Tolerance of *Pinus taeda* and *Pinus serotina* to low salinity and flooding: Implications for equilibrium vegetation dynamics

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Abstract

Questions: 1. Do pine seedlings in estuarine environments display discrete or continuous ranges of physiological tolerance to flooding and salinity? 2. What is the tolerance of *Pinus taeda* and *P. serotina* to low salinity and varying hydrologic conditions? 3. Are the assumptions for ecological equilibrium met for modeling plant community migration in response to sea-level rise?

Location: Albemarle Peninsula, North Carolina, USA.

Methods: *In situ* observations were made to quantify natural pine regeneration and grass cover along a salinity stress gradient (from marsh, dying or dead forest, to healthy forest). A full-factorial greenhouse experiment was set up to investigate mortality and carbon allocation of *Pinus taeda* and *P. serotina* to low-salinity conditions and two hydrology treatments over 6 months. Treatments consisted of freshwater and two salinity levels (4 ppt and 8 ppt) under either permanently flooded or periodically flushed hydrologic conditions.

Results: Natural pine regeneration was common (5-12 seedlings per m^2) in moderate to well-drained soils where salinity concentrations were below ca. 3.5 ppt. Pine regeneration was generally absent in flooded soils, and cumulative mortality was 100% for 4 and 8 ppt salinity levels under flooded conditions in the greenhouse study. Under weekly flushing conditions, mortality was not significantly different between 0 and 4 ppt, confirming field observations. Biomass accumulation was higher for *P. taeda*, but for both pine species, the root to shoot ratio was suppressed under the 8 ppt drained treatment, reflecting increased below-ground stress.

Conclusions: While *Pinus taeda* and *P. serotina* are commonly found in estuarine ecosystems, these species display a range of physiological tolerance to low-salinity conditions. Our results suggest that the rate of forest migration may lag relative to gradual sea-level rise and concomitant alterations in hydrology and salinity. Current bioclimate or landscape simulation models assume discrete thresholds in the range of plant tolerance to stress, especially in coastal environments, and consequently, they may overestimate the rate, extent, and timing of plant community response to sea-level rise.

Keywords: Climate change; North Carolina; Sea-level rise.

Nomenclature: Radford et al. (1968).

Introduction

The ability of plant species to tolerate environmental stress is especially important in coastal and riverine wetlands where gradients in hydrology or salinity determine dominant vegetation patterns (Kozlowski 1997; van Eck et al. 2005). Sea-level rise due to climate change is anticipated to have a strong influence on future vegetation patterns primarily as flooding and salinity increase inland (Church et al. 2001; DeLaune et al. 1987). Predicting the effects of sea-level rise on ecosystem function, structure and composition requires a detailed knowledge of individual species life histories, physiological tolerances, and potential adaptation to environmental stress. While some species may have a narrow range of tolerance to salinity, others may be more tolerant to a range of salt concentrations or have adaptations that enable their survival as conditions change. Field and greenhouse studies can provide a detailed understanding of the salinity and hydrologic regime that salt-marsh and coastal strand species can tolerate (Kozlowski 1997; Kozlowski et al. 2002). However, there is much less known about the tolerance of freshwater plant species that are subject to more subtle gradients of salinity and salt spray. Detailed life history information for estuarine species is needed to fully model the dynamics of vegetation in response to sea-level rise (Shao et al. 1996) and to design restoration strategies that are resilient to global change (Keddy 1999).

In the southeastern United States, the combination of large landscapes with low elevations have created extensive regions vulnerable to inundation (Titus et al. 2001). Coastal North Carolina (USA) has some of the highest rates of sea-level rise globally due to the combination of local isostatic adjustment and eustatic rise contributing to rates of up to 4.3 mm.a^{-1} (Douglas et al. 2002). The dynamics of many ecosystems are frequently modeled based on the assumption that they are in equilibrium with their environment and that their response to constant global change will be gradual, as determined by discrete bioclimatic limits (Guisan et al. 2005). Plant migration and community composition may not necessarily respond

at the same rate as change in the environment, however, due to dispersal limitations, resilience or tolerance to gradual environmental stress, or amelioration of underlying stress by facilitation from other plant species (Araujo et al. 2006; Davis 1989; Gavin et al. 2006). If wetland species are temporarily able to maintain their geographic position in response to gradually changing water tables and soil chemistry, then equilibrium assumptions will need to be re-evaluated to consider these interactions on plant community migration. For example, lenticel development has been observed in some pine seedlings as a mechanism to cope with flooded soils (Kozlowski 1997), resulting in their ability to survive in either hydric or mesic soil conditions. Similarly, woody species adaptations to increased salinity have been observed through either changes in life history strategy (Stanton et al. 2000) or physiological mechanisms such as salt extrusion (Kozlowski 1997) allowing them to survive periodic flooding.

In coastal regions from Virginia to Texas, identified by Titus & Richman (2001) as vulnerable to sea-level rise, *Pinus taeda* and *P. serotina* are ecologically dominant and commercially important (Little 1971; Wahlenberg 1960; Woodwell 1958). Both species are common to forest and woodland communities immediately adjacent to grass-dominated estuarine marshes, with *P. serotina* often dominating on organic peat soils and *P. taeda* more common on mineral soils. These forest communities will be among the first affected by projected sea-level rise and its effects on increasing groundwater tables and soil salinity. Several studies have evaluated the tolerance of these species to sea level-related environmental change, including *P. taeda* seed viability (Johnson et al. 1993), seedling survival (Johnson et al. 1993; Tolliver et al. 1997), and adult phenology or survival (Blood et al. 1991; Conner et al. 2005; Kirwan et al. 2007) to salt-water flooding.

These studies, however, are limited toward understanding current vegetation dynamics as they were conducted at either high salinity levels (10-30 ppt) (Johnson et al. 1993), over short experimental time periods (Johnson et al. 1993; Tolliver et al. 1997), or did not considered periodic flooding (Pezeshki 1992). Few examined conditions directly comparable to those characteristic of micro-tidal, oligohaline estuaries characterized by low salinity, and infrequent flooding that are found around the world (Costa et al. 2003; Moorhead et al. 1995). In addition, experimental and observational data for *P. serotina* are more scarce, with no existing studies for salt tolerance and only one study on flood tolerance (Hunt 1951). The combination of a lack of experimental evidence and treatment factors that, in addition, differ from field conditions, limits our ability to predict plant physiological response to sea-level rise.

We conducted this study to investigate the influence of low-salinity conditions, typical to oligohaline estuaries along the mid-Atlantic coast, on pine survival and growth. We used a combination of field surveys and a greenhouse experiment to investigate the range of salinity and flood tolerances suitable for *P. taeda* and *P. serotina* regeneration. Field conditions were replicated in a greenhouse setting to quantify inter- and intra-specific mortality and carbon allocation to better understand community dynamics and physiological responses to environmental stress. We tested the hypothesis that in field and greenhouse settings, estuarine pine species show tolerance to low levels of salinity and flooding rather than discrete thresholds that restrict their survival.

Methods

Study area

Field surveys were conducted in northeastern North Carolina on the Albemarle Peninsula, a 5000 km[2] low-lying, estuarine landscape surrounded by the Albemarle and Pamlico Sounds (Fig. 1). The Outer Banks Barrier Island chain restricts the exchange of water between the Atlantic Ocean and estuaries creating micro-tidal, low salinity conditions (Moorhead et al. 1995). *Cladium jamaicense* and *Juncus roemerianus*, *Pinus taeda* pocosin and *Pinus serotina* flatwoods are the predominant plant communities (Christensen 2000; Schafale et al. 1990). Fire and hurricanes are frequent, periodic disturbances with fire having substantial impacts on the rates and trajectory of succession (Frost 1995). Ca. 30 - 50% of the land area is below 1 m relative to sea level (Poulter et al. in press) resulting in the development of extensive
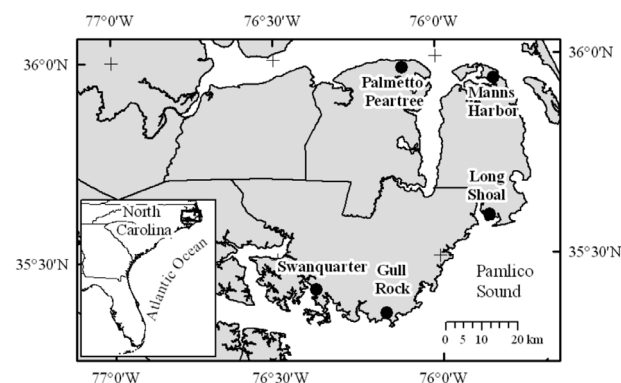

Fig. 1. Location of study area on the Albemarle Peninsula in northeastern North Carolina. Sampling was focused on five replicated transects to quantify natural regeneration of *Pinus taeda* and *P. serotina* across salinity and hydrology gradients dominant in coastal marsh-woodland ecotones.

freshwater peat deposits with high groundwater tables. The climate is 'humid sub-tropical' with a mean annual temperature of 16.6 °C and mean annual precipitation of 1265 mm.a^{-1}. Groundwater salinity is generally low (this study) reflecting the low salinity in the adjacent Sounds (5-15 ppt) (Buzzelli et al. 2003). Groundwater levels are generally at or within 10 cm of the soil surface (this study), are generally anaerobic and highly reduced, as characterized by the gley-soils found throughout the region.

Field surveys

During the winter of 2003, five locations along the shoreline of the Peninsula were selected for vegetation surveys (Fig. 1). At each location, 3 plant communities were identified (marsh, transition or dying forest, and healthy forest) and 7 randomly located 12-m radius plots (450 m^2) per vegetation community were established (however, at two sites, Palmetto Peartree and Long Shoal Marshes, no marsh community plots were established due to logistical problems). In each plot, five smaller, 1-m^2 subplots were surveyed (in each quadrant of the main plot) for natural pine seedling regeneration (< 2.5 cm diameter and < 1.35 m tall) and estimates of grass cover. Within each community, 3 groundwater monitoring wells (PVC-wellscreens) were installed to a depth of 2 m and monitored for water-surface height (relative to the soil surface) and salinity. Specific conductance was measured with a YSI-conductivity probe and converted to salinity units (ppt). Groundwater-well dynamics were monitored monthly for 12 months (June 2003 to June 2004) by manually measuring the difference between the soil surface and water level.

Greenhouse experiment

A full-factorial, randomized block design was established to test the interaction between salinity and hydrology on *P. taeda* and *P. serotina* survival and growth. We established four replicates of each treatment with seven individual seedlings per replicate for both *P. taeda* and *P. serotina*. Three salinity levels corresponding to field values (0, 4, and 8 ppt), and two hydrology treatments (flooded (2 cm above soil surface) and drained (where a container was water-filled once a week with treatment solution and allowed to drain over 5 minutes)). *P. taeda* and *P. serotina* seeds were acquired from the North Carolina Division of Forestry and germinated at the Duke University Greenhouse in January 2004. *P. taeda* seeds were first soaked and stratified in cold storage for 30 days; however pond pine seeds did not require stratification. Seeds were germinated in a Petri dish and were transplanted to individual sand-filled cups (7 cm diameter and 20 cm depth cup) 1 month after germination. Individual cups (14, with 7 individuals per species) were placed in each plastic container (16-l volume). Salinity concentrations were created by mixing Instant Ocean salts (Aqua Craft Incorporated) with tap water. Temperature-corrected conductivity and salinity were also measured to validate the salinity concentration. When the seedlings were three months old, salinity was increased gradually, to 4 ppt in week one and to 8 ppt in week two of the treatment for the higher salinity treatment. Each treatment was replicated 4 times for a total of 24 containers and 336 seedlings. Once each week, survival was noted, and containers were watered with their corresponding salt treatment. After 24 weeks of treatment, the plants were watered for an additional two weeks with freshwater to measure potential recovery. The seedlings were destructively harvested in November, 2004 (seedling age = 10 months) to ascertain below and above-ground biomass (oven-dry weight).

Statistical analysis

Following the field surveys, total natural pine regeneration, and the mean and standard deviation of annual water table height and groundwater salinity was summarized for each plant community. We applied a two-variable changepoint model using a model similar to the Bayesian change point method in Qian et al. (2003) to investigate the interaction between salinity and hydrology on natural pine regeneration across all five sites. Natural pine regeneration was modeled as a Poisson random variable and the expected number of seedlings modeled as a step function of variable z. This variable (z) represents the observed interaction between water table height (cm) and groundwater salinity (ppt). A Markov Chain Monte Carlo (MCMC) method (Qian et al. 2003) was used to estimate $\hat{z}$ and model coefficients. Credible intervals were generated from the results of the MCMC approach.

The greenhouse experiment data were analysed using a multilevel ANOVA model (Gelman 2005; Qian et al. in press). Cumulative mortality (as a probability), total above and below-ground biomass, and root to shoot ratio were used as response variables. Treatment, species, and block were used as covariates to explain variation in the selected responses. An interaction term between treatment and species was also evaluated (but was not significant for any response). The multilevel ANOVA approach uses Bayesian analysis (MCMC) to calculate variance partitioning rather than sum of squares (Qian et al. in press). *Post-hoc* multiple comparisons are investigated by graphically comparing the estimated effects and their 95% credible intervals represented by an error bar (see Fig. 4). When the two intervals do not overlap, the

effects are significantly different at $\alpha = 0.05$ (see Qian & Shen (in press), online Supplementary Materials). In the same figure, the overall mean is referenced as the 0 line (the vertical gray line at 0 in Fig. 4a). When the treatment effect 95% credible interval does not include 0, we can confidently conclude that the effect is larger (or smaller) than the overall mean.

Results

Natural pine regeneration

The density of pine seedlings ranged from 0 to 12 individuals/m^2 across all sites, with an average 2.7 individuals/m^2. Average annual groundwater salinity ranged from 0 to 5.2 ppt (Fig. 2a), with lower values during the winter when evapotranspiration was low and higher precipitation diluted the groundwater. Pine seedlings were most frequent where groundwater salinity was less than ca. 3.5 ppt, however, low levels of regeneration were recorded up to 5.2 ppt. There was high variability in the relationship between salinity and pine regeneration, with regeneration not always present in what would be considered freshwater sites. The lack of regeneration at the freshwater sites corresponded to higher water table levels (Fig. 2b) where, in general, permanently flooded soils prevented pine seedling establishment. The interaction between salinity and height of the water table was more important than each factor alone (Fig. 2c) with the changepoint model identifying a salinity threshold of ca. 5 ppt at low water-table levels and 0 ppt at higher (saturated) water-table levels.

Greenhouse results

The cumulative probability of mortality after 6 months of treatment (when the seedlings were 8-9 months old) ranged between 3.5% to 100% depending on salinity and flooding combination (Fig. 3). No post-treatment recovery of seedlings was observed during the two-week freshwater amendment. There was no significant dif-
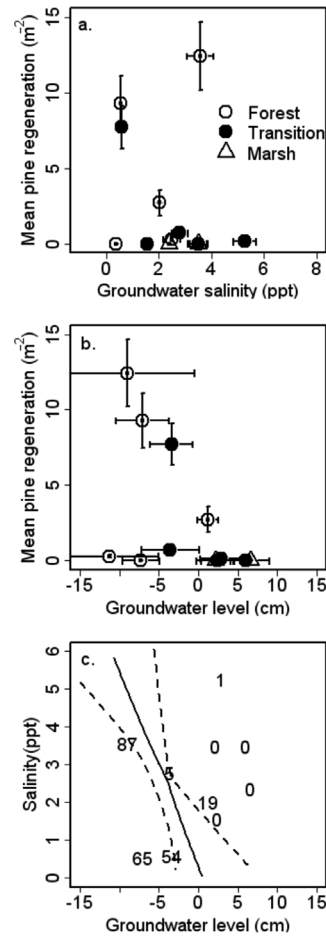

Fig. 2.a. Natural pine regeneration in the field was not observed above salinity concentrations greater than 4 ppt. **b.** When water was consistently above the soil surface, pine regeneration was unsuccessful. Natural pine regeneration was abundant at low salinity concentrations in soils with relatively low water tables (**c**), flooded soils, even with low salinity, contained or harbored no observations of natural pine regeneration. The number indicates the number of seedlings observed in the field surveys.
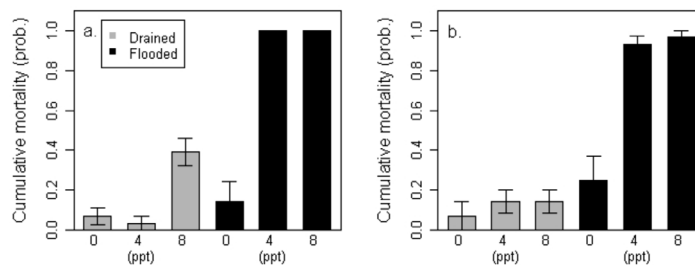

Fig. 3. Cumulative probability of mortality at the end of the greenhouse experiment for *Pinus taeda* (**a**) and *P. serotina* (**b**). Error bars represent standard error and letters indicate statistically significant differences, with the same letter indicating no difference.
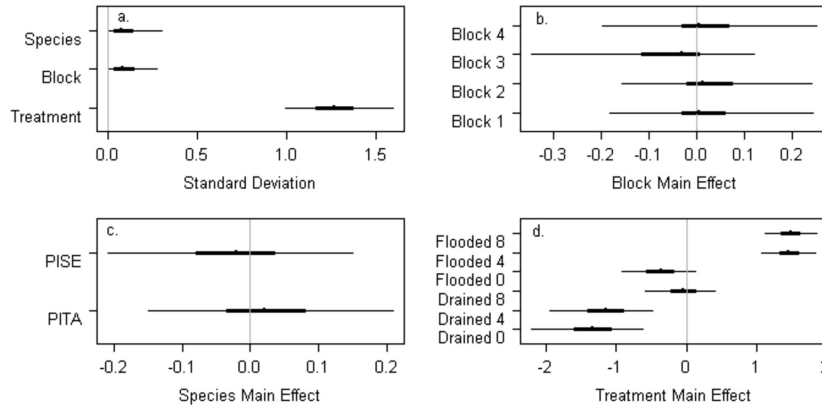
Fig. 4. Summary plot for main effects (**a**) and covariates – block effects) (**b**), species effects (**c**), and treatment effects (**d**). The covariate plots (**b**, **c**, **d**) compare each treatment effect to the overall mean. The thin horizontal line represents the 95% credible intervals, when these do not overlap, then the effect is significantly different at ($\alpha = 0.05$). The thin vertical line at $y = 0$ is used to identify the direction of the covariate influence relative to the overall mean. For example, the main effect Treatment (**a**) explains the majority of the variability in the model, no Block or Species differences exist, but the Flooded 8 and 4 ppt treatments are significantly different to the rest of the Treatments.

ference in mortality between *P. taeda* and *P. serotina* for any of the treatments (Table 1). There were, however, significant treatment differences for mortality, total biomass and the root to shoot ratio. Both flooded salinity treatments (4 and 8 ppt) resulted in 100% mortality after approximately 2.5 months (temporal data not shown), while mortality averaged around 10% for the drained salinity treatments for both species (Fig. 3). Freshwater flooding did not significantly increase mortality for either species, and the level of mortality was statistically similar between freshwater flooded and the drained freshwater treatment.

Total seedling biomass ranged between 0.1 to 3.8 g (dry weight) although mean biomass by treatment was lower (0.1 to 1.78 g). Treatment and species had significant effects on total biomass (Table 1) with salinity and freshwater flooding both decreasing biomass. Pond pine had consistently lower biomass than *P. taeda* for all treatments (Fig. 5). However, no species differences were observed for the root to shoot ratio, and belowground biomass allocation was suppressed by salinity and freshwater flooding (Table 1).

Discussion

Observed range of salinity and flood tolerance

Our field observations revealed that *Pinus taeda* and *P. serotina* were able to establish and survive in salinity conditions up to 5 ppt in semi-flooded to well-drained soils. These results are supported by similar studies investigating woody species tolerance to low salinity levels (Conner et al. 1997) but are the first such data for pond pine. As the field surveys did not consider the potential effects of interspecific competition from grasses on pine regeneration, our results may represent a conservative estimate (or over-estimate, if facilitation is significant) of the ability of the pine species studied here to regenerate under saline conditions. Our field observations were confirmed by the greenhouse experiment demonstrating that both pine species were able to tolerate weekly flushing of low-salinity water representing the irregular, wind-driven flooding typical to the Albemarle and Pamlico estuaries (Moorhead et al. 1995). The tolerance displayed by *P. taeda* and *P. serotina* to low-salinity conditions is consistent

Table 1. Results from multilevel ANOVA model. A negative sign indicates that the effect resulted in a significant ($\alpha = 0.05$) decrease in the response variable, a positive sign resulted in an increase in the response variable. If a treatment effect did not cause any difference from the mean conditions, it was indicated by n.s. For the flooded 4 and 8 ppt treatments, mortality was 100% and no measurements were made for biomass and root to shoot ratio.

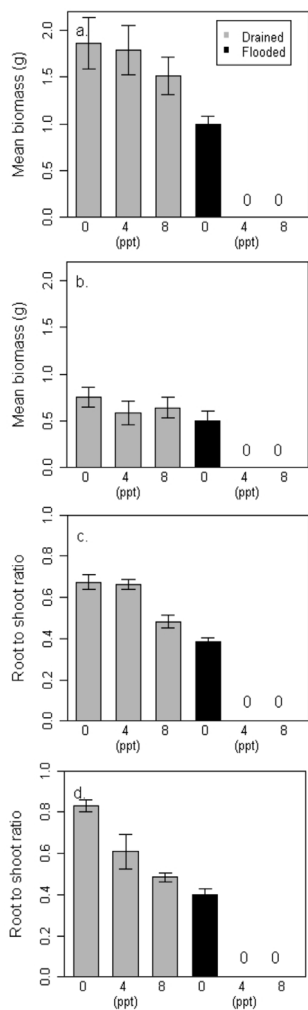|	Response variable treatment effect (relative to mean experiment effect)							
	Drained (ppt)			Flooded (ppt)			Species effect	
	0	4	8	0	4	8	*P. taeda*	*P. serotina*
Cumulative mortality	-	-	n.s.	n.s.	+	+	n.s	n.s
Total biomass	+	n.s.	n.s.	-	no data	no data	+	-
Root to shoot ratio	+	+	-	-	no data	no data	n.s	n.s

Fig. 5. Total biomass response for *Pinus taeda* (**a**) and *P. serotina* (**b**), and root to shoot ratio for *P. taeda* (**c**) and *P. serotina* (**d**). Cumulative mortality for the 4 and 8 ppt flooded treatments was 100%, consequently, no end of experiment biomass data were analysed. Error bars represent standard error.

for both species although as expected, this pattern was more marked for pond pine (an ombrotrophic wetland species) than for *P. taeda*. This growth response was most likely due to decreased conductance and its effects on photosynthesis. The flooding treatment (0 ppt) also caused a decrease in total biomass for both species, similar to other studies that have shown negative effects on conductance from saturated soils (Kozlowski 2002; McLeod et al. 1996; Pezeshki et al. 1996, 1999. Both pine species in this study have shown physiological adaptations to water-logged soils that involve the development of lenticels (Kozlowski 1997), and it appears that in our study, while permanently flooded soils affected growth rates, this did not significantly affect mortality.

Regardless of salinity and flooding treatment, no species differences were observed between *P. taeda* and *P. serotina* mortality. Previous work on *P. taeda* and *P. serotina* (Hunt 1951) also found no species difference in mortality for flood tolerance. Total *Pinus serotina* biomass was lower than *P. taeda*, however, confirming differential rates of carbon accumulation between the species, with *P. taeda* generally faster growing and more tolerant of low levels of salinity. The salinity and flooding treatments also caused a significant shift in carbon allocation away from the roots to the stem. Increased below-ground stress from salinity and flooding – or possibly from a reduction in stress from excess water availability (Megonigal et al. 1992) – are plausible causes of differential biomass allocation across treatment.

Implications for equilibrium responses to gradual environmental change

The geographic distribution of a species has long been observed by a wide range of environmental conditions rather than by discrete boundaries (Whittaker 1956). This concept has important implications for modeling species response to global change, especially when species tolerance and adaptation to stress are poorly understood and where stress gradients occur across small spatial scales. We show that pine seedlings are able to establish and survive within a range of low-salinity conditions in well-drained soils contrary to the notion that discrete salinity boundaries result in either marsh or forest communities (Park et al. 1988). Under the environmental conditions experienced in Albemarle and Pamlico Sounds, pine regeneration and forest survival may continue, despite gradually rising sea level, due to physiological tolerance to low salinity levels. Additional field evidence for pine tolerance to periodic low-salinity flooding comes from observations of hurricane related storm surge events, where, for example, Hurricane Isabel (in 2003) was associated with a storm surge that flooded much of the southern and eastern edges of the Albemarle Peninsula.

with observations of long-term vegetation dynamics on the Peninsula from aerial photographs that suggest the geographic position of treeline has been relatively stable in undisturbed areas since 1932 in spite of an ca. 20 cm rise in sea level over this period (Poulter 2005).

Woody species response to salinity is wide ranging and can change based on the life-history phase of a plant; seedlings are generally more sensitive to salinity while adults may show a wider range of tolerance (Kirwan et al. 2007; Kozlowski 1997). Most commonly, physiological responses include a decrease in conductance resulting from lower osmotic potential resulting in a decrease in photosynthesis and growth rates (McLeod et al. 1996; Willis et al. 2004). We observed significantly lower biomass for the drained 4 and 8 ppt salinity treatments

Most of the observed tree mortality from Isabel at the study sites was from wind damage, and very little mortality was symptomatic of salt-damage (pers. observ.).

Landscape simulation models typically use empirically-derived (or estimated) discrete thresholds for plant species tolerance to salinity and flooding (Park et al. 1988; Reyes et al. 2000; Shao et al. 1996). These modeling approaches will inevitably result in gradual shifts in plant community zonation if the forcing from environmental change occurs gradually, as is the case with sea-level rise (Church et al. 2001). For example, Shao et al. (1996) and Park et al. (1988) classify pine forest as intolerant (or a 0 ppt threshold) to salinity from salt spray or hydrology, in contrast to our experimental and field observations that suggest an upper limit between 3-5 ppt depending on flood duration. Furthermore, experimental research by Williams et al. (1998) show that resprouting strategies may increase the success of regeneration of freshwater species located in areas periodically flooded by salt water. The combination of physiological tolerance and life history strategies suggests that thresholds and bioclimate approaches (that often underestimate potential species ranges by quantifying *realized* rather than *fundamental* niche (Guisan et al. 2005)) may fail to recognize important mechanisms inherent to plant community resilience and environmental change.

In general, the sharp boundaries between marsh and woodland communities in coastal wetlands has created the impression that the range of freshwater-species tolerance to environmental stress is small, and that gradually changing salinity and hydrology will lead to gradual plant community migration. However, in the wetlands we studied, low salinity shoreline gradients create conditions whereby estuarine species may tolerate gradually changing water chemistry, resulting in rates of forest migration lower than predicted by current models. Equilibrium assumptions are valuable tools for investigating the statistical relationship between species or plant communities and climate (Guisan et al. 2000), but recent research has questioned the validity of the assumptions underlying equilibrium models (Pearson et al. 2003) suggesting that mechanistic approaches that incorporate species physiology directly may be more suitable for predicting potential species range or fundamental niche (Guisan et al. 2005; Hickler et al. 2004; Hijmans et al. 2006). This study suggests that equilibrium dynamics at the local-scale may be less important in certain coastal wetlands than previously considered given the range of physiological responses to salinity and flooding that we observed. As a result of pine species tolerance to low-salinity and flooding forest migration may lag gradual sea level rise in flat terrain, and occur at a later stage when physiological limits are reached.

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