.5). The incremental root biomass varied by depth. Age was a significant effect within treatment heights, whereas hydrologic regime was not (Table 2.5). The exception to this was in the -30 cm water-table depth treatment, where hydrologic regime had a significant effect on incremental root biomass ($F = 3.11$, $p = 0.033$). The root biomass in the upper 15 cm of the soil profile was significantly different among water-table depth treatments ($F = 12.782$, $p < 0.001$) and between ages ($F = 43.258$, $p < 0.001$), (Figure

2.16). Root-to-shoot ratio did not vary significantly by water-table depth or hydrologic regime, but 6-month old seedlings had a significantly lower root- to-shoot ratio than 18-month old seedlings ($F = 34.649$, $p < 0.001$).

The growth response and biomass allocation of the mangrove seedlings generally tracked the gradient of soil moisture through the soil profile. The minimum and maximum available moisture in the upper 15 cm of the soil profile, sampled at various times throughout the study when the substrate surface was the closest or furthest possible distance from the water table, varied among water-table depth treatments (Table 2.5). The optimum range of water-table depths for seedlings appears to be between -15 and -30 cm based on final mangrove seedling heights (Figure 2.17). The percent moisture at the time of harvest varied significantly across the different soil depths, but did not differ between the two age classes (Figure 2.18). We compared the percent moisture in the midpoint of the upper 15 cm of the soil profile between treatments (Table 2.5) and determined that water-table depth had a significant effect on soil moisture in the upper 15 cm of soil ($F = 50.558$, $p < 0.001$).

Table 2.2. Summary ANOVA table for the water-table depth experiment. Significant effects are denoted with an asterisk (*).

	Aboveground Biomass	Belowground Biomass	Final Leaf Count	Total Leaf Area
Age	$F = 5.77$ $p = 0.018^*$	$F = 36.963$ $p < 0.001^*$	$F = 40.989$ $p < 0.001^*$	$F = 0.03$ $P = 0.868$
Water-Table Depth	$F = 39.13$ $p < 0.001^*$	$F = 17.79$ $p < 0.001^*$	$F = 15.116$ $p < 0.001^*$	$F = 50.67$ $p < 0.001^*$
Age x Water- Table Depth	$F = 3.57$ $p = 0.009^*$	$F = 1.57$ $p = 0.188$	$F = 0.73$ $p = 0.573$	$F = 2.10$ $p = 0.086$

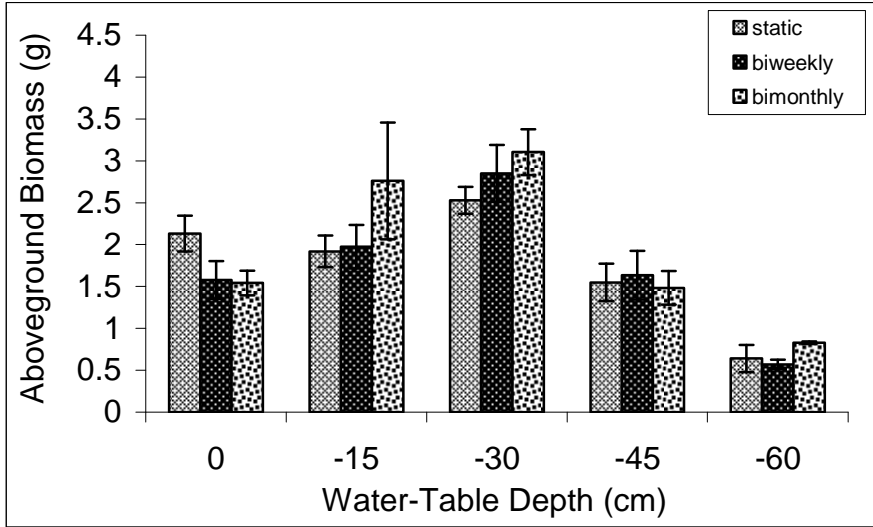


Figure 2.11. Aboveground biomass per 6-month old mangrove seedling (mean ± 1 SE).

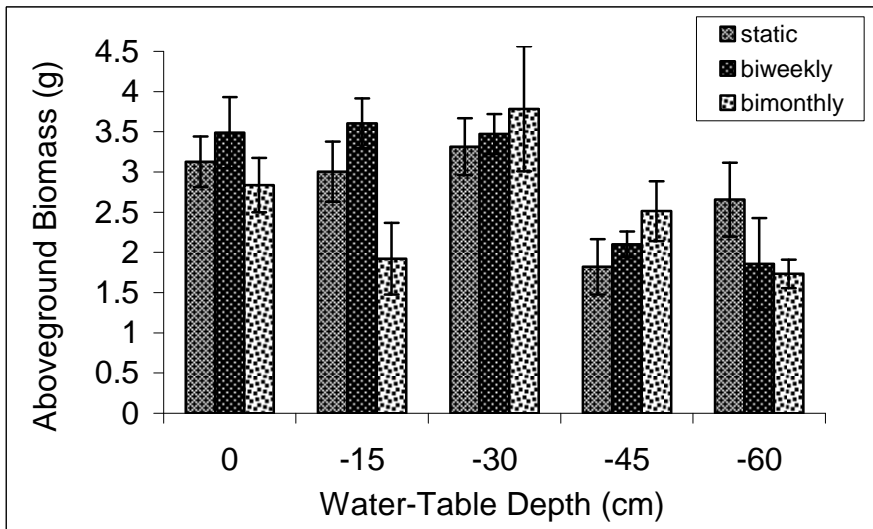


Figure 2.12. Aboveground biomass per 18-month old mangrove seedling (mean ± 1 SE).

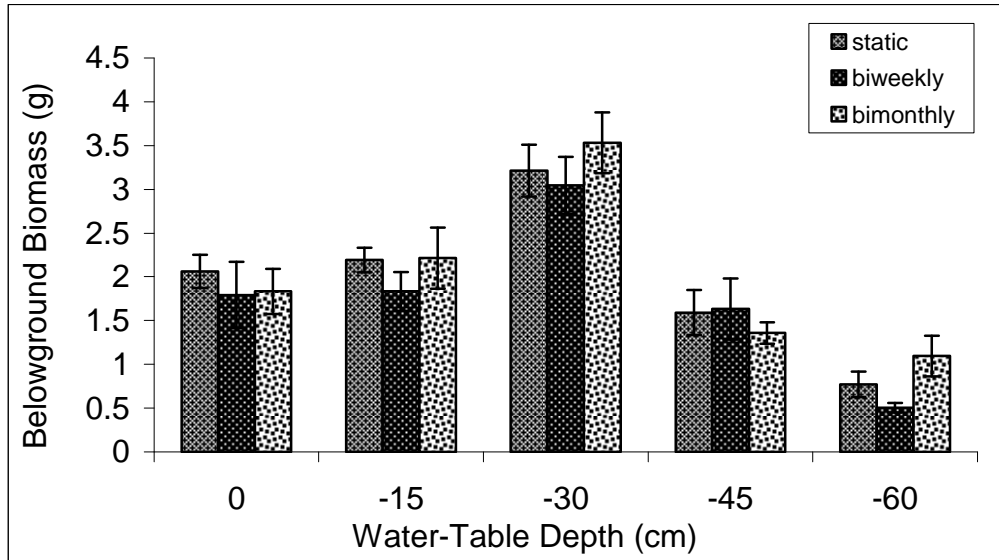


Figure 2.13. Total belowground biomass per 6-month old mangrove seedling (mean \pm 1 SE).

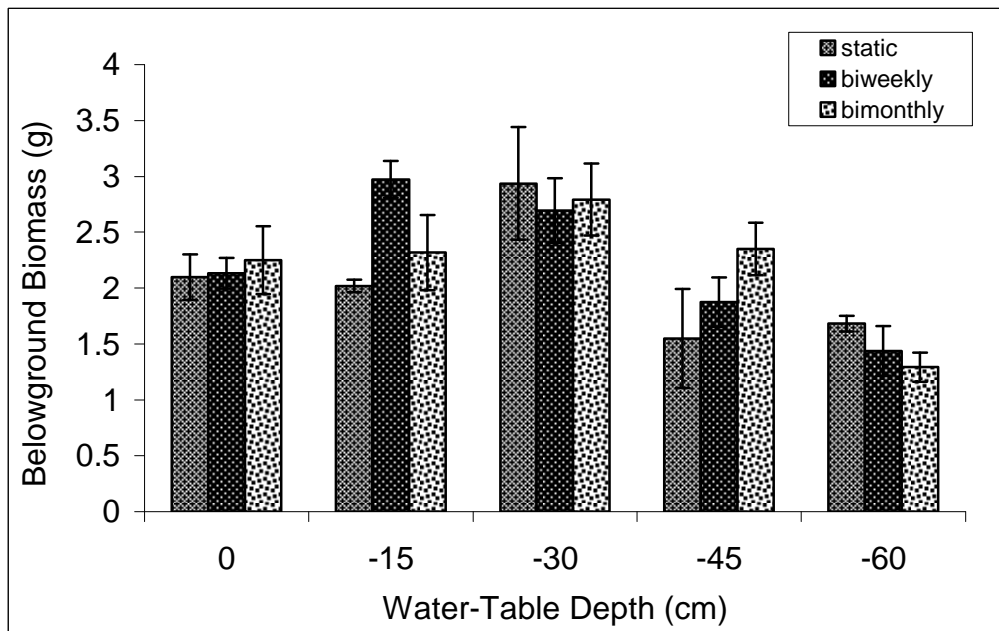


Figure 2.14. Total belowground biomass per 18-month old mangrove seedlings (mean \pm 1 SE).

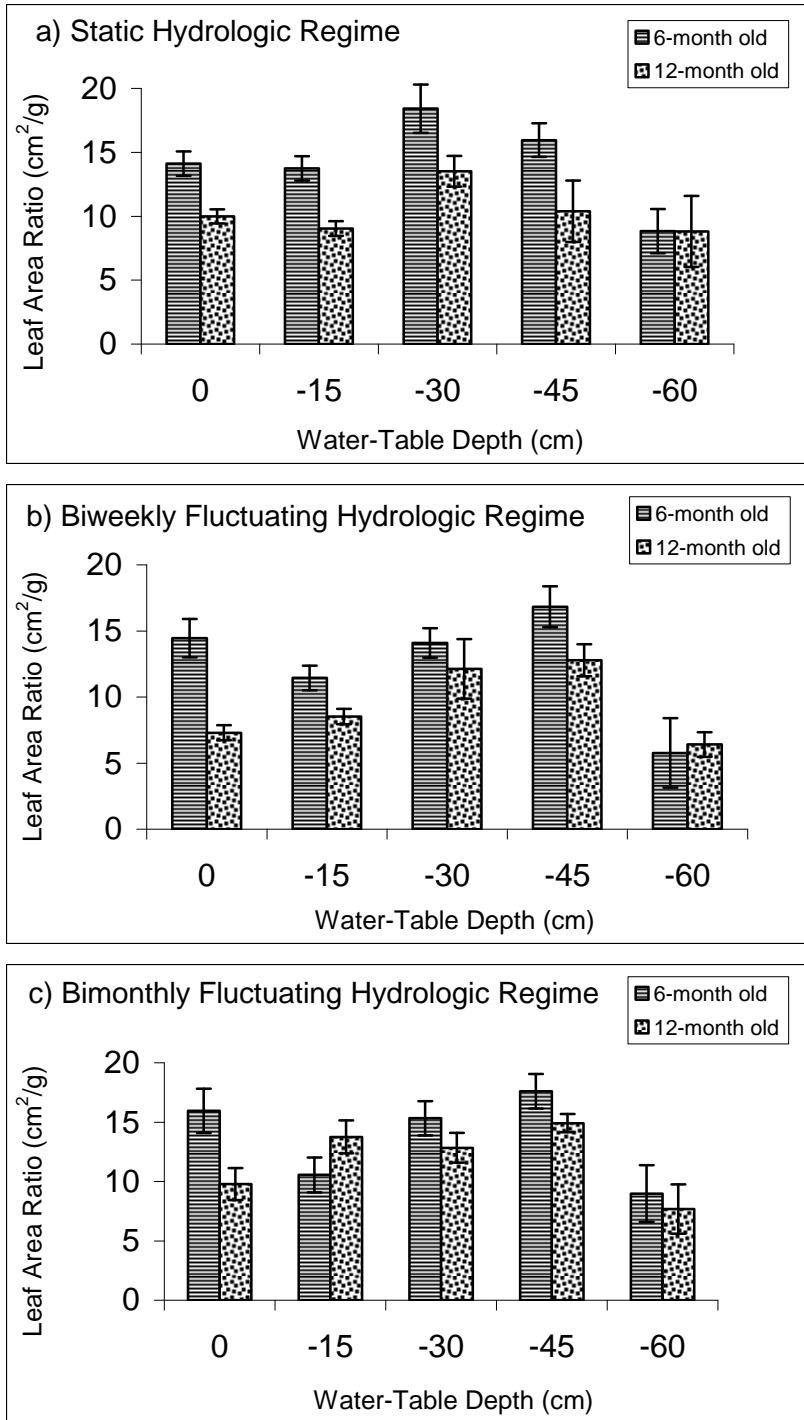


Figure 2.15. Leaf area ratio (LAR) per mangrove seedling (mean \pm 1 SE) as a function of seedling age class, water-table depth, and hydrologic regime (panels). Leaf area ratio = [Total leaf area (cm²) / total seedling biomass (g)].

Table 2.3. Mean rates of net CO₂ assimilation, stomatal conductance, and water-use efficiency measured at mid-study and at the end of the study (mean ± 1 SE).

	Net CO ₂ Assimilation ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	Stomatal Conductance ($\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$)	Water-Use Efficiency
4 months	9.14 ± 0.31	0.20 ± 0.01	54.28 ± 3.94
6 months	9.14 ± 0.29	0.16 ± 0.01	63.27 ± 1.72

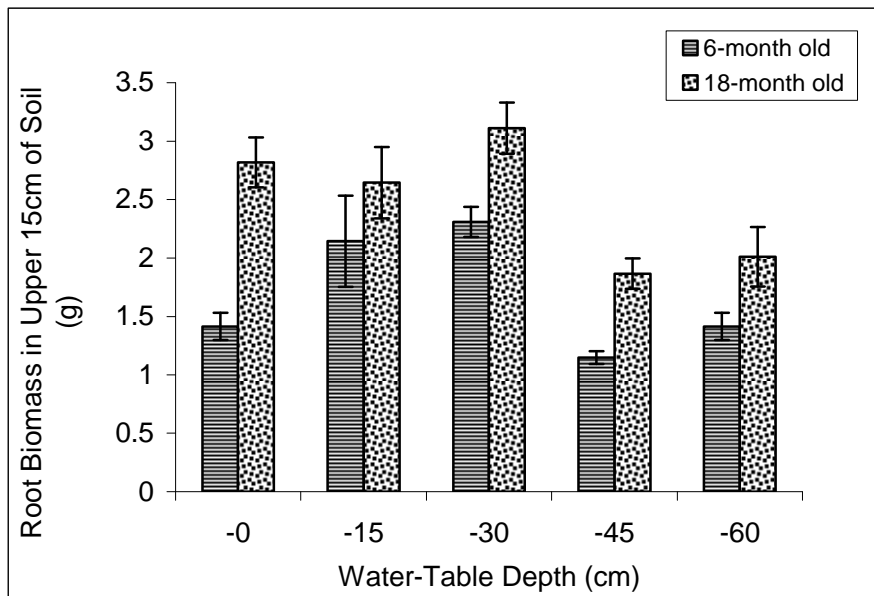


Figure 2.16. Root biomass per mangrove in top 15 cm of soil profile (mean ± 1 SE).

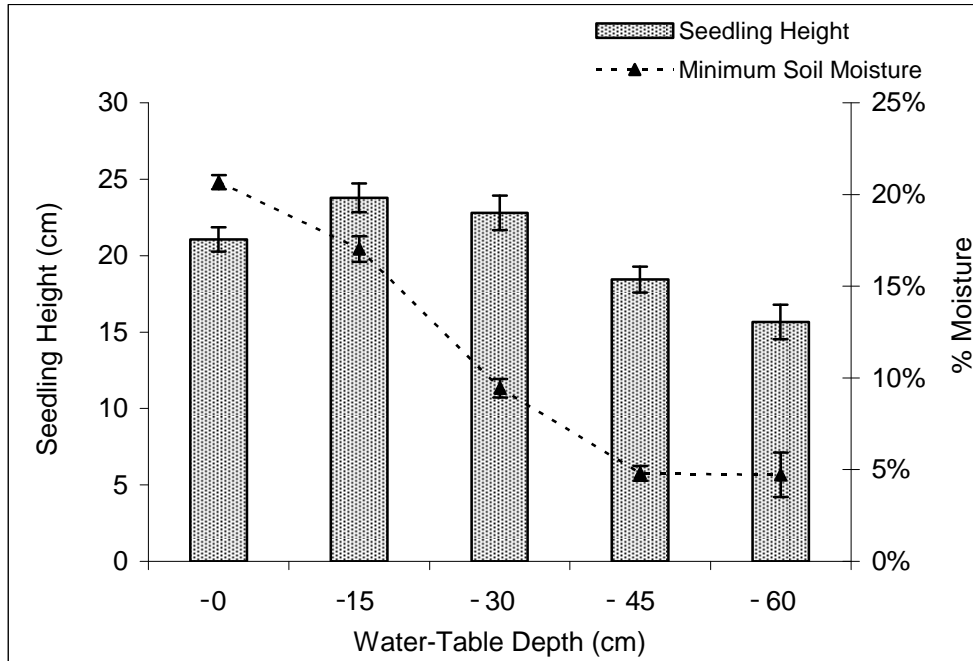


Figure 2.17. Optimal soil moisture for mangrove growth as a function of water-table depth, shown here as the range of average minimum percent soil moisture values of the upper 15 cm of the soil profile (dashed line) and average height per seedling (bars) (means \pm 1 SE). Age class did not significantly affect minimum percent moisture, and as such, seedling heights are averaged between age classes for each water-table depth treatment.

Table 2.4. Moisture extremes of the upper 15 cm of soil profile resulting from the various water-table depths and hydrologic regimes. Minimum percent moisture was collected at the maximum time the water table had “fluctuated” and plants were 15 cm above the midpoint; maximum percent moisture was collected at the maximum time the water table had “fluctuated” and plants were 15 cm below the midpoint. Values are the mean \pm 1 SE.

Water-Table Depth	Minimum % Moisture	Maximum % Moisture
-0 cm	20.67 \pm 0.39	44.95 \pm 2.05
-15 cm	17.03 \pm 0.69	23.72 \pm 1.28
-30 cm	9.44 \pm 0.50	20.27 \pm 0.66
-45 cm	4.8 \pm 0.40	13.57 \pm 0.36
-60 cm	4.72 \pm 1.22	6.7 \pm 0.35

Table 2.5. Repeated-measures analysis of variance (ANOVA) by water-table depth for root biomass and percent moisture (both collected over 15 cm increments). Significant effects highlighted with an asterisk (*).

	Main Effects	Root Biomass		% Moisture	
		F-ratio	p-value	F-ratio	p-value
-0cm	Water-Table Depth	234.277	<0.001*	NA	NA
	Age	32.966	<0.001*	0.983	<0.001*
	Hydrologic Regime	0.183	0.889	6.812	0.006*
-15cm	Water-Table Depth	96.412	<0.001*	23.267	<0.001*
	Age	0.939	0.364	0.847	0.368
	Hydrologic Regime	0.625	0.581	12.232	<0.001*
-30cm	Water-Table Depth	439.051	<0.001*	8.418	0.001*
	Age	17.734	<0.001*	0.694	0.506
	Hydrologic Regime	3.11	0.033*	3.572	0.014*
-45cm	Water-Table Depth	391.389	<0.001*	45.195	<0.001*
	Age	33.672	<0.001*	0.761	0.52
	Hydrologic Regime	0.668	0.606	2.632	0.025*
-60cm	Water-Table Depth	120.037	<0.001*	75.613	<0.001*
	Age	27.146	<0.001*	0.737	0.477
	Hydrologic Regime	1.441	0.261	1.287	0.294

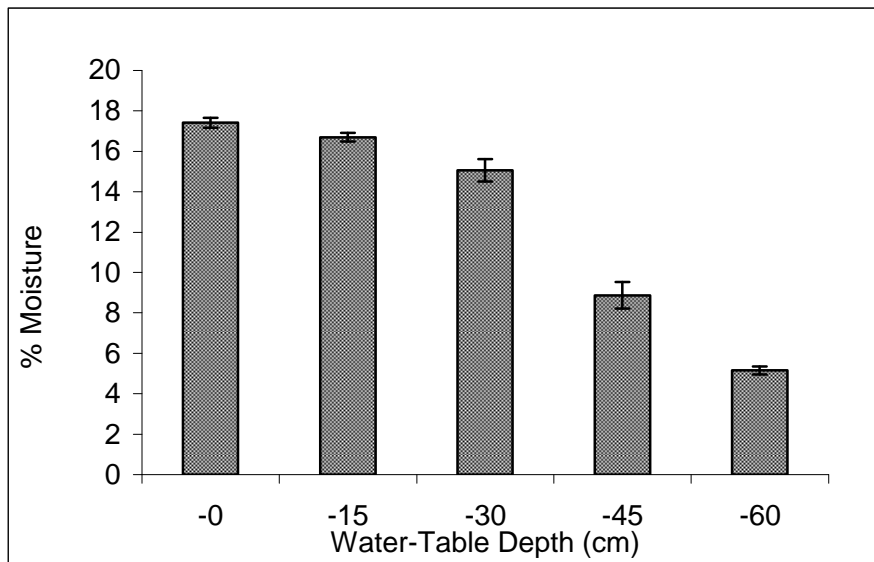


Figure 2.18. Percent moisture in the upper 15 cm of the soil profile at the time of harvest (mean \pm 1 SE).

Discussion

Elevated Salinity Levels

Salt tolerance is one trait that may be displayed by stress-tolerators (Grime 1977), which refers to plants capable of withstanding various environmental stressors, thereby allowing them to grow in specialized niches (Grime 1977; Diaz et al. 2004). Black mangroves are tolerant of high salinity levels; they are in fact the most salt tolerant of the new world mangroves (Patterson and Mendelssohn 1991; Saenger 2002). This is evident not only in their distribution throughout the neotropics, where they typically occur upslope of red mangroves in less frequently flooded substrates that are generally more saline (Chapman 1976; Tomlinson 1986; Imbert et al. 2000), but also in our findings that young seedlings did not die in porewater salinities of 72 ppt. Salt crystals were visible on the leaves by the second week of the study, showing the active excretion of salt by the salt glands in response to increasing concentrations of salt ions in the water. One recognized tradeoff in the tolerance to elevated salinity levels is a slower rate of resource allocation and growth due to added energy expenditure in the production of compatible solutes to lower cytoplasmic water potential (Ball 1996; Lambers et al. 1998; Mitsch and Gosselink 2000). In addition to slow growth rates, salinity stress response can be manifested in the loss of (older) leaves in an attempt to both translocate excess salt ions to expendable tissue (Cram et al. 2002) and minimize leaf area to reduce evapotranspiration (Lambers et al. 1998).

In the current study, ontogenic differences between age classes played a role in the significant differences in above- and belowground biomass, which may be important to wetland managers depending on the goals, timeframe, and budget of the restoration project. Twenty-four month old seedlings had more leaves at the beginning of the study (11.63 +/-1.25) than 12-month old seedlings (8.2 +/-0.5). Initial average height of 24-month olds (21.72 cm +/-1.81) was also greater than 12-month olds (14.68 cm +/-0.78). These age class differences may be important for 24-month old seedlings to be able to capture more light energy (more leaf area), and therefore initially fix more carbon per seedling than 12-month old seedlings, as well as possessing a height advantage in areas that may be subjected to sand burial. At the end of the salinity tolerance experiment, although aboveground biomass of the 24-month old seedlings was greater than the 12-month olds under freshwater conditions (0 ppt), it is important to note that when grown at the 24 ppt salinity level the 12-month old seedlings were able to produce an equivalent amount of aboveground biomass as the 24-month old seedlings. Therefore, at sites not expected to experience hypersaline conditions nor significant sand burial (as discussed below), 12-month old seedlings will likely perform as well as more expensive 24-month old seedlings. Both age classes displayed the greatest number of leaves per seedling when grown under the 24-ppt salinity level, thereby further substantiating that this salinity level is in the optimum range for vigorous black mangrove seedling growth.

When plants experience physiological drought (as may occur with actual drought or the initial phases of salinity stress), photosynthate is often allocated to root growth to increase the ability to uptake fresh water (Ball 1988). Twelve-month old seedlings had the greatest root biomass in 24 ppt in relation to the other salinity levels. Average root-to-shoot ratios for both age classes were lowest at 0 and 24 ppt. In the absence of salt stress, these seedlings increased vegetative growth because water was not limiting and growth rates were maximized. In the salinity levels beyond

those optimal for growth, both age classes displayed increases in root-to-shoot ratios in an apparent attempt to reduce leaf area (reduce transpirational water loss) while increasing allocation to root biomass (increase root surface area for water uptake). This indicates some degree of physiological drought stress; plants allocate more resources to belowground biomass at the expense of aboveground biomass in increasingly saline conditions (Ball 2002).

Sand Burial

Sedimentation is a major process in the mangrove environment (Twilley 1995; Furukawa and Wolanski 1996). Whether along a tidal creek or inland on a barrier island, sediment deposition is an important modulator in dynamic coastal systems (Lee et al. 1996; Ellison 1998). Given the frequency of tropical storms and hurricanes in coastal Louisiana, these events can be major sediment re-distribution events (Turner et al. 2006). Barrier islands are the first land masses to absorb the force of hurricane wind and storm surge, thus, the plant communities that comprise the beach, dune, swale, and backbarrier marsh grow in sediment that is constantly being reworked. In fact, mangroves are well adapted to moderate rates of sedimentation on the magnitude of 10 mm/year (see Ellison 1998 for review). Sediment burial can be differentiated as rapid accretion when it exceeds this rate of deposition. It has been reported that the lethal depth of burial in adult mangroves occurs when sediment covers the pneumatophores, smothering them and preventing the roots from respiring aerobically (Hutchings and Saenger 1987; Terrados et al. 1997; Ellison 1998). Since the development of pneumatophores does not occur until the seedling is mature, and depends to some extent on the degree of soil saturation (Saenger 2002), we investigated the lethal threshold in these younger black mangrove seedlings.

Moderate depths of sand burial did in fact stimulate growth in the first several weeks as the overall growth rates increased until mid-study and were at a maximum up to and around day 26, or ordinal date 87. Interestingly, 6-month old seedlings had a greater combined growth rate in the first 14 days post-burial; their response was more immediate than the 18-month old seedlings. The intrinsic growth rate of an organism may be the single most predictive factor in recovery following disturbance, regardless of the intensity or frequency (Haddad et al. 2008). Black mangrove seedlings, though slow-growing as compared to herbaceous plants, apparently have the capacity to upregulate growth in response to moderate levels of sand burial in an effort to recover. The response of black mangrove seedlings to sediment burial is consistent with other salt marsh plants that are stimulated by moderate sediment burial, such as *Spartina alterniflora* (L.) (Deng 2008) and *Puccinellia maritima* (Langlois et al. 2001). An important finding of our study is that regardless of age class, mortality only occurred once the seedling was completely buried. Therefore, 6-month old seedlings can perform as well or better than 18-month old seedlings when subjected to moderate sand burial events that do not completely bury the seedlings.

Fluctuating Water Table

The hydrology of the mangrove environment is a master environmental driver that modulates the edaphic conditions through the frequency, depth and duration of flooding. The influence of the tides and precipitation are dictated by the elevation of a site, which in turn affects the available moisture, pH, salinity, redox potential, and availability of nutrients and ions present in the soil (McKee 1993). Mangrove restoration projects are most likely to fail when suboptimal substrate

elevations at a site prevent the proper hydrology, and therefore optimal edaphic characteristics, for mangrove growth (Crewz and Lewis 1991; McKee 1993; Turner and Lewis 1997; Platong 1998; Ellison 2000). If the project substrate elevation is not well-suited for mangrove restoration efforts (either too high and hypersaline or too low and waterlogged), the restoration may fail unless other, better-suited species are planted at these suboptimal elevation areas. We strongly recommend adaptive management approaches in the restoration of any coastal ecosystem.

The availability of fresh water to plants on a barrier island is determined by the depth of the freshwater lens that is perched on top of the denser salt water. This freshwater lens is controlled by precipitation and tidal action. Meteorological events and frontal passages can overwhelm astronomical tides, altering the height and duration of normal tidal oscillations and temporally changing the depth from which plants access the fresh water on the barrier island. The amount of stress that a plant undergoes to meet its water demand is further dictated by the elevation at which it is growing. In our current study, we determined that mean water-table depth was a much more important factor in the determination of mangrove growth and biomass allocation than temporal hydrologic fluctuations (of +/- 15 cm) around that mean. Water-table depth significantly affected above- and below-ground biomass, total leaf area, and leaf area ratio. Soil moisture appears to be the driving force resulting in the differences we observed in biomass production, allocation, and physiological response (Table 3.3). Mangrove seedlings of both age classes had the greatest biomass when grown at a -30 cm water table; total, aboveground, and belowground biomass were all reduced in the two shallower water-table depths (0 and -15 cm), as well as in the two deeper water-table depths (-45 and -60 cm). Consistent with other findings of the effects of flooding on black mangrove root allocation (Pezeshki 1997), waterlogged soil did not trigger a response of increased root biomass allocation.

However, our results also appear to indicate that black mangrove seedlings are less robust to soil moisture limitations (drought) than to flooding stress. Average soil moisture in the top 15 cm of the deepest water-table treatment (-60 cm) was less than 10%, and unlike dune species of Louisiana barrier islands such as sea oats (*Uniola paniculata*) that increase root:shoot and rooting depth in drier soil conditions (Hester and Mendelssohn 1989), root biomass and rooting depth were significantly less than the other, shallower water-table depths. The maximum rooting depth that any of the plants reached in the -60 cm water-table depth treatment was -30 cm. In contrast, the maximum rooting depth of plants in the intermediate water-table treatments (-15 and -30 cm) were deeper than -45 cm (i.e., roots actually grew into the water table). Therefore, our results suggest that optimal black mangrove substrate elevation is in the upper-intertidal and high marsh zones, which is congruent with the patterns of black mangrove zonation in Louisiana, Florida, and throughout the neotropics (Chapman 1976; Patterson and Mendelssohn 1991). In this part of their range, black mangroves are located at higher elevations than lower-intertidal species with which they co-occur, such as *Spartina alterniflora* in Louisiana and *Rhizophora mangle* in Florida and the Caribbean (Tomlinson 1986; Ellison and Farnsworth 1993; Patterson et al. 1997).

The effect of soil moisture limitation on seedling leaf number and leaf area was evident in the deepest water-table depth treatments. The leaf area of plants grown at a -60 cm water-table was dramatically reduced in response to the limited water availability. Our measurements of photosynthesis and stomatal conductance were affected by this because in many cases it was not possible to analyze these variables in leaves smaller than 3.0 cm². We measured 46 fewer plants

in the second set of measurements (6 months into the study) than in the first set (4 months) because so many leaves were below this measurement threshold of 3.0 cm² leaf area. Regardless, overall average water-use efficiency in those plants we were able to measure on both occasions was greater by the end of the study, as the prolonged water limitation apparently resulted in an acclimation response of reduced stomatal aperture and hence reduced stomatal conductance and increased water conservation. An important note, as pointed out in a review by Krauss et al. (2008), is that the estimate of water-use efficiency under flooded conditions (and drought) is different under fresh versus saline conditions. Under saline conditions, physiological drought is exacerbated, and the plant may regulate its water-use efficiency accordingly. Age-specific patterns of biomass allocation may also differ under freshwater and salt water flooding (Pezeshki et al. 1990), as energy is required to synthesize osmotic compounds (compatible solutes) within the mangrove to regulate internal water balance under saline conditions (Naidoo 1985). Thus, our estimates of photosynthesis and stomatal conductance likely represent a “best case” scenario for mangrove seedling water-use efficiency and do not include the interaction of flooding and salinity or drought and salinity.

As expected, the effect of seedling age did not contribute to differences in soil moisture. Although the belowground biomass of 18-month old seedlings was significantly greater than that of the 6-month old seedlings, the soil moisture profiles were similar. Soil moisture decreased with distance from the water table. Further, the different hydrologic regimes (fluctuating versus static) did not significantly affect the average soil moisture profiles.

Summary

Advice from practitioners of mangrove ecosystem rehabilitation includes defining the optimal hydrologic regime, describing any “propagule limitation” or barriers to natural dispersal, and integrating the mangroves into the landscape to improve the success of mangrove restoration projects (Lewis 2005). The first step to designing restoration should be elucidating the reasons why black mangroves may not currently occur in certain regions of the southeastern Louisiana salt marsh and barrier island plant communities. Black mangrove propagule production does not appear limiting, although it may be lower in hurricane or other high-disturbance years than in normal years, and so the observed distribution of black mangroves is either due to dispersal limitations, abiotic factors relating to physiological tolerance, or biotic factors/interactions, such as competition.

In Louisiana backbarrier marshes black mangroves often occur in association with smooth cordgrass, *Spartina alterniflora*. Black mangroves have the ability to outcompete this salt marsh sympatric species at elevations that are not permanently flooded (Patterson et al. 1993). They may in fact establish more readily in higher elevation sites if salt-tolerant species like *Sesuvium portulacastrum*, *Batis maritima*, and *Distichlis spicata* are present to act as facilitators to establishment (McKee et al. 2007b; Milbrandt and Tinsley 2006). Other biotic interactions include the potentially devastating effects of propagule herbivory, though in this region of the black mangrove range this is not as prominent as it is elsewhere (see Cannicci et al. 2008 for review).

Our research on elevated salinity level, sand burial, and fluctuating water-table depths has delineated the upper and lower bounds of survival and growth in black mangrove seedlings

ranging from 6 months to 24 months of age. The judicious use of propagules, in conjunction with seedlings, is advisable if we assume that these propagules have the ability to establish within the constraints of the 6-month old seedling tolerances to abiotic factors reviewed in this report. This is a valid assumption, given that black mangrove propagules have long-distance dispersal potential that would not be possible without adequate and efficient internal metabolic regulation (Nettel and Dodd 2007). It has been reported that propagule establishment is compromised only at salinity levels above 75 ppt (McMillan 1971). Propagules are supplied with maternal nutrients and carbohydrates from the maternal plant, and as a primary successional species, propagules are adapted to harsh establishment conditions.

The arrival and establishment of propagules is critical, but the long-term persistence and expansion of a healthy black mangrove population depends on several important factors, including sufficient reproductive output and dispersal of propagules to the area, retention of stranded propagules, and favorable abiotic factors of salinity, sedimentation, and hydrology. Black mangroves represent a key component in barrier island and coastal salt marsh ecosystems throughout their range and are robust to a wide range of environmental conditions. As such, they are a promising facet of barrier and coastal salt marsh restoration in Louisiana. The information provided in this report should facilitate future rehabilitation and management efforts.

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Appendix

Figure A1. Diagrammatic Louisiana Black Mangrove Restoration Template. Abiotic and biotic factors pertinent to restoration success are delineated on the left and right side of the diagram, respectively. Factors outlined in double black box are those that were specifically addressed and quantified in this NOAA CREST report. Factor ranges are provided in Appendix Table A1.

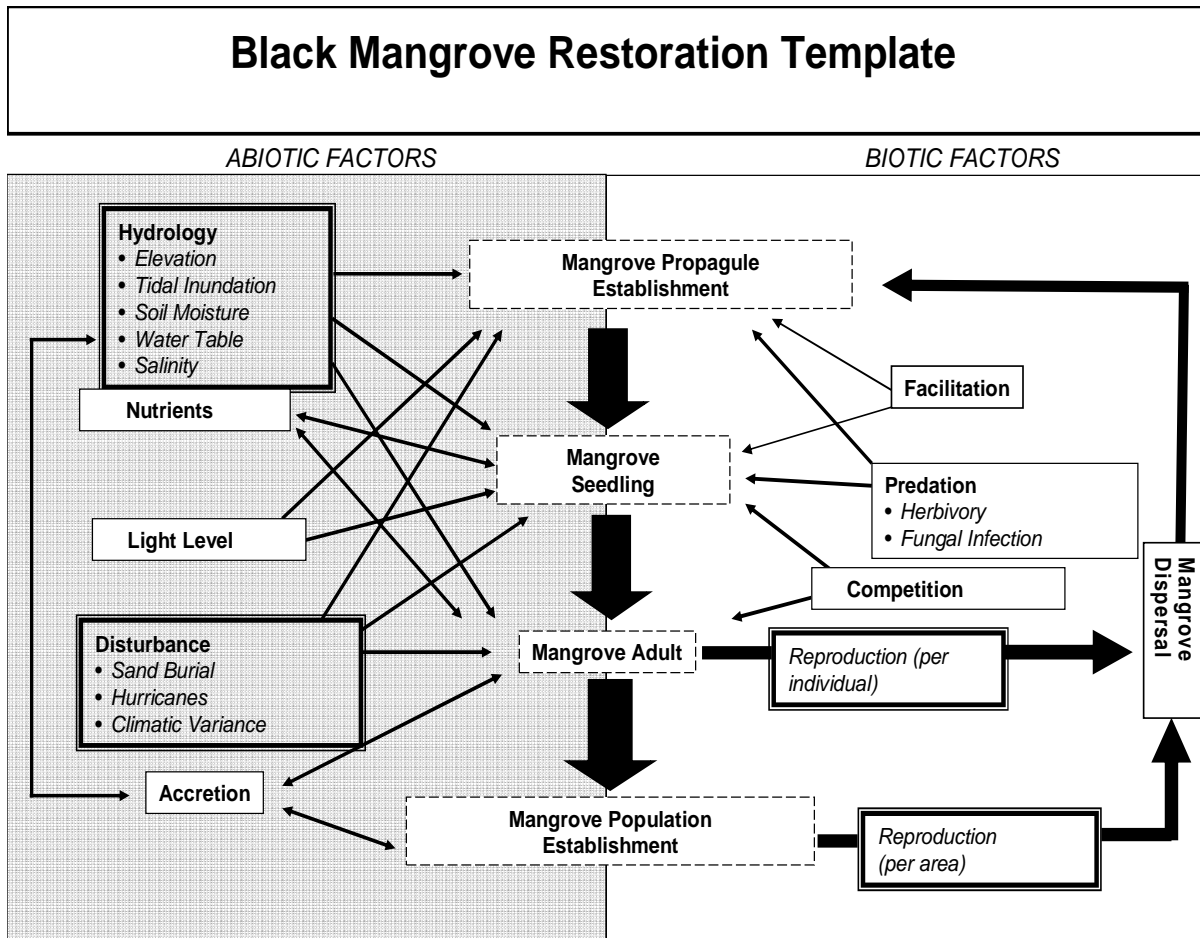


Table A1. Summary of key physiological tolerance ranges utilized in the development and optimization of our Louisiana Black Mangrove Restoration Template. All data presented are the result of NOAA CREST funding. Additional relevant literature from other geographic regions and studies are being compiled as a companion table.

Life History Stage	Environmental Constraint/Factor(s)	Recommendation	Location, Researcher(s), Date
Propagule	Elevation, Flooding	Plant above MHT (elevation > 0.8m MWL). Enclosures may increase establishment at lower elevations by preventing re-dispersal of propagules.	Caminada-Moreau; Hester et al. 2007
	Light Level	60% light transmission is optimal for survival; 20 - 60% transmission optimal for growth.	Caminada-Moreau; Hester et al. 2007
	Potential Propagule Fungal Infestation	Store propagules in salt water. Use of various fungicides often not effective. Evaluate fungal source; often common under winter greenhouse conditions.	Personal observation
Seedling (6, 12, 18, 24-month olds)	Salinity Level	24 – 48 ppt for optimal growth (12-mo old seedlings prefer 24 ppt, 24-mo olds prefer 24 - 48 ppt). Sublethal effects evident above 72 ppt. Lethal at 96 ppt.	Source Population: Caminada-Moreau. Greenhouse study. Hester et al. 2009
	Sand Burial Depth	All seedling age classes can survive a burial event as long as some leaf tissue remains exposed; 5-10 cm sand stimulates burial.	Source Population: Caminada-Moreau. Greenhouse study. Hester et al. 2009
	Hydrologic Regime, Elevation (Water-table depth)	Hydrologic regime (fluctuating, static) has no effect. Elevations between 15-30 cm above the water table best for establishment of 6- and 18-mo old seedlings.	Source population: Caminada-Moreau. Greenhouse study. Hester et al. 2009
Adult Sexual Reproductive Output	Hurricane Disturbance year vs. Normal year	Average propagules/m ² of canopy = 23 to 147 in Hurricane disturbance year. In a non-hurricane year, propagules/m ² of canopy = 163 to 214.	Caminada-Moreau. Hester et al. 2009