Chapter 4: Freshwater Forested Wetlands and Global Climate Change

by

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Abstract: Sea-level rise is likely to cause both direct and indirect effects on forested wetlands, and both types of potential impacts were investigated. The direct effects of increased flood durations and salinity levels were assessed through a series of experiments on 10 major wetland tree and shrub species. Results of this work showed that certain species and groups of species (e.g., the bottomland oaks) are highly susceptible to the combination of flooding and salinity stress. Other species, such as baldcypress, are more tolerant, but they, too, will not survive long in salinity much greater than 1/6 the concentration of seawater. Indirect effects that were found to be potentially important include an increase in the level of defoliation by the fruittree leafroller, an insect already causing significant damage to baldcypress in southern Louisiana and a possible increase in the distribution and abundance of Chinese tallow, a highly invasive exotic tree species that was found to be tolerant to combined salinity and flooding stresses during simulated storm surges. In addition to providing information needed for predicting the likely impacts of sea-level rise, the results of this research also point to promising management responses. One possibility, for example, is to make use of the high level of variation in salt tolerance found in baldcypress by developing planting material capable of surviving on sites with elevated soil salinity levels. Such an approach, ideally combined with at least partial restoration of original hydrologic regimes, may provide a powerful tool for managers interested in restoration of degraded coastal wetlands.

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Study Areas

Research on the effects of global climate change on freshwater forested wetlands focused primarily on the northern Gulf of Mexico coast. In this region, several hundred thousand hectares of forested wetlands occur within the coastal zone and at low elevations—often less than 2 m above mean sea level (Salinas et al. 1986; DeLaune et al. 1987). Forested wetlands at such low elevations and so close to the coast are believed to be among those most at risk from short-term changes in climate. Furthermore, many of these forests are already threatened by factors similar in some respects to those that may result from global change, such as alterations in hydrology and saltwater intrusion (Fig. 4-1). The northern gulf coast, and southern Louisiana in particular, therefore offered the prospects of a grand "natural experiment" on the potential impacts of global climate change. Additional work was carried out in coastal South Carolina, where saltwater intrusion is also a problem and major hurricanes may have profound effects on coastal wetlands.

Plant Community Types Studied

Wharton et al. (1982) classified southeastern forested wetlands into 75 community types, including red maple, Atlantic white cedar, and cypress-tupelo swamps; pocosins; hydric hammocks; and Carolina bays. Evaluating the potential impacts of global change on all these types of forested wetlands was not feasible. We decided to focus most of our research on cypress-tupelo swamps because of their extent within the coastal zone, ecological and economic importance, and potential for global change-related losses. Some additional work was carried out on important species found in bottomland hardwood wetland types that occur in the immediate vicinity of cypress-tupelo swamps.

Cypress-tupelo swamps, which are dominated by baldcypress (*Taxodium distichum* var. *distichum*), water tupelo (*Nyssa aquatica*) and/or swamp tupelo (*Nyssa biflora*) occur along nearly all the major rivers flowing into the northern Gulf of Mexico and along the Atlantic coast from Florida to Maryland (Larsen 1980). There are approximately 650,000 ha of cypress-tupelo swamps within the Coastal Plain Province of the south-central United States (McWilliams and Rosson 1990) and at least 160,000 ha within the coastal zone of southern Louisiana (Salinas et al. 1986).

Cypress-tupelo swamps are important in part because they perform many of the same functions as terrestrial forests, such as providing nesting sites, feeding areas, and travel corridors for numerous species of migratory birds. In southern Louisiana, they are frequently used as nesting sites for colonies of wading birds (Keller et al. 1984) and are where 93% of bald eagle nests were found in a survey (Harris et al. 1987). Because of their linkages to both upland and aquatic habitats, they also perform functions that distinguish them from upland forests, such as providing shelter for juvenile fish and exporting organic matter

Figure 4-1. Louisiana gulf coast forests currently experiencing increased flooding or saltwater intrusion or both. Source: Modified from Pezeshki et al. 1990.

directly to adjacent estuaries (Wharton et al. 1982; Mitsch and Gosselink 1993).

Cypress-tupelo swamps are freshwater ecosystems, with salinity levels generally less than 0.5 ppt. In some coastal swamps, however, changes in hydrology and sedimentation have resulted in elevated salinity levels. In areas where salinity levels remain above 2 to 3 ppt for much of the growing season, many trees die or show signs of severe stress (Wicker et al. 1981).

Research Focus

The integrating element of all our research on freshwater forested wetlands was the potential impacts of sea-level rise. The most direct effects of sea-level rise are believed to be increases in flooding of coastal wetlands and increases in salinity levels of soil and surface water. Most of the research was therefore aimed at elucidating the effects of these stressors on some of the major tree species found in cypress-tupelo swamps. Another global change factor believed to be important is increased intensity and/or frequency of hurricanes and other large storms (Emmanuel 1987). Consequently, the potential impacts of storm surges (i.e., large pulses of salt water) were also investigated.

Additionally, the direct effects of flooding and salinity appear highly likely to result in a number of indirect effects on cypress-tupelo communities, such as changes in patterns of herbivory, the possible rise in importance of exotic species, and changes in plant species composition due to differences in tolerance and competitive ability under altered site conditions. While the indirect effects were evaluated to a substantially lesser degree than the direct effects of sea-level rise, some of our research does have implications for understanding these effects.

Direct Effects of Sea-level Rise

Determining the effects of salinity and flooding on major cypress-tupelo swamp tree species was the main goal of two major studies. One study evaluated species-level responses of 10 species and the other focused on intraspecific variation in responses of one particularly important species (baldcypress).

Species-level Responses to Flooding and Salinity

Species-level responses were evaluated primarily through a series of experiments on the effects of flooding alone, salinity alone, and combinations of the two stressors (Conner 1995). Specifically, the experiments were designed to determine the impact of flooding and salinity on survival, growth, and biomass allocation of seedlings of major canopy and subcanopy species, and the impact of simulated storm surges on seedlings of major species. Additional research on the physiological responses of the seedlings, although not funded directly by the U.S. Geological Survey Biological Resources Division, was carried out in cooperation with scientists from the University of Georgia's Savannah River Ecology Laboratory. Results of that work are highlighted in the accompanying box, *Ecophysiological Responses to Flooding and Salinity.*

Experiments on seedling response to various treatment combinations of flooding and salinity were conducted in each of 3 years, with different species being evaluated during each year. Species included in the study were baldcypress, water tupelo, black tupelo (*Nyssa sylvatica* var. *sylvatica*), green ash (*Fraxinus pennsylvanica*), Chinese tallow (*Sapium sebiferum*), buttonbush (*Cephalanthus occidentalis*), Nuttall oak (*Quercus texana*), swamp chestnut oak (*Q. michauxii*), overcup oak (*Q. lyrata*), and water oak (*Q. nigra*). Most of the experiments were conducted over the latter half of one growing season by using seedlings growing in small plastic pots.

These experiments clearly demonstrated that substantial differences in tolerance to flooding and salinity stress exist among species. All four species of oaks, for example, were found to be highly sensitive to flooding with even low level (2 ppt) salinity (Conner et al. 1998). Swamp chestnut oak and water oak showed signs of stress (e.g., leaf necrosis or loss, tip dieback) when flooded with 2 ppt water for only one week. After 11 weeks, both species had 100% mortality. Nuttall oak and overcup oak did not show signs of stress until weeks 7 and 9, respectively, but all of these seedlings were also dead by the end of the 5-month experiment. Seedlings of all the oak species died within 7 weeks of flooding with 6 ppt water (Conner et al. 1998).

In contrast, baldcypress, water tupelo, and Chinese tallow had high survival rates and good growth when flooded with low salinity water (Fig. 4-2). When flooded with 2 ppt water, all three species had 100% survival and height growth that was not significantly different than that for seedlings flooded with fresh water and tended to have only slightly reduced diameter growth (Conner 1994, 1995; McLeod et al. 1996; Conner et al. 1997; see box).

In general, these experiments suggest that species already well adapted to long flood durations handle the additional stress of low-level salinity better than species somewhat less tolerant to flood. Species such as buttonbush, baldcypress, and water tupelo were among those least affected by flooding with 2 ppt water (Conner 1994; McCarron et al. 1998). This pattern was less clear when trees were flooded with higher salinity water or when the extremely rapid increase in salinity associated with some hurricanes was simulated. Chinese tallow, for example, was found to be more tolerant of these treatments than baldcypress and water tupelo, which are both more flood tolerant than Chinese tallow (see section on "Potential for Invasion of Chinese Tallow").

Based on the results of the 3 years of experiments, a general classification of tolerance to salinity can now be

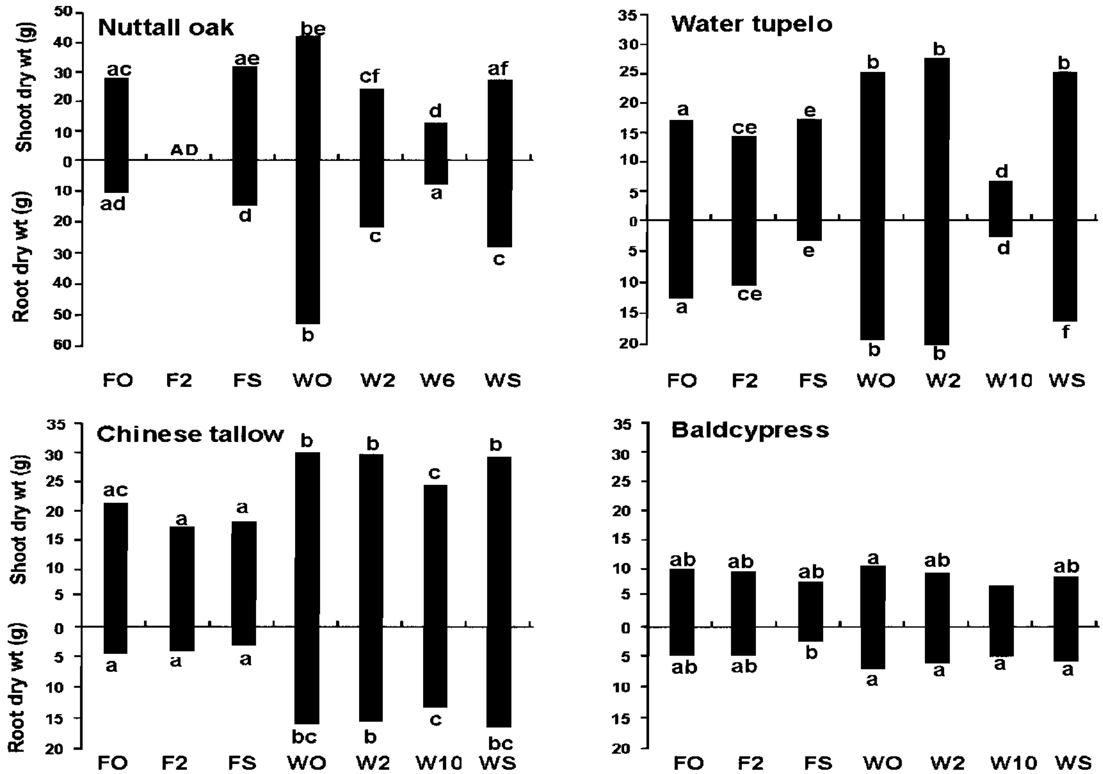

Figure 4-2. Effects of flooding and salinity on shoot and root biomass of Nuttall oak, baldcypress, water tupelo, and Chinese tallow (±SE). F indicates flooded (water levels were maintained at about 5 cm above the soil surface), and W indicates well-watered (seedlings were watered regularly but without flooding or saturating the soil). F0 = flooded with 0 ppt water, F2 = flooded with 2 ppt water, FS = surged with 32 ppt water, W0 = watered with 0 ppt water, W2 = watered with 2 ppt water, W6 = watered with 6 ppt water, W10 = watered with 10 ppt water, WS = surged with 32 ppt water; and AD = all dead, no measurements taken. Unlike letters indicate statistical differences at 5% level for treatments by seedlings. Source: Conner 1995.

developed (Table 4-1). Also, existing rankings of flood tolerance, which are often based on limited or anecdotal evidence, can be supported by more quantitative evidence.

These experiments have substantially improved our ability to rank tolerance and better predict the impacts of saltwater intrusion. In addition, they have provided new insight into how responses to events such as hurricanes may vary depending on site conditions just prior to an event. For example, the effects of a storm surge may be less severe in cases where the soil is already saturated and more severe when the soil is initially well drained. In experiments involving the responses of baldcypress seedlings of differing ages to simulated storm surges, trees showed stress much more quickly and showed less indication of recovery when the soil was well drained prior to surging. Salinity levels in saturated soils do not become as elevated initially and drop to tolerable levels faster following a surge than they do in well-drained soils (Fig. 4-3).

Intraspecific Variation in Responses to Flooding and Salinity

Knowledge of species-level responses is crucial for predicting global change-related impacts on the extent, structure, and function of forested wetlands. There may be situations, however, where it is equally important to understand how responses to flooding and salinity vary within a species. Substantial variation in tolerance to saltwater intrusion within a species may mean that the species will be able to respond to altered conditions more effectively. Also, the existence of such variation might have important implications for the development of management responses to saltwater intrusion.

Ecophysiological Responses to Flooding and Salinity

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Measurement of the physiological activity of plants can provide early information about a specific stress response before it is apparent in leaf morphology or biomass. These measurements may be more revealing than traditional evaluation tools, but they must be interpreted carefully since a single physiological process must be considered within the larger context of how that process affects growth and survival. With any variable used to detect stress, multiple aspects may need to be considered. Of interest is the initial response(s) to the stress, but probably of greater importance is the long-term response (e.g., if photosynthesis is reduced, is the reduction proportionate to the length of time the plant is exposed to the stress, or does recovery occur?).

Seedlings of 10 woody species demonstrated several response patterns based on their initial and long-term reactions to freshwater flooding in laboratory experiments. Baldcypress and buttonbush showed neither an initial reduction in photosynthesis nor any long-term impact. Water tupelo and green ash showed a significant initial reduction in photosynthesis but no cumulative effect over time. Both of these groups would survive long-term exposure to this particular stress. For a third group of species (overcup oak, water oak, Nuttall oak, and Chinese tallow, photosynthesis was not reduced until 2 weeks after the initiation of the flooding. This impact increased with length of exposure. Finally, a fourth response type was observed in black gum and swamp chestnut oak; photosynthesis was initially reduced with an increasing impact over time. Since photosynthesis was increasingly impacted over time in both of the two latter groups, these species are not adapted to flooding and would eventually perish if the stress continued.

As the salinity of the floodwater increased to 2 ppt, as might occur when sea level rises and floods coastal areas, the respective tolerances among the species did not differ greatly, but photosynthesis was reduced in all species. Again, baldcypress showed no significant initial reduction in photosynthesis, but by 4 weeks a significant reduction in photosynthesis was observed. Photosynthesis of buttonbush was similar to that of water tupelo and green ash with significant initial reduction and no cumulative effect over time. The response of the other six species to flooding with brackish water was similar to that of freshwater flooding, but with a greater reduction in photosynthesis and, ultimately, mortality of all individuals of these six species.

In conditions similar to those observed during hurricane storm surges (i.e., high salinity of short duration), photosynthesis of all 10 woody species was severely reduced. Buttonbush was the least impacted species but was only slightly more resistant than black gum, baldcypress, water tupelo, Chinese tallow, or green ash, all of which were still surviving several weeks after the simulated storm surge. The four oak species had severely reduced photosynthesis and all died within 2 weeks of the stress.

As flooding of coastal areas increases because of sea-level rise, photosynthesis will be affected differently in these species based primarily on their flood tolerances, even if the floodwater is of low salinity (2 ppt). This finding suggests that the flooding associated with sea-level rise is more important than small increases in salinity, while large increases in salinity will be very harmful to all of these species.

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Table 4-1. Flood and salinity tolerance rankings for tree species investigated by Conner (1995).

		Salinity tolerance	
Species	**Flood tolerance**[1]	**Low-level+flooding**[2]	**Storm surge**[3]
Baldcypress	Most tolerant	Tolerant	Moderately tolerant
Water tupelo	Most tolerant	Weakly tolerant	Moderately tolerant
Buttonbush	Most tolerant	Weakly tolerant	Moderately tolerant
Black tupelo	Most tolerant	Intolerant	Moderately tolerant
Chinese tallow	Tolerant	Intolerant	Moderately tolerant
Overcup oak	Tolerant	Intolerant	Intolerant
Green ash	Moderately tolerant	Weakly tolerant	Moderately tolerant
Nuttall oak	Moderately tolerant	Intolerant	Intolerant
Water oak	Weakly to moderately tolerant	Intolerant	Intolerant
Swamp chestnut oak	Weakly tolerant	Intolerant	Intolerant

[1] Based on rankings by McKnight et al. 1981 and Hook 1984, except for Chinese tallow.
[2] Based on responses to flooding with 2 ppt water, such as may occur during early stages of saltwater intrusion.
[3] Based on responses to simulated storm surge treatments during flooding, such as may occur as a result of hurricanes.

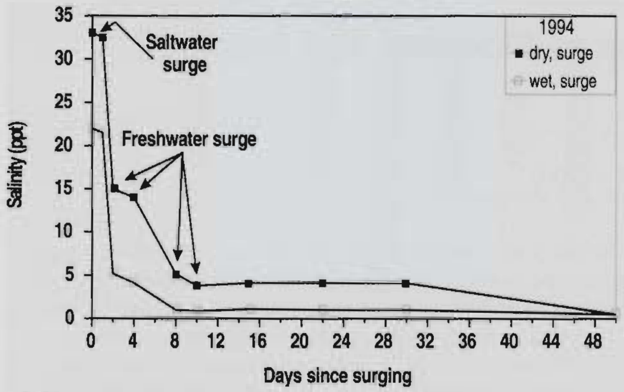

Figure 4-3. Salinity levels in surge tanks after flooding with saltwater and subsequent freshwater additions (the "storm surge" treatment referred to in the text). Source: Conner 1995.

Figure 4-4. Saltwater-intrusion-affected swamp in St. Bernard Parish, Louisiana, with one living, apparently healthy baldcypress. Photo credit: J.A. Allen, U.S. Geological Survey.

Anecdotal evidence and personal observations provided good reason to believe that baldcypress was a species with considerable intraspecific variation in salt tolerance. Pezeshki et al. (1990) indicated the existence of stands and individual baldcypresses that were apparently salt tolerant. Also, in some southern Louisiana baldcypress stands where most trees have succumbed to saltwater intrusion, some individuals are still apparently thriving (Fig. 4-4). Since this work was initiated, evidence of variation in salt tolerance has also been supported by a greenhouse trial (Javanshir and Ewel 1993) and field observations in North Carolina (Yanosky et al. 1995).

The first phase in this study was a search for living baldcypress trees found in habitats with elevated salinity levels. The coastal zone of southeastern Louisiana (from the Mississippi line to the east levee of the Atchafalaya River) was searched by using light aircraft, boats, and ground observations. A portion of Mobile Bay, Alabama, was also searched. Trees were selected primarily based on the salinity level of surface water where they were found and secondarily on their form. Many trees that were apparently salt-tolerant were found during the course of the search, including several growing in areas where the surface water salinities ranged from 6 to 8 ppt (Allen et al. 1994).

Seed was collected from 10 of these trees and, for comparison, from five baldcypress trees growing in areas not subject to saltwater intrusion. Seedlings were then produced from each of the parent trees. The seedlings from each parent tree are hereafter referred to as "families" (more technically they are "open-pollinated families," since the source of the pollen was not controlled and therefore only one parent is known). Seedlings from each of the 15 families were subjected to flooding with water of salinity levels ranging from 0 to 8 ppt, and their survival, growth, and physiological performance were monitored.

The results of this study demonstrated that there is indeed statistically significant variation in salt tolerance within the baldcypress species (Allen 1994). Tolerance was assessed in a number of ways, including the ability to survive under elevated salinity levels, the ability to maintain healthy leaves, and through the use of indices combining various responses. One such index, referred to as the Potential Survival Index or PSI, was based on survival and leaf area at the two highest salinity levels (6 and 8 ppt) relative to the survival and leaf area at the two lowest salinity levels (0 and 2 ppt). The PSI was devised to assess future survival by combining first-year survival with a measure believed to be indicative of the likelihood of future survival (amount of leaf area remaining at the end of the first growing season).

The calculated PSI values ranged from 106 to 2,941 units (Table 4-2), suggesting a wide range in apparent tolerance to salinity among the 15 families. The overall mean

Table 4-2. Potential Survival Index (PSI) by family.

Family	PSI	Rank
Brackish sources		
CB2	720	6
CB3	2941	1
FA1	651	7
FA2	2042	2
FA3	2027	3
FA4	646	8
PB1	295	13
SG2	1177	5
VE2	1572	4
VE3	429	11
Mean	1250	
Freshwater sources		
BO2	106	14
LS1	464	9
PR1	337	12
SW1	464	9
SW2	439	10
Mean	362	
Overall mean	954	

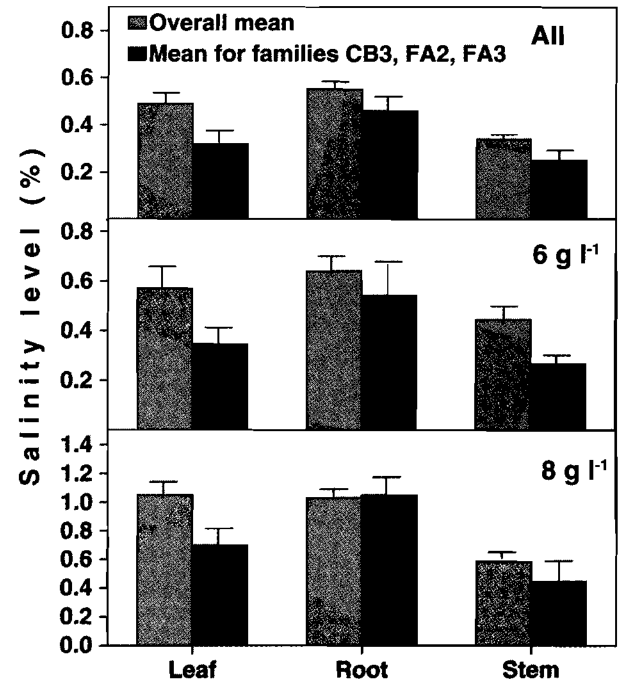

Figure 4-5. Means by tissue type and salinity level for sodium concentrations for all 15 families and for the most salt-tolerant families CB3, FA2, and FA3. Source: Allen 1994.

PSI for the 10 families from sites with elevated salinity levels was about 3.5 times higher than the mean for the 5 families from totally freshwater locations. All of the most highly tolerant families came from parent trees located on saline sites, as might be expected if salt tolerance is a genetically controlled and therefore heritable characteristic.

Physiological responses evaluated in this study included net photosynthesis and stomatal conductance, leaf water potential, chlorophyll fluorescence, and ion accumulation in leaf, stem, and root tissue. Statistically significant variation among families was found for most of these response variables, but overall there was little apparent relationship between physiological performance and the various measures of salt tolerance (Allen et al. 1997). The exception was in the accumulation of sodium (Na^+) and chlorine (Cl^-) ions in shoot (stem and leaf) tissue, which was found to have moderately strong negative correlations with PSI. The tolerant families had lower concentrations of sodium when averaged across all salinity levels, and the differences were even more pronounced when the means were compared at the highest salinity levels (Allen et al. 1997; Fig. 4-5). High concentrations of sodium and chlorine in leaf tissue may cause water stress, ion toxicity or imbalances, and hormonal imbalances (Greenway and Munns 1980; Poljakoff-Mayber 1988), so the ability to exclude these ions from leaf tissue is probably the most critical difference between the most tolerant families and the more salt-sensitive families.

Beginning late in 1995, a follow-up study on intraspecific variation in salt tolerance of baldcypress was initiated. This new study contained four components: a physiology experiment designed to evaluate short-term responses to a rapid saltwater influx; an evaluation of intraspecific variation in germination of baldcypress seed under different levels of soil salinity; a determination of intraspecific growth variation in the root elongation of baldcypress under several salinity regimes; and an evaluation of intraspecific variation in survival and growth in the field along a salinity gradient.

Results of the first, and subsequent, components of this study provide further evidence of significant intraspecific variation in salt tolerance of baldcypress. Four open-pollinated families were subjected to rapid influxes of saline water (4 and 6 ppt), and gas exchange and water potential responses were measured. Two of the families, both of which exhibited relatively high salt tolerance in the earlier study (Allen 1994; Allen et al. 1994), were able to maintain significantly higher stomatal conductance and transpiration rates than the other two families (Krauss et al. 1996).

In the second study, seed germination of eight families of baldcypress were evaluated within a controlled environment. Seeds were sown in soil saturated with water from four different salinity concentrations (0, 2, 4, and 6 ppt) and monitored over 65 days for successful germination. Not only was intraspecific variation significant (Fig. 4-6), but also three families from brackish-water sources, with a combined mean germination capacity of 22.3% across all salinity concentrations, tended to have higher germination relative to the two freshwater checks, which averaged 11.6% germination capacity (Krauss et al. 1998). Germination trials offer a cost-effective means of screening large numbers of baldcypress genotypes for potential salt tolerance.

Root growth response to flooding and salinity often varies considerably from shoot growth response. As a result, the third study evaluated the intraspecific variation in root elongation of five baldcypress families at three concentrations of floodwater salinity (0, 4, and 6 ppt). Although root growth from all families was impacted negatively by an increase in floodwater salinity, certain families had a greater degree of root elongation than others tested (Krauss et al., 1999a). Once again, although confounded slightly by the performance of one family at 6 ppt, seedlings from brackish-water sources experienced greater root elongation than seedlings from freshwater sources when evaluated across all three salinity concentrations. Genotypes of baldcypress with greater root growth may experience better survival as well as positive biomass increment in salt-impacted wetlands.

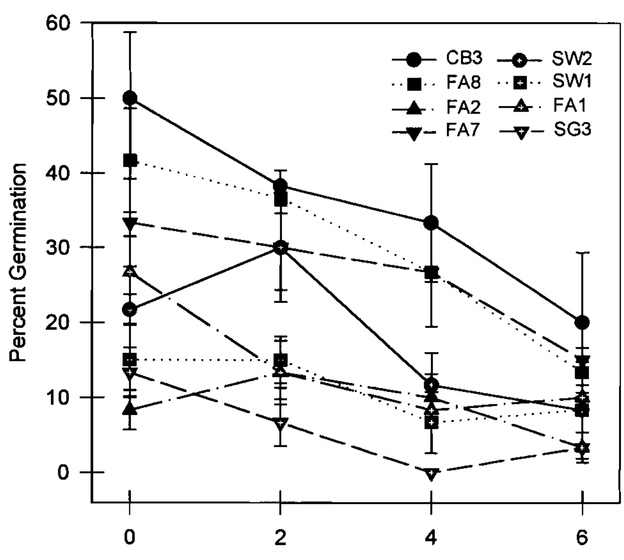

Figure 4-6. Intraspecific variation in baldcypress seed germination at four soil salinity concentrations. Families SW1 and SW2 represent the two freshwater source collections. Source: after Krauss et al. 1998 (permission to reproduce granted to authors by Kluwer Academic Publishers, Inc.).

The final study in the series of four involved a field trial, or provenance test, to evaluate the feasibility of using controlled environment experiments as a mechanism for salt tolerance screening. Three plantations, containing seedlings from 10 families, were established on sites impacted by saltwater intrusion in southeastern Louisiana. Survival, growth, and tissue ion concentrations were monitored through one growing season. Although intraspecific variation in survival was not significant, variation did exist for height, diameter, and volume growth increment (Krauss 1997). In addition, families exhibited differential abilities to exclude Cl^- or take up K^+ and $Ca2^+$ at salinities as high as 4 ppt, which may give some insight into mechanisms of salt tolerance in baldcypress (Krauss et al. 1999b).

Indirect Responses to Sea-level Rise

Relationship of Flooding to Insect Herbivory on Baldcypress

Since 1983, widespread defoliation of baldcypress has occurred in southern Louisiana each spring. The cause of this defoliation was determined to be feeding by larvae of the fruittree leafroller (*Archips argyrospila*), a wide-ranging species of moth native to the United States (Goyer et al. 1990; Fig. 4-7). The fruittree leafroller is a close relative of the spruce budworm (*Archips fumiferana*) (Goyer et al. 1990), one of the most economically destructive insect pests in North American forests. Although well known as a pest in orchards, the fruittree leafroller had not been previously reported to affect baldcypress. There is, however, consistent host-related behavioral as well as genetic differences in the moths affecting baldcypress (Goyer et al. 1995).

The first recorded infestation of the fruittree leafroller on baldcypress was in the Atchafalaya Basin, primarily in a three parish area southwest of Baton Rouge. Defoliation appeared to be most extensive in areas with permanent or near-permanent flooding (Goyer and Chambers 1997), suggesting that the existing defoliation problem may become more severe if sea-level rise results in greater areas of baldcypress being exposed to increases in flood duration.

Given the already serious nature of the problem and the prospects for its being compounded by sea-level rise, a study was developed to delineate the extent of defoliation of baldcypress by the fruittree leafroller and broadly categorize the levels of defoliation within the affected areas, assess potential impacts on natural regeneration by comparing defoliation on mature trees to that on immature trees, and contrast defoliation levels and refoliation rates under different flooding regimes (permanently flooded, seasonally flooded, and nonflooded).

Aerial surveys conducted annually since 1984 addressed the first objective (Fig. 4-8). In recent years, approximately 125,000 ha were defoliated to the extent as to cause significant growth loss. These numbers are dramatically higher than

Figure 4-7. Full-grown fruittree leafroller caterpillars on baldcypress foliage. Photo credit: R.A. Goyer, Louisiana State University.

in the mid-1980's (Fig. 4-8). The aerial surveys also clearly documented an eastward expansion of the annual defoliation, to the point where it reached the outskirts of New Orleans (Fig. 4-9) and now affects the Lake Pontchartrain Basin. Because the basin contains very extensive stands of baldcypress that are already under stress from a variety of human-induced alterations in hydrology and saltwater intrusion (Pezeshki et al. 1990), the potential for damage caused by severe levels of defoliation seems high.

The work on defoliation of mature and immature trees demonstrated that small and/or suppressed trees were most frequently and severely defoliated by the fruittree leafroller. The effect of repeated defoliation also appears to be more severe on these trees, which were found to have high levels of branch mortality and a reduced capacity to refoliate and recover from repeated defoliation (Table 4-3). In addition, over a 6-year period, 28% of these small trees growing in open patches died. These results suggest potentially critical effects of the fruittree leafroller on future natural or artificial regeneration of baldcypress.

While there was an indication of increased levels of defoliation in areas concurrent with increased flooding, there was little difference between sites flooded permanently and those seasonally flooded (Fig. 4-10). Also, there was no difference in observed amounts of refoliation that could be attributed to differences in flooding regime (Goyer and Chambers 1997). Growth, however, of baldcypress was significantly less in defoliated/flooded areas than in areas not defoliated and/or not flooded (Fig. 4-11).

Potential for Invasion of Chinese Tallow

A number of experiments on two native species, baldcypress and water tupelo, and one exotic species, Chinese tallow, showed that Chinese tallow had greater tolerance to some stresses associated with sea-level rise. Chinese tallow is already a common invader of forested wetlands in coastal regions of the Southeast and may be poised to become even more prominent in areas undergoing stress due to rising sea level or storm surges.

In one experiment, seedlings of three species—baldcypress, water tupelo, and Chinese tallow—were subjected to flooding with saline (10 ppt) water. After 6 weeks, Chinese tallow showed no signs of stress, while 90% of the water tupelo and 60% of the baldcypress had dead tops (McLeod et al. 1996; Conner et al. 1997).

In a simulated storm surge experiment with baldcypress and Chinese tallow, nearly 100% of the seedlings exhibited signs of stress within 4 weeks, but all survived until the end of the growing season. However, there were pronounced differences in ability to fully recover from this stress. After seedlings exposed to the simulated storm surge in late September overwintered in their tanks (with a

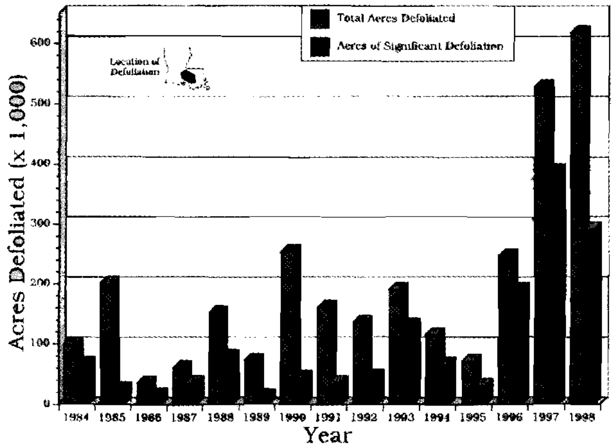

Figure 4-8. Amount of defoliation (acres) by fruittree leafroller. Source: Goyer, unpublished data.

Table 4-3. Annual dieback (%) of understory baldcypress saplings <10 cm diameter in open patches. Southern Louisiana 1992-97[a] (means only).

Year	Mean % (n=50)	Number dead
1992	31.0	0
1993	39.9	0
1994	46.0	2
1995	55.4[b]	4
1997	65.5[b]	13
Change (%)	34.3[b]	28.3

[a] Each year all saplings were 80-100% defoliated by fruittree leafroller.
[b] Dead trees removed from calculations.

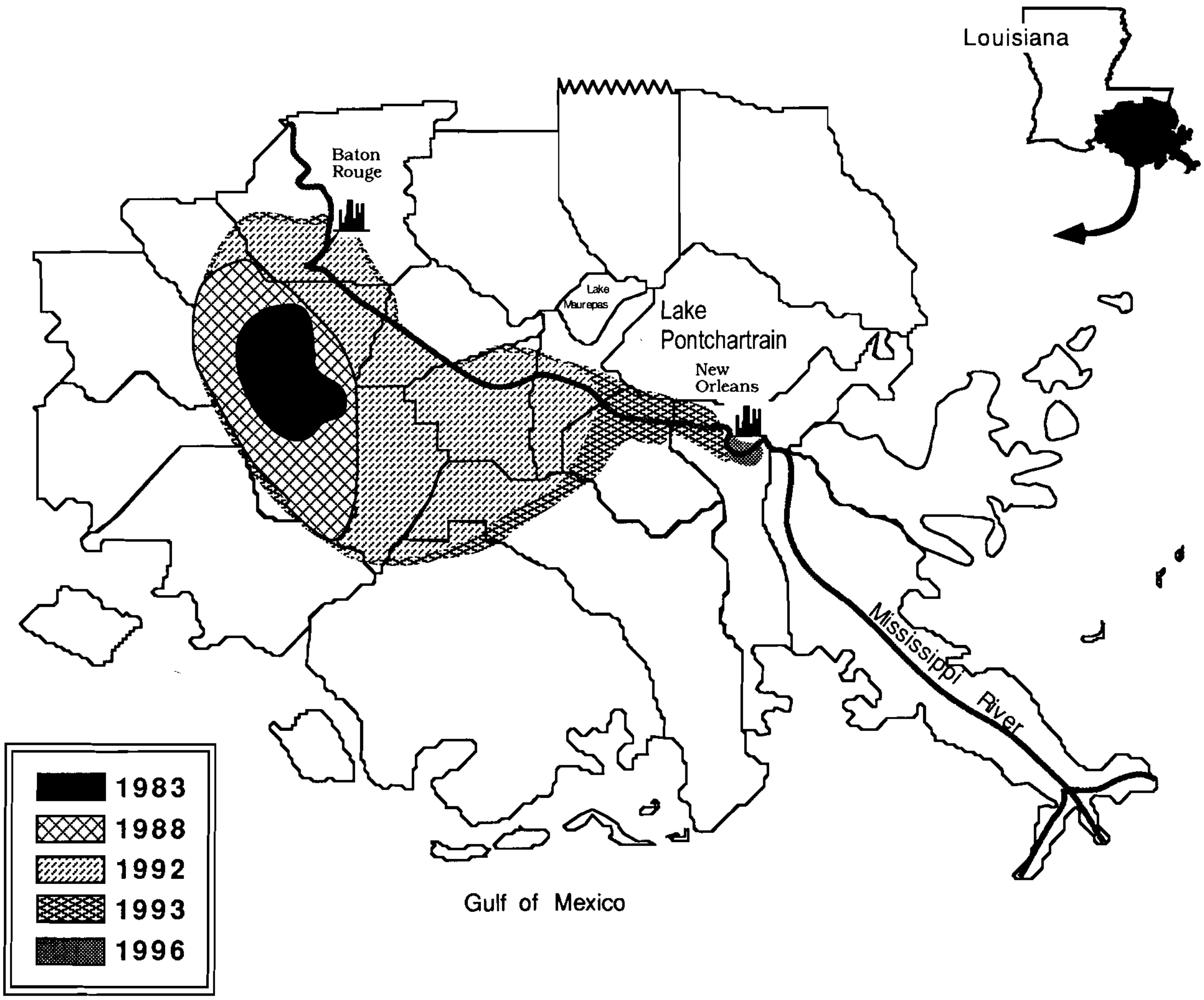

Figure 4-9. Extent of fruittree leafroller defoliation in 1983, 1988, 1992, 1993, and 1996. Source: Goyer, unpublished data.

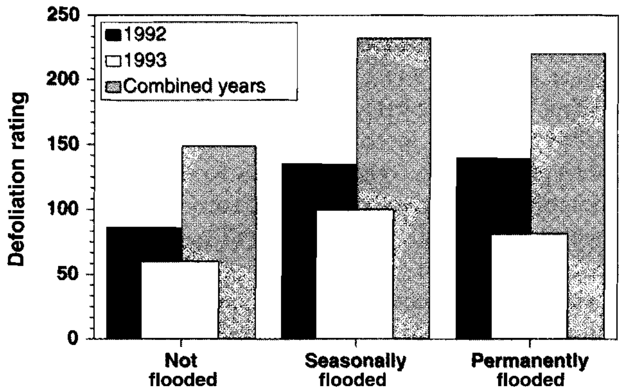

Figure 4-10. Baldcypress defoliation rating for three hydrological regimes, Bayou Chevreuil, Louisiana. Source: Goyer and Chambers 1997.

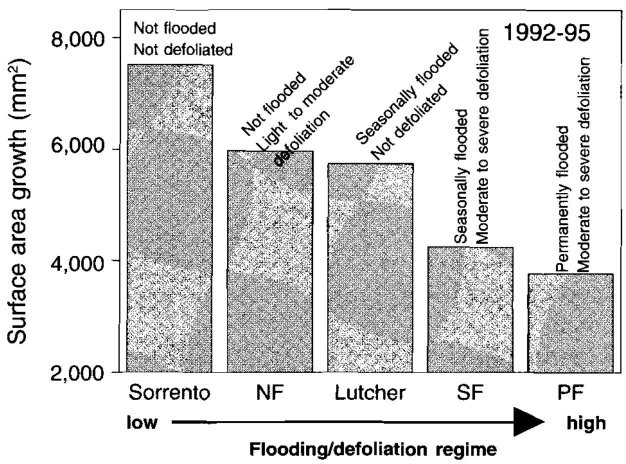

Figure 4-11. Surface area growth of baldcypress as influenced by flooding and insect herbivory (after data from Goyer 1996; Table 4-3).

residual tankwater salinity level of 2.5 ppt, down from an initial high of 21 ppt), clear differences were seen between the two species. Only one-third of the baldcypress seedlings survived to the next spring, and those that did survive had dead tops, with sprouting occurring at the water line. On the other hand, all but two of the Chinese tallow survived and resprouted the following spring with only partial top dieback (Conner et al. 1997).

Implications

Potential Species Responses to Sea-level Rise

The uncertainty surrounding the specific effects of global climate change presents a significant challenge to scientists concerned with their potential impacts on coastal wetland habitats. A major goal of the research on coastal freshwater forested wetlands, therefore, was to develop information on the potential responses of key tree species to a range of different conditions. As a result, the implications of a range of global climate change scenarios can be evaluated.

It is possible, for example, that sea-level rise will result in a gradual increase in flooding and/or salinity in coastal forested wetlands. The results of the work described herein suggest that some types of forested wetlands, especially those dominated by baldcypress, may be able to persist for many years under these conditions. Previous work has shown that in the South, baldcypress is one of the most tolerant species of long flood durations and relatively deep flooding (Hook 1984). It has now also been demonstrated to be tolerant of permanent flooding with water of low salinity (Allen et al. 1994; Conner 1995). Furthermore, baldcypress has been shown to have substantial intraspecific variation in salinity tolerance at the seedling stage (Allen et al. 1994) and at the seed germination stage (Krauss et al. 1997).

If the change in salinity levels is rapid or large pulses of saltwater intrude into freshwater systems during hurricanes, the impacts are likely to be much more rapid and dramatic, even for tolerant species such as baldcypress. None of the native species investigated were found to be capable of tolerating sustained flooding with salinity levels greater than 8 ppt, and some (the oaks) were found to succumb rapidly at salinity levels of 6 ppt.

The relative inability of the native species to tolerate higher levels of salinity and especially periodic pulses of salinity may provide an opportunity for exotic species to become increasingly prominent. Chinese tallow is one species that appears likely to benefit from the hydrological and salinity changes that may occur. It has many other characteristics that allow it to become an invasive species, such as rapid growth rate, early and prolific seed production, readily dispersed seed, moderately high shade tolerance, and an ability to grow on a wide range of soil types (National Academy of Sciences 1983; Jones and McLeod 1989, 1990; Jubinsky 1995). That it is also relatively tolerant of large pulses of salt water suggests that, following hurricanes and other major storms, it may come to dominate some sites now occupied by native species. Because there is evidence that Chinese tallow invades forested wetlands disturbed by hurricanes but not currently affected by sea-level rise (Doyle et al. 1995), it may also become an important invader in some areas defoliated by the fruittree leafroller.

While the lower elevation forests along the coast are likely to be the first to experience increases in flood durations and salinity associated with a gradual increase in sea level, slightly higher elevation wetlands may actually succumb more rapidly. Oaks and associated species often are found on low ridges no more than 30 to 60 cm above surrounding swamps (Conner and Flynn 1989; Conner 1988).

Because oaks were found to be so vulnerable to flooding with even low level salinity (2 ppt), they may well exhibit stress sooner than trees in the deeper swamps.

Development of Management Responses

Research described in this chapter also provides potentially valuable guidance for the restoration of forested wetlands subjected to saltwater intrusion. As mentioned earlier, many sites in southern Louisiana are currently subject to saltwater intrusion (Fig. 4-1); many more such areas may exist in the future as sea level rises and saltwater intrusion reaches farther inland.

Although restoration of original hydrologic regimes (i.e., freshwater and seasonally to semipermanently flooded) is undoubtedly the single best strategy for restoring forested wetlands, results of some of the work described above suggest that the development of moderately salt-tolerant planting material may be a useful complementary approach. This approach is analogous to that advocated by Epstein et al. (1980) and others for agriculture on saline soils. Epstein et al. (1980) believed that an "engineering approach" to the salinity problem was no longer adequate by itself and should be combined with a "genetic approach" involving the development of salt-tolerant crops.

Our first steps towards developing moderately salt-tolerant varieties of baldcypress demonstrated that considerable variation in salt tolerance exists within the baldcypress species. However, this work was conducted primarily under greenhouse and controlled environment conditions. Ultimately, managers will be interested in the performance of salt-tolerant seedlings in the field. The cooperative study initiated between Louisiana State University and the National Wetlands Research Center to test the performance of several families of baldcypress under field conditions is therefore of critical importance. The field trial involving 1,200 seedlings of 10 families, planted on three sites with differing salinity levels, began in January of 1996 and early results are promising (Krauss et al. 1999b). Also, a related study seeks to determine the suitability of developing selected salt-tolerant or salt-intolerant varieties to survive fruittree leafroller infestation. The results of these studies will hopefully provide a strong impetus for the active restoration of sites affected by saltwater intrusion throughout the southeastern coastal zone.