Vulnerability of Coastal Wetlands in the Southeastern United States: Climate Change Research Results, 1992-97

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By

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Abstract: As part of the USGCRP research framework on coastal lands and ecosystems, the Biological Resources Division of the U.S. Geological Survey (National Wetlands Research Center) entered into partnership with Rice University, Louisiana State University, Duke University, Clemson University, University of Southwestern Louisiana, University of Georgia, and the Virginia Institute of Marine Science (College of William and Mary) to (1) document the current state and vulnerability of coastal ecosystems including an assessment of past changes in land cover, (2) develop an understanding of the processes which underlie these changes, and (3) predict the extent of future alterations to these habitats and the consequences for the sustainability of the resource and land base. This document summarizes the initial findings of our collaborative efforts. Overall, the studies exemplify an integrated approach addressing questions at the species, community, and landscape levels of organization and focusing on factors related to hydroperiod, sea-level rise, disturbance events, and coastal marsh submergence.

Key Words: Climate change, sea-level rise, coastal ecosystems, subsidence, disturbance events, hydroperiod

Chapter 1:
Overview of Coastal Wetland Global Climate Change Research

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The potential impacts of climate change are of great practical concern to those interested in wetland resources. In particular, land managers need a better understanding about the potential environmental consequences of climatically induced changes and how management practices may influence or preserve critical habitat and mitigate potential ecosystem change. The U.S. Global Change Research Program (USGCRP) was undertaken to provide a stronger scientific basis for understanding, predicting, assessing, and responding to the causes and consequences of changing climate. Among the areas of greatest risk in the United States are low-lying coastal habitats and ecosystems along the northern Gulf of Mexico and southeast Atlantic coasts. These areas are vulnerable to the effects of climate-related change because of their elevation relative to sea level, low relief, and exposure to a host of human-induced stresses.

The Intergovernmental Panel on Climate Change (IPCC) has developed a range of scenarios for future greenhouse gas and aerosol precursor emissions which, when coupled with "best estimate" values of climate sensitivity and ice melt sensitivity to warming, project an increase in mean global sea level ranging from 15-95 cm by the year 2100 with a projected global mean mid-range increase of 50 cm (Intergovernmental Panel on Climate Change 1995b). That increase will result in widespread inundation of coastal areas, loss of coastal wetlands, and loss of many economic support functions those ecosystems provide. Indeed, sea-level rise that has occurred since 1940 has already inundated areas of the southeastern U.S. coastal zone. A projected additional 30% loss of coastal wetlands with a 50 cm increase in sea-level is of tremendous economic and biological importance (OTA 1993). Coastal wetlands provide essential habitat for many endangered and threatened species as well as supporting an economically important sports fisheries. The coastal areas of Louisiana alone provide the natural resource base for a fish and shellfish industry of over $1-billion-per-year.

Partners

As part of the USGCRP research framework on coastal lands and ecosystems, the Biological Resources Division of the U.S. Geological Survey (National Wetlands Research Center) entered into partnership with Rice University, Louisiana State University, Duke University, Clemson University, University of Southwestern Louisiana, University of Georgia, and the Virginia Institute of Marine Science (College of William and Mary) to:

(1) document the current state and vulnerability of coastal ecosystems including an assessment of past changes in land cover, (2) develop an understanding of the processes which underlie these changes, and (3) predict the extent of future alterations to these habitats and the consequences for the sustainability of the resource and land base.

This document summarizes the initial findings of our collaborative efforts. Overall, the studies exemplify an integrated approach addressing questions at the species, community, and landscape levels of organization and focusing on factors related to hydroperiod, sea-level rise, disturbance events, and coastal marsh submergence.

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Climate Change and Threatened Coastal Habitats

Coastal wetlands are particularly vulnerable to the effects of global climate change. Located on the interface between land and water, wetlands will be affected by large-scale climatic shifts. For example, subsidence (the rate at which land is sinking with respect to sea level) and sea-level rise (caused by thermal expansion of oceans and melting of polar ice caps and glaciers) are currently not being balanced by accretion (sediment accumulation) in many wetlands along the northern Gulf of Mexico Coast, resulting in increased flooding, saltwater intrusion into freshwater wetlands, and erosion of the coastline. Through natural processes, many coastal wetlands maintained their relative elevation to gradual increases of 1-2 mm per year in sea-level rise over the last several hundred years, but these rates are projected to increase twofold to threefold during the next century (Intergovernmental Panel on Climate Change 1995b).

Global change models for the southeastern United States predict a change in the temperature regime but no reliable changes in precipitation patterns (Giorgi et al. 1994). Regional models have predicted a 3 to 4° C increase in temperature region wide; however, all coupled ocean-atmospheric models used in the IPCC's Second Assessment Report predict an increase in precipitation over mid to high latitude regions as a result of a warmer climate. Variations in patterns of precipitation and temperature can affect the growth of individual trees, tree species population dynamics, ecosystem structure, and the geographic distribution of low lying forests and forest communities lying at the interface between terrestrial and aquatic systems.

Underlying the predicted climatic change is an overall increase in carbon dioxide concentrations in the atmosphere. The current evidence suggests that high concentrations of atmospheric carbon dioxide will affect atmospheric and oceanic processes that will have an impact on coastal wetlands (Edgerton 1991). Curtis et al. (1989) showed that salt marsh communities directly respond to increased atmospheric carbon dioxide with increases in biomass production. Although these increases may appear to be positive effects, the long-term response of vegetation to elevated carbon dioxide levels is still uncertain. Translating the responses at the cellular and leaf level in controlled experiments to community and ecosystem responses is difficult (Solomon and Shugart 1993). Increased atmospheric carbon dioxide concentrations should also result in a linearly proportional increase in dissolved carbon in coastal waters, which may potentially affect the biology and ecology of submersed plant communities.

Global climate models also include predictions about the nature of tropical storms (Emanuel 1987; Knutson et al. 1998). The coastal zones of the Gulf of Mexico and parts of the southern Atlantic Ocean are particularly vulnerable to hurricanes as evidenced from historical patterns of storm tracks and the consequences of recent storms (Guntenspergen and Vairin 1996; Michener et al. 1997). Freshwater marshes are susceptible to pulses of salt water during storms. Coastal forests are susceptible to direct damage from wind and storm surge sufficient to alter forest structure and diversity. Animal communities are locally susceptible to high winds and flooding associated with storms. And coastlines are susceptible to geomorphic changes and erosion. Although the IPCC (1995) concluded that the science is currently inadequate to state whether or not tropical storm frequencies or intensities will increase, some global climate change models predict changes in the frequency and intensity of tropical storms (Emanuel 1987).

The coastal zone of the southeastern United States consists of a matrix of open water, different wetland types, and upland. This matrix provides habitat for distinct groups of wildlife. Each of these habitat types requires an improved understanding if we are to predict and plan for changes caused by climate-induced environmental alteration.

Submersed aquatic vegetation (SAV), both freshwater communities and seagrasses, provide food for wintering diving ducks and habitat for fish. These communities are quite sensitive to changes in their physical environment. Scenarios for future climate change would affect the location, extent, composition, and productivity of these communities. Coastal emergent marshes provide habitat for a different array of waterfowl and terrestrial wildlife as well as serving as a vital nursery habitat for fish and shellfish. These habitats are particularly vulnerable to the effects of submergence, saltwater intrusion, and tropical storm activity. Forested wetlands and upland forested systems provide important habitat for colonial nesting birds, raptors, wintering and resident waterfowl, deer and other mammals, and Neotropical migrants. Lowland forests are sensitive to altered hydrology, salinity, and tropical storms.

Scientific assessments of current resource condition, an understanding of the large-scale processes operating in these systems, and an ability to predict the vulnerability and adaptability of natural and managed systems to the consequences of the long-term variations of the physical environment have long been needed. The research described in this document provides some understanding of climate change impacts on U.S. coastal wetlands.

Goals

The wetland global change research program in the U.S. Geological Survey was organized in a hierarchical framework to: (1) identify sensitive ecosystems and critical processes, (2) understand their current condition, (3) develop new tools and technology to identify sensitive systems and measure critical processes, (4) develop predictive tools which model the vulnerability of habitats to environmental

changes, and (5) develop management recommendations to ameliorate the potential environmental impacts associated with global climate change. Research in the Gulf of Mexico and South Atlantic Coastal Plain has concentrated on land managed by the Department of the Interior's U.S. Fish and Wildlife Service's (USFWS) National Wildlife Refuge System and by the National Park Service (NPS). In this region, the USFWS manages 65 national wildlife refuges, and NPS manages 27 national parks. Climate change is projected to have significant regional impacts on resource management and use of these public lands. Southeastern coastal wetlands have also been high priority areas for state fish and wildlife agencies because of the renewable resource base associated with these unique and vulnerable habitats.

Submersed Aquatic Plant Communities

Communities of submersed aquatic vegetation (SAV) found in marine, estuarine, and freshwater environments within the northern Gulf of Mexico coastal zone provide critical habitat for fish, shrimp, wintering waterfowl, and endangered species including sea turtles and manatees; reduce erosion; and improve water quality.

Field and laboratory experiments conducted by USGS scientists addressed the possible impact of elevated dissolved inorganic carbon, sea-level rise and salinity increases, and increased physical disturbance by storms on the ecology and function of submersed aquatic plant communities. Studies on the effects of elevated dissolved organic carbon examined the photosynthetic response of phytoplanktonic, benthic microalgae, and macrophyte components of these habitats as a potential measure of shifts in the organization and structure of the submersed aquatic plant community. Increased atmospheric carbon dioxide is likely to lead to increased concentrations of dissolved carbon and thus lead to widespread changes in the productivity of these communities, changes in the food quality of these species for fish and wildlife, changes in the growth patterns of the plant species, changes in species composition, and possible extirpation of SAV by competition with phytoplankton and epiphytes.

Greenhouse experiments with wild celery (*Vallisneria americana*) and shoalgrass (*Halodule wrightii*) exposed to increased levels of dissolved inorganic carbon resulted in changes in biomass allocation, ratio of carbon to nitrogen in certain tissues, and enhancement of epiphytic growth on the seagrass species. These experiments did not result in increased growth of the two species in the short-term, however.

Rates of photosynthesis increased in experimental treatments with three freshwater SAV species: wild celery, coontail (*Ceratophyllum demersum*), and hydrilla (*Hydrilla verticillata*) as well as shoalgrass exposed to higher concentrations of dissolved carbon dioxide. The results

of experiments with shoalgrass are particularly significant because seagrass photosynthesis is often thought to not be limited by dissolved inorganic carbon concentrations because of the abundance of carbonate carbon in the water column. In these experiments, the lack of response by widgeon grass (*Ruppia maritima*), another species of submersed aquatic macrophyte, was likely a result of elevated levels of dissolved inorganic carbon as well as free carbon dioxide.

The distribution and abundance of submersed aquatic vegetation along salinity gradients has long been recognized for many coastal areas so we can associate general groups of species with broad salinity zones. Our understanding of the mechanisms underlying these patterns, however, is limited. Community composition at any location reflects the salinity tolerances of individual species as well as the biotic interactions among species. Although these salinity tolerances have been determined for many North American SAV species, there is little information on the relative importance of biotic interactions in structuring SAV communities, particularly under changing environmental conditions. Greenhouse studies assessed the salinity tolerance of six of the most common SAV species found in the coastal waters of the United States. They represented a range of habitat types (from freshwater to brackish). Additional experiments determined how potential distribution patterns might be altered by competitive interactions. Species known to be strong competitors dominated at low salinities and did not grow well at the high end of the salinity gradient because of a physiological intolerance to high salinity conditions. Species tolerant of high salinities proved to be weak competitors at low salinity. Species presence appears to result from an interaction between tolerance to the physiological stress associated with high salinity levels and the ability to compete and grow well in the presence of other plant species. Predictions for alterations in the salinity of any coastal area can be derived from physical information on local geomorphology, watershed freshwater inputs, volume of the tidal prism, and predicted sea-level rise. This information can then be used to predict changes in the SAV community structure.

An increase in the severity or frequency of tropical storms associated with global climate change could have acute impacts on coastal SAV communities. Studies which examined the role of chronic physical disturbance in patterns of seagrass distribution and abundance in coastal Louisiana were initiated so that predictions about the responses of coastal SAV to increases in storm disturbance could be made. These field studies indicated that seagrass community structure can be controlled by frequent and relatively minor overwash sediment deposition events. One seagrass species, turtlegrass (*Thalassia testudinum*), was found in protected areas characterized by nutrient-rich sediments of high organic content and low sand content.

Another dominant seagrass species, manatee grass (*Syringodium filiforme*), was found in patches characterized by sandy sediments. Increasing the deposition of sandy beach and offshore sediments in seagrass beds will result from a rise in the frequency of low intensity storms. The chronic effects of the predicted increases in sediment deposition from storm-generated waves is expected to cause a shift in community structure and species composition of these habitats to species commonly found after disturbance.

Coastal Marshes

The loss of coastal wetlands in the southeastern United States has accelerated in the face of relative sea-level rise during the past 50 years. Although many coastal wetlands have maintained their elevations relative to sea level in spite of a 1-2 mm per year rise in mean sea levels, local geomorphic processes complicated by human activities have led to the submergence of coastal wetlands and contributes to rates of coastal wetland loss in south Louisiana exceeding 65 km^2 per year. Areas in south Louisiana with high local rates of subsidence are currently experiencing relative sea-level rise rates up to 10 times the current global mean sea-level rise. U.S. Geological Survey scientists and their collaborators have sought to evaluate the potential for the submergence and subsequent loss of a range of saline and brackish marsh types relative to the local rate of sea-level rise.

Along the coast of the United States, marsh submergence can only be prevented if sediment accumulation and biogenic processes result in a vertical buildup of the marsh surface that keeps pace or exceeds the rate of relative sea-level rise. Surface elevation lagged behind sediment deposition at 7 of the 12 coastal wetlands monitored by USGS scientists. Four of the sites which exhibited significant loss of elevation relative to sea level had high rates of sediment accumulation, suggesting that subsurface processes in the top few meters of the soil as well as biogenic and external physical forces (storms) affected surface elevation. It is quite likely that estimates of marsh loss based only on tide gauge records and rates of sediment accumulation underestimate actual rates of subsidence. Predicting the potential for coastal marsh submergence caused by sea-level rise requires site-specific information and an improved understanding of the interactions among marsh vegetation, soil, and hydrologic processes. These initial findings cannot be extrapolated to all southeastern coastal wetlands. Information on local environmental factors, including coastal geomorphology, sediment supply, and frequency of major storms as well as trends in mean sea-level rise are needed to identify specific coastal wetlands at risk of submergence caused by global climate change.

Duke University and USGS scientists also found that as sea level rises and lower elevation sites are submersed and lost, marsh build-up and expansion can occur on the upslope landward marsh boundary, creating new wetland habitat and replacing lost marsh. The slope of the coastal plain as well as the rate of sea-level rise and sedimentation are key factors controlling the upslope movement of coastal wetlands. Horizontal migration can be impeded, however, if the slope of the surface is too steep or if barriers to new marsh formation exist upslope (e.g., sea walls, roads, or buildings).

Duke University and USGS scientists modeled the movement of the marsh edge in North Carolina's Pamlico Sound. Their results imply that the movement of the marsh edge occurs in a series of dynamic events rather than in a gradual constant manner. These "transgression" events are separated by longer periods of relatively little marsh edge movement. Upland movement of the marsh is associated with disturbance of the upland vegetation associated with major tropical storms or fire. The general model implies that upslope marsh movement is driven not only by sea-level rise but also by local environmental conditions. Marsh managers should not rely on short term estimates of upslope marsh movement as a tool which would predict coastal marshes at risk for submergence. To avoid a net loss of marsh habitat, they should employ management techniques, including the removal of upslope barriers, which would enhance marsh development upslope and minimize the potential for marsh submergence and net habitat loss.

Net Loss of Coastal Habitat

At St. Marks National Wildlife Refuge in northwest Florida, elevation and water depth are key factors controlling habitat type. The ability to predict landward transgression of coastal marsh caused by sea-level rise depends on knowledge of the current vegetation distribution and relation to topographic gradients. Field data were collected to establish correlations between vegetation distribution and surface elevation. These data were combined with the development of landscape models and new satellite technology to provide important tools for research and policy purposes that allow for effective land and water management, risk assessment, and cumulative impact analysis.

New satellite remote sensing techniques were developed to produce a fine scale resolution topographic map of the low lying coastal marsh. Color infrared photography, satellite imagery, and satellite radar images were combined to create additional maps of the marsh and upland vegetation of the refuge. A digital elevation model of St. Marks NWR was constructed to track the process and pattern of coastal inundation for given sea-level rise projections. Sea-level rise projections adopted from the IPCC (1995) indicate that major portions of the St. Marks coastal zone will be permanently flooded, bringing about a migration of vegetation community types and loss in total area and proportion of some habitats. Model results suggest that there is a large land base that will be quickly converted from coastal salt

and freshwater marsh to open water, which will approach the scale of marsh loss that has been experienced in south Louisiana. There will be some shift of emergent marsh into forested zones. Site geomorphology and the slope of the land will present an effective barrier to the establishment and growth of specific plant communities because of lack of suitable habitat conditions. The landform in this area increases sharply in slope from the sea inland, effectively squeezing area available for forest and marsh.

Coastal Forested Wetlands

Forested wetlands at low elevations are among the coastal communities that are considered most vulnerable to losses due to potential changes in sea level. Many of these forests are already threatened by alterations in hydrology and saltwater intrusion. USGS scientists and their collaborators from Clemson University and the University of Georgia examined the effects of potential increases in flood durations and salinity levels through a series of growth and physiological experiments with 10 major wetland tree and shrub species.

Measures of plant physiological activity using experimentally simulated environmental conditions predicted to occur under different climate change scenarios were good predictors of whole plant growth responses that may not be evident for years or decades. Baldcypress (*Taxodium distichum*) was relatively tolerant to permanent flooding but relatively intolerant to exposure to saline waters. Oaks, which usually occur on ridges no more than 30-60 cm above the surrounding swamps, were vulnerable to a combination of flooding and salinity stress in experimental studies. Chinese tallow (*Sapium sebiferum*), a highly invasive exotic tree species, was tolerant to the combined salinity and flooding stresses associated with simulated storm surges. Flooding was more important than small increases in salinity in the growth and survival of most tree species tested, whereas large increases in salinity were harmful to all of the species tested regardless of flooding regime. It is evident that large-scale shifts and/or losses in wetland forest communities are likely to occur over the next 50 years if current trends in sea-level rise continue. Genetic studies conducted with baldcypress, however, also suggested that new varieties can be developed that might be planted in restoration projects and partially mitigate the effects of salinity intrusion. Significant variation in salt tolerance existed among baldcypress populations. Greenhouse and field experiments demonstrated that this tolerance has a genetic component and is heritable. These findings imply that restoration of baldcypress forests may be possible in degraded sites where existing populations have been killed by low-level saltwater intrusion.

At Big Thicket National Preserve in southeast Texas, scientists from Rice University established a long-term monitoring effort to detect coastal forest response to climate change. Permanent plots were established to quantitatively document the dynamics of forest structure and the responses to changes in storm intensity, flooding, and fire frequency. Long-term monitoring data suggest that increases in drought associated with changing climatic regimes may significantly alter understory seedling populations in bottomland forests, recruitment into the sapling layers, and ultimately influence overstory canopy structure. Flooding, hurricanes, and even low-intensity storms which result in openings in the forest canopy will influence the responses of these forests to climatic shifts by accelerating natural successional processes. Increased disruptions to the forest canopy will also provide recruitment opportunities for exotic species enhancing their rate of invasion into natural stands.

A series of related studies was initiated to determine potential changes in the growth and geographic distribution of forest tree species. Tree ring analyses from sites across the wet-dry transition zone from western Louisiana to central Texas suggest that many forest tree species do not alter their growth rates near the edges of their range. These results combined with forest tree dynamics from the permanent plots imply that seedling establishment and survival may be more important in limiting the geographic ranges of tree species than the growth and survival of adults.

Exotic species can be expected to increase in importance throughout forest stands in the coastal plain with increased levels of disturbance and canopy gap formation. The costs to control exotic species will continue to rise in national parks and other managed natural areas. Other shifts in species composition are also expected to occur. Increased disturbance from changes in the frequency and intensity of tropical storms may favor early successional, shade-intolerant species at the expense of shade-tolerant ones. Land managers will be faced with intensive efforts to maintain the natural character of their preserves.

Mangrove ecosystems predominate the coastal areas in the lower Florida peninsula where hurricanes commonly occur. Landscape simulation models developed by USGS scientists confirmed that hurricane disturbance has also contributed to the structural composition of modern mangrove forests across south Florida and Everglades National Park. Modeling future climate change scenarios with the results of this research suggests that increased damage associated with stronger storms will likely result in future mangrove forests of smaller stature than present day stands and that shifts in species dominance to stands composed of red mangroves (*Rhizophora mangle*) are likely to occur.

Assessment

The research findings summarized in this document reveal both the scale and scope of potential global change impacts on plant communities of low-lying coastal

margins. While there remain many uncertainties regarding the regional and local responses to changes in climate, current studies of plant communities and landforms of the coastal zone of the southeastern United States provide strong evidence of the potential effects of relative sea-level rise and changes in tropical storm activity. Predictive models and new developments in remote sensing technology can be used to project the impacts and interactions of global change variables on land cover and geomorphology of the coastal zone. We cannot as yet verify the ultimate and cumulative effects on species, populations, and communities. In the southeastern coastal plain, however, we have documented trends in the changing dynamics of plant communities, loss of coastal wetlands, and erosion of barrier islands that can be related to more than 50 years of environmental change, regardless of causative factors. Future research should provide a more thorough understanding of wetland response to long-term environmental change.

Chapter 2:
Global Climate Change
and Communities of Submersed Vegetation:
Research Summary of Selected Environmental Impacts

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Abstract: Communities of submersed aquatic vegetation (SAV) are important components of many freshwater, brackish, and marine aquatic ecosystems. They provide erosion protection by baffling the impacts of waves, remove nutrients and other pollutants from river and runoff inputs to coastal areas, and provide nursery habitat for fish, shrimp, and other species, as well as forage for wintering waterfowl and endangered species such as sea turtles and manatees. Submersed aquatic plant communities, though, are susceptible to long-term environmental changes that are predicted to accompany global climate change. Our research was aimed at determining the responses of SAV to increased dissolved inorganic carbon, higher sea levels, and increased frequency and intensity of tropical storms. We found that photosynthesis of macrophytes changed little or not at all in response to bicarbonate additions, but photosynthesis did increase in response to additions of dissolved carbon dioxide for most species tested. The photosynthesis of benthic microalgae and of phytoplankton at saline sites was not affected by additions of either dissolved carbon dioxide or bicarbonate, but at freshwater sites, the addition of carbon dioxide did enhance phytoplankton photosynthesis. Increased dissolved inorganic carbon may also alter species allocation of biomass by increasing the proportion of belowground biomass relative to aboveground biomass. Experiments on the effects of sea-level rise indicate that at freshwater to oligohaline sites, species that are strong competitors will likely dominate, while salt-tolerant species will dominate areas with higher salinity. Our research on the effects of storm disturbance on SAV suggests that increased storm activity may favor seagrasses that dominate in sandy, nitrogen-poor sediments because of the increased likelihood of storm overwashes.

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Introduction

Communities of submersed aquatic vegetation (SAV) occur in all types of aquatic ecosystems within the northern Gulf of Mexico coastal zone. One of the most widely recognized values of SAV is as fish and wildlife habitat (Stevenson and Confer 1978; Zieman 1982; Zieman and Zieman 1989). Submersed aquatic vegetation serves as a critical food resource for waterfowl and as important feeding and nursery grounds for many commercially and recreationally important finfish and shellfish. In fact, changes in distribution of waterfowl populations (Kemp et al. 1984; Wicker and Endres 1995) and commercial landings of blue crabs (Orth and van Montfrans 1990) have been correlated with abundance of SAV. Submersed aquatic vegetation also provide critical habitat for threatened and endangered species such as sea turtles and manatees. The importance of SAV to aquatic ecosystems extends to physical and chemical functions as well. The leaves of submersed plants reduce waves and currents (Fonseca et al. 1982; Fonseca 1989) and root and rhizome systems bind sediments, both of which enhance shoreline stabilization. Finally, nutrient uptake and particulate sedimentation within SAV beds effectively ameliorate water quality (Ward et al. 1984; Short and Short 1984). Changes in SAV thus have profound implications for fish and wildlife, shoreline geomorphology, and biogeochemical cycles of aquatic ecosystems.

Primary production within beds of SAV is derived from many sources (Fig. 2-1). Phytoplankton, benthic microalgae, and epiphytes, in addition to macrophytic vegetation, contribute to the production of organic matter. Any of the latter three groups may dominate primary production within the SAV community depending on location, type of SAV, and time of year (Morgan and Kitting 1984; Jensen and Gibson 1986; Mazella and Alberte 1986; Murray and Wetzel 1987; Moncreiff et al. 1992). The magnitude of production and the diversity of primary producer groups within SAV communities is a principal reason for their high biological diversity and value as feeding and nursery areas.

Submersed plant communities are distributed throughout the coastal zone of the northern Gulf of Mexico. Species of SAV restricted to fresh and brackish waters occur in the shallow areas of estuaries and river deltas along the gulf coast (Handley 1995); their greatest coverage occurs in large, shallow bays and in the shallow flats that form at river mouths. Marginal bands of SAV often line the shores of small tributaries and creeks, and small patches can be found in quiet zones along the edges of large rivers (Stout 1990). The composition of freshwater and brackish SAV communities is diverse; 24 species were identified in surveys of habitats in Mobile Bay, Alabama (Stout 1990). Many beds exist as mixed communities, although monodominant stands, particularly of invasive, nonnative species, are also common. Eurasian milfoil (*Myriophyllum spicatum*) and hydrilla (*Hydrilla verticillata*) are nonnative species found in this region. These species are often considered nuisance aquatic plants because of the dense, nearly impenetrable mats of vegetation they form.
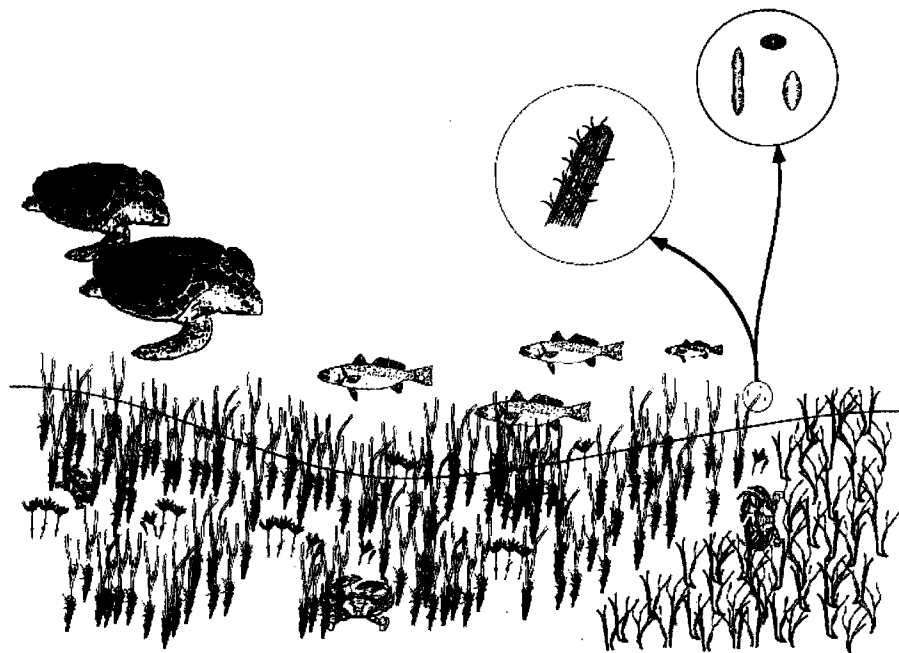

Figure 2-1. Important components of a typical submersed aquatic vegetation ecosystem, including marine animals, macrophytes, epiphytes, and phytoplankton.

Seagrasses, or marine SAV species, form the most extensive SAV systems along the northern gulf coast. Five seagrass species grow in this region: turtlegrass (*Thalassia testudinum*), manatee grass (*Syringodium filiforme*), shoalgrass (*Halodule wrightii*), star grass (*Halophila engelmannii*), and paddle grass (*Halophila decipiens*). Widgeongrass (*Ruppia maritima*), a submersed plant with a broad salinity distribution, occurs with seagrasses in the lower salinity areas of the marine environment. Seagrass beds are often quite heterogeneous, with individual species exhibiting patchy distributions within expansive, continuous seagrass beds. As such it is difficult to assign overall dominance in the gulf to a particular species (Kenworthy 1994). The most recent estimate of total seagrass coverage in the shallow, nearshore waters of the Gulf of Mexico coastal states is 1.02 million ha (Duke and Kruczynski 1992). The largest seagrass beds in this region occur in Florida Bay (550,000 ha; Zieman and Zieman 1989), the Big Bend area of Florida between St. Marks and Tarpon Springs (300,000 ha; Iverson and Bittaker 1986) and the Laguna Madre of Texas (73,000 ha; Onuf 1995). Most of the remaining seagrass beds are within estuarine areas of Florida and Texas (Handley 1995). Isolated patches and narrow bands occur in sounds protected by the barrier islands of Louisiana, Mississippi, and Alabama. The largest continuous seagrass bed in this region is found in Chandeleur Sound of coastal Louisiana (5,657 ha; Handley 1995).

Effects of Global Climate Change

The distribution and abundance of SAV habitats in the northern Gulf of Mexico have declined precipitously during the past 50 years, most notably from widespread deterioration of water quality (Neckles 1994). The productivity, distribution, and composition of submersed plant communities are also susceptible to stresses associated with a changing global climate (Rizzo and Neckles 1993). Increases in concentration of dissolved inorganic carbon (including both carbon dioxide [CO_2] and bicarbonate [HCO_3^-]) may affect SAV directly and may have indirect effects through influences on attached and unattached algae in SAV systems. A rise in sea level will increase the depth of water at any given position and will cause inland and upstream intrusion of salt water, both of which will affect existing SAV. The direct effect of temperature on plant physiological processes may ultimately influence SAV community composition and the latitudinal distribution of species. In addition, if changes in global climate result in a warmer tropical ocean, the frequency and intensity of tropical storms likely will increase (Emanuel 1987), which would further increase the inland extent of saltwater penetration. Any increase in the frequency or intensity of physical disturbance from storms may also have direct effects on SAV habitats. The environmental effects of a changing

global climate may exacerbate existing human-caused stresses on SAV and accelerate habitat alteration or loss. There is, however, little information from which to predict the direction and magnitude of potential changes in SAV associated with global change. Therefore, minimizing and adapting to the effects of a changing global environment require foremost a better understanding of potential SAV responses to these environmental variables.

The research results summarized here address the possible effects of elevated dissolved inorganic carbon, sea-level rise and salinity increases, and increased storm disturbance on various aspects of the ecology of SAV ecosystems. Each section includes a brief background statement followed by a research summary. Research on the effects of elevated dissolved inorganic carbon examined the growth response of two macrophyte species and the photosynthetic responses of the phytoplanktonic, benthic microalgal, and macrophytic components of these habitats. Studies on sea-level rise and salinity increase focused on the effects of these variables on macrophyte survival, competition, and community structure. The effects of disturbance on the community structure of seagrass communities was undertaken to evaluate the possible long-term effects of increased storm activity.

Effects of Increased Carbon Dioxide Concentration

There is overwhelming evidence that high concentrations of atmospheric carbon dioxide will directly impact global vegetation. Most studies to date have focused on terrestrial or emergent plants, where common responses to elevated levels of carbon dioxide include increased photosynthesis and biomass, enhanced root growth relative to shoot growth, and elevated tissue carbon-to-nitrogen ratios (e.g., Cure and Acock 1986; Mooney et al. 1991; Dahlman 1993). Although an increase in concentration of atmospheric carbon dioxide causes a linearly proportional increase in that of dissolved carbon in aquatic environments (Wetzel and Grace 1983), comparatively little information exists on responses of submersed plant communities to carbon dioxide enrichment and the potential ecosystem consequences.

The size of the total pool of dissolved inorganic carbon is a result of complex interactions between biota, atmospheric carbon dioxide partial pressure, temperature, pH, alkalinity, and salinity. The dissolved inorganic carbon pool is partitioned into carbon dioxide, bicarbonate, and carbonate (CO_3^{2-}; Fig. 2-2). The distribution of dissolved inorganic carbon among these three fractions depends strongly on pH, which is expected to decrease slightly as a result of carbonic acid formation from increased dissolution of carbon dioxide (Wetzel and Grace 1983). The variability in dissolved inorganic carbon concentrations and the distribution among the major constituents is much
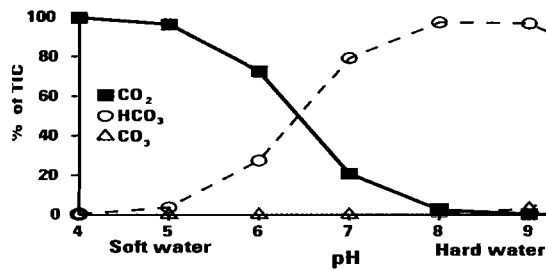
Figure 2-2. Relationships between dissolved inorganic carbon constituents (carbon dioxide bicarbonate), pH, and alkalinity (soft water to hard water) in aquatic ecosystems (after Wetzel 1975).

greater in fresh water than marine systems because of the constant ionic composition and buffering capacity of seawater.

The limited research available typically has found an increase in SAV photosynthesis with carbon dioxide enrichment (e.g., Beer and Wetzel 1981; Titus and Stone 1982; Nielsen and Sand-Jensen 1989; Rattray et al. 1991; Durako 1993; Madsen et al. 1993). Submersed plant species exhibit a wide range of responses, however. All SAV take up carbon dioxide preferentially during photosynthesis, but most can also use bicarbonate to some degree. In general, species that are inefficient bicarbonate users show the greatest photosynthetic response to carbon dioxide increases (Madsen et al. 1993). Thus, although total dissolved inorganic carbon can limit SAV photosynthesis and growth, an unfavorable partitioning of dissolved inorganic carbon among constituents can also limit some species (Vadstrup and Madsen 1995). Increased concentrations of carbon dioxide may not only increase primary production of organic matter but also, by altering the outcome of competition, lead to shifts in species composition.

Epiphytic algae can limit the supply of dissolved inorganic carbon to SAV leaf surfaces by increasing the thickness of the layer through which carbon must diffuse (Sand-Jensen et al. 1985) and by actual carbon uptake. These algae are also susceptible to carbon limitation of photosynthesis and would be expected to respond positively to increased availability of carbon dioxide. One potential consequence is enhanced algal growth and a shift in the balance between epiphytes and macrophytes.

Wetzel and Grace (1983) summarized the literature on the response of autotrophs to carbon dioxide enrichment by making generalized predictions on the magnitude of the response. They predicted a doubling of photosynthesis for both marine and freshwater macrophytes (single plant responses) with a doubling of carbon dioxide concentration, for optimal conditions of light and water mixing. They predicted no increase for marine phytoplankton and a response for freshwater phytoplankton ranging from no response to an increase of about 1.5 times ambient. While there was a limited data base on SAV responses, there were even fewer

studies on phytoplankton and no studies on the benthic microalgal components of SAV habitats.

Macrophyte Photosynthetic Responses to Elevated Dissolved Inorganic Carbon

Initial quarterly studies of the photosynthetic response of macrophytes to elevated carbon dioxide and bicarbonate were carried out for *Vallisneria americana, Halodule wrightii, Ceratophyllum demersum,* and *Ruppia maritima.* Additional, more intensive sampling was conducted for *Ceratophyllum demersum, Hydrilla verticillata,* and *Vallisneria americana.* Species collected from saline sites included *Halodule,* a true seagrass from Galveston Bay, and *Ruppia,* from a brackish environment at Rockefeller National Wildlife Refuge (NWR), Louisiana. The other species were collected from freshwater environments (a pond at the National Wetlands Research Center, Lafayette, Louisiana, and Vermilion Lake and Spreafico Lake, Louisiana), a wetland in Cameron Parish, Louisiana (*Vallisneria*), and Lake Martin, Louisiana (*Ceratophyllum* and *Hydrilla*).

Only *Ceratophyllum* showed significant responses to addition of bicarbonate: enhancement in one experiment and inhibition in another. The instance of enhancement probably resulted from an increase in inorganic carbon substrate at a time when this species may have been using bicarbonate as a primary carbon source. Conversely, the inhibition probably resulted from a decrease in free carbon dioxide, the preferred carbon source for plants, as a result of an increase in pH from the bicarbonate addition. The generalized lack of response to bicarbonate additions suggests either that plants are exclusively using free carbon dioxide as a primary carbon source or that ambient concentrations of bicarbonate are already sufficient to maximize photosynthesis in plants using this less desirable carbon source.

Typical curves of the response of macrophyte photosynthesis as a function of increasing concentration of dissolved inorganic carbon (as added carbon dioxide) are shown in Fig. 2-3. In a number of cases, photosynthesis was still increasing even at the maximum added concentration of 2-4 times ambient. *Vallisneria* photosynthesis increased with carbon dioxide additions in all nine experiments, while *Ruppia* photosynthesis increased in 0 of 3 experiments. *Halodule* responded in 2 of 4 experiments, *Ceratophyllum* in 20 of 26 experiments, and *Hydrilla* in 7 of 14 experiments. The results for *Halodule* are particularly significant because seagrass photosynthesis is often thought to be not limited by dissolved inorganic carbon because of the abundance of bicarbonate in marine environments. *Hydrilla* and *Halodule* responded to carbon dioxide additions principally during the most active phase of growth in spring and early summer. With the exception of January 1995, *Ceratophyllum* responded consistently to carbon dioxide addition until the summer of 1995.
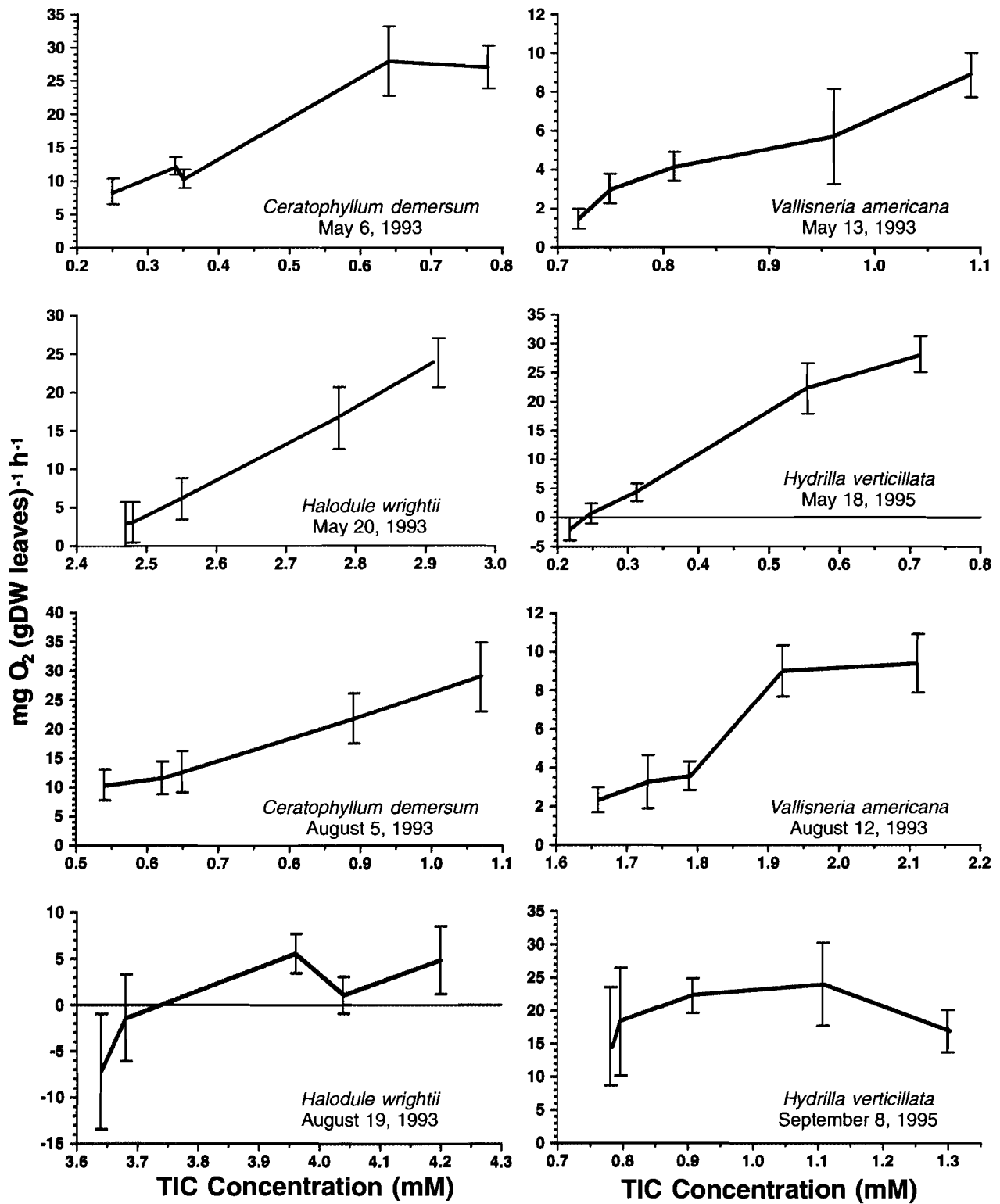
Figure 2-3. Growing season photosynthetic responses of four macrophyte species to increasing concentrations of dissolved inorganic carbon, added as carbon dioxide. The lowest concentration represents ambient concentrations at the collection site.

In fall of 1992, *Hydrilla* was discovered in Lake Martin. It covered about 50% of the lake surface by the end of summer 1994 and reached virtually complete surface coverage by the end of July 1995 (Fig. 2-4). Weekly monitoring samples at our littoral collection site showed a significant decrease in pH and increase in free carbon dioxide from 1994 to 1995. These conditions may have alleviated carbon dioxide limitation in this species during most of the latter half of 1996. The lack of response by *Ruppia* probably also resulted from the high concentrations of dissolved inorganic carbon and free carbon dioxide.

There was a more than threefold difference among species in the mean response to carbon dioxide addition in our experiments (Fig. 2-5). Photosynthesis by *Ceratophyllum* and *Hydrilla* doubled with addition of carbon dioxide, while *Vallisneria* and *Halodule* photosynthesis increased nearly threefold. The maximum response of *Ceratophyllum*, *Vallisneria*, and *Halodule* exceeded
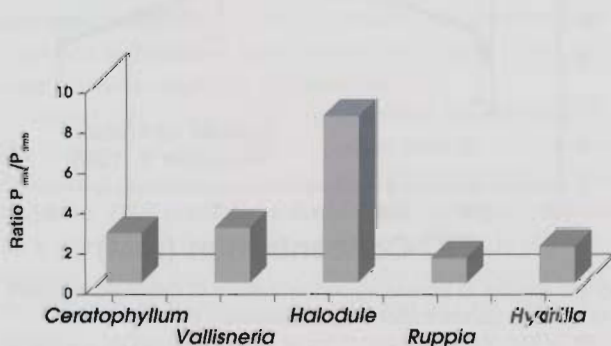
sixfold, while the maximum for *Hydrilla* was only threefold, underscoring the important differences among species.

Regression analyses indicated that factors such as temperature and the ambient rate of photosynthesis, an indicator of plant condition, were also important in controlling the responses of SAV to increased carbon dioxide concentrations. Consequently, both environmental and life history factors are important in determining when and how strongly a species will respond to an increase in carbon dioxide. The importance of temperature in controlling this response is particularly important since global temperatures are expected to increase along with concentrations of carbon dioxide.

Benthic Microalgal and Phytoplankton Photosynthetic Responses to Elevated Dissolved Inorganic Carbon

The benthic microalgal and phytoplankton studies also began as quarterly studies at all the macrophyte study sites (except Rockefeller NWR, where no benthic microalgal studies were conducted). Monthly phytoplankton sampling began in late 1993 and expanded to include lake sites that had no SAV but represented large differences in ambient dissolved inorganic carbon concentrations. Sites at Galveston Bay, Rockefeller NWR, and Cameron Parish all had high concentrations of dissolved inorganic carbon. Lake Martin and Vermilion Lake, Louisiana, had moderate dissolved inorganic carbon concentrations, the NWRC pond had high concentrations, and Spreafico Lake had low dissolved inorganic carbon concentrations.

Addition of either carbon dioxide or bicarbonate had no effects on the photosynthesis of benthic microalgae. At two freshwater sites, sediment regeneration of carbon dioxide greatly exceeded autotrophic demand, so it is unlikely that carbon dioxide would become limiting to photosynthesis in these environments. At a marine site, demand was much greater than regeneration, but concentrations of dissolved inorganic carbon, principally as bicarbonate, were high and probably supplied benthic microalgal requirements. Because of their microscopic size and high surface-to-volume ratio, benthic microalgae make much more efficient use of the less preferred bicarbonate carbon source than do macrophytes.

The number of experiments in which phytoplankton photosynthesis increased as a result of carbon dioxide addition is shown by site in Fig. 2-6. There was no increase in photosynthesis from additions of either carbon dioxide or bicarbonate at either site with measurable salinity. Photosynthesis was enhanced by carbon dioxide addition in most experiments at each of the freshwater sites except the NWRC pond, the site highest in dissolved inorganic carbon concentration. Even at that site, however, photosynthesis increased on two occasions. In contrast to the macrophyte experiments, phytoplankton photosynthesis was increased by bicarbonate additions on several occasions at three of

Figure 2-4. Lake Martin, Louisiana, showing complete surface coverage by *Hydrilla verticillata* in late summer 1995. Boating became impossible on the lake, and fish kills ensued. Invasions by such exotic species may be abetted in an environment enriched in dissolved carbon dioxide.

Figure 2-5. Photosynthetic enhancement as measured by the ratio of ambient photosynthesis (P_{amb}) and photosynthetic rates enhanced by carbon dioxide enrichment (P_{max}) for five species of submersed aquatic vegetation.

**Figure 2-6.** Total number of experiments per site and number of experiments in which phytoplankton photosynthesis increased because of carbon dioxide addition. The phytoplankton communities represent a salinity gradient from marine to freshwater and, for freshwater sites, a gradient of high to low dissolved carbon dioxide.

the four freshwater sites where bicarbonate additions were carried out. Also, additions of both carbon dioxide and bicarbonate caused inhibition of photosynthesis in a number of experiments. Inhibition by bicarbonate may result from the associated increase in pH, which can actually reduce concentrations of free carbon dioxide. Conversely, communities using only one dissolved inorganic carbon source may undergo brief metabolic shut down (i.e., inhibition) while shifting to an enzyme system capable of using the more abundant or energetically favorable dissolved inorganic carbon substrate when its availability is suddenly increased.

The increase in photosynthesis due to carbon dioxide addition is shown in Fig. 2-7. For experiments in which there was an increase with carbon dioxide addition, the level of increase was between 1.5 and 2.0 for three of the four freshwater sites. This level is slightly higher than that predicted by Wetzel and Grace (1983).
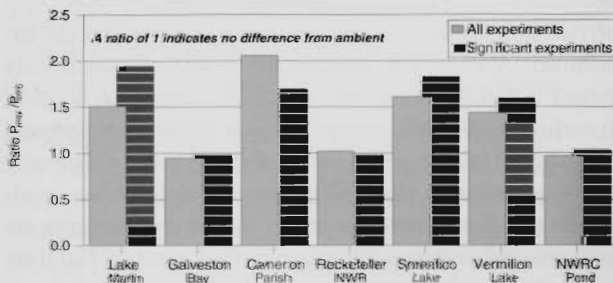
Macrophyte Growth Responses to Elevated Carbon Dioxide

Studies of various vegetation types have indicated that the initial metabolic impacts of increases in carbon dioxide diminish substantially as plants acclimate to higher ambient concentrations. Therefore, although our laboratory experiments showed significant effects of short-term increases in dissolved inorganic carbon concentrations on SAV photosynthesis, these effects might not necessarily translate into longer-term effects on growth and production. To assess the potential responses of a freshwater and a marine species of SAV to elevated dissolved inorganic carbon, we used mesocosms, or large experimental systems designed to simulate natural ecosystems. Because the photosynthesis of all species increased most consistently in response to carbon dioxide additions during our laboratory experiments, we focused on this dissolved inorganic carbon constituent for our longer term measurements (Fig. 2-8).

Our experimental mesocosms were planted with intact sods of either *Halodule wrightii* from coastal Texas or *Vallisneria americana* from coastal Louisiana. Conditions were maintained in the tanks to mimic the natural environment as closely as possible. The tanks were filled with water at the same salinity and depth as at the collection sites. The experimental treatment consisted of continuous aeration of the tanks with ambient or carbon-dioxide enriched air for six weeks. Dissolved inorganic carbon concentrations in the air and water were monitored daily.

Contrary to the results of other studies, carbon dioxide enrichment did not affect total macrophyte biomass (Fig. 2-9a) or final shoot density (Fig. 2-9b) for either species. However, consistent with a large body of research on other systems, the final ratio of aboveground to belowground biomass decreased with carbon dioxide enrichment (Fig.

Figure 2-7. Photosynthetic enhancement as measured by the ratio of ambient photosynthesis (P_{amb}) and photosynthetic rates enhanced by carbon dioxide enrichment (P_{max}) for phytoplankton communities from the various seven study sites.

Figure 2-8. Mesocosms set up in a greenhouse at the National Wetlands Research Center. Such mesocosms enable studies of macrophyte responses to discrete variables such as carbon dioxide concentration or salinity.
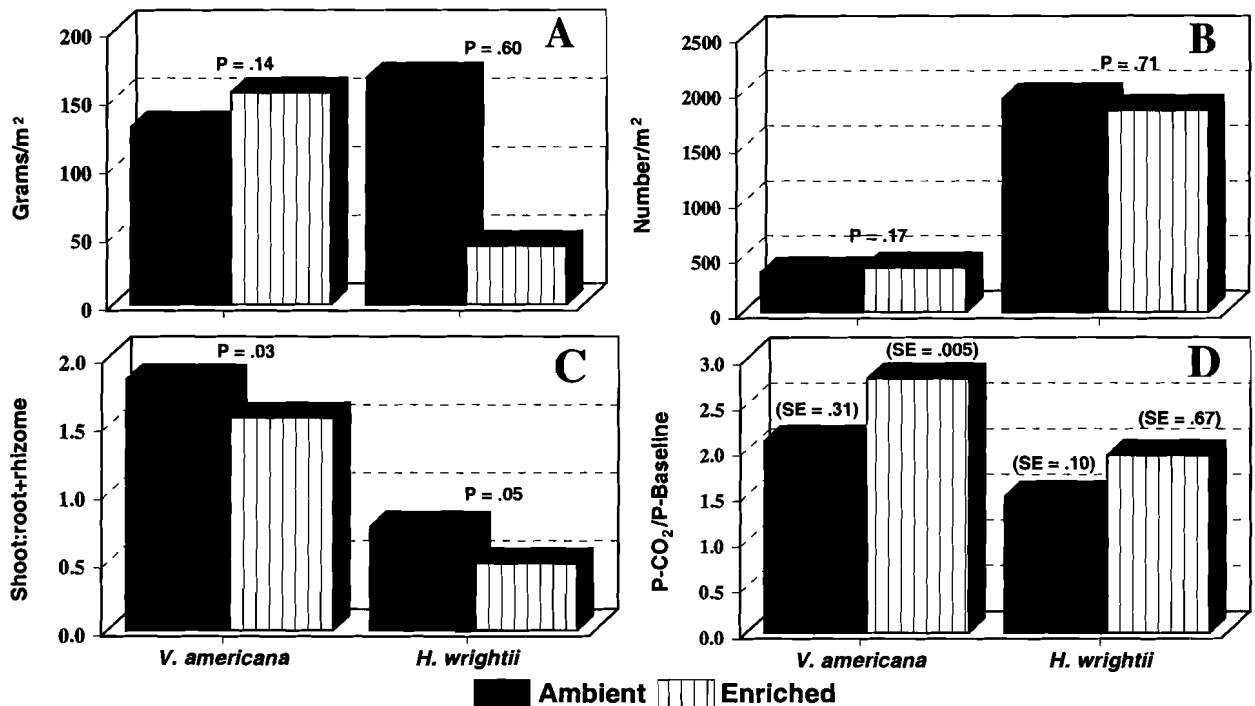
Figure 2-9. Growth responses to elevated carbon dioxide for two species of submersed macrophytes. Responses are shown after 6 weeks of growth under either ambient or enriched concentrations. A. Total macrophyte biomass. B. Macrophyte density. C. Ratio of shoot to root+rhizome biomass. D. Potential for altered photosynthetic capacity as determined by the enhancement of photosynthesis by carbon dioxide addition (P-CO_2) relative to rates with no carbon dioxide addition (P-Baseline).

2-9c), indicating increased biomass allocation to root and rhizome tissue. Thus carbon dioxide enrichment does have longer term consequences for these species. The lack of overall growth responses may have been due to the timing of the experiment (plants were already near peak biomass at the onset of treatment). Also, a longer experiment may have made a greater difference in total biomass. Alternatively, plant growth may have been subject to limiting effects of factors other than carbon dioxide, although tissue nutrient concentrations and carbon-to-nitrogen ratios suggest that growth was not nitrogen limited.

Both species did exhibit an increase in photosynthetic capacity following growth under elevated carbon dioxide concentrations (Fig. 2-9d). Higher primary production with increased concentrations of carbon dioxide may benefit consumer organisms. Similar responses by nuisance canopy forming species, however, would cause recreational and socioeconomic problems by killing fish and hindering boating (Fig. 2-4). The relatively low biomass of epiphytes on *Vallisneria* did not increase with carbon dioxide enrichment, but the epiphyte biomass on *Halodule* nearly doubled. This increase of epiphyte biomass on *Halodule* suggests the potential for a shift in balance between epiphytes and seagrasses with rising concentrations of atmospheric carbon dioxide. In eutrophic waters where nutrient limitations

to algal growth are alleviated, rising carbon dioxide concentrations could result in excessive epiphytic growth and ultimately in SAV declines.

The ratio of carbon to nitrogen in *Vallisneria* leaf tissue increased with carbon dioxide enrichment, whereas in *Halodule* leaf tissue it remained unchanged. We can only speculate on the cause of the difference between species. Differences in epiphyte response may have been partly responsible, that is, *Halodule* leaves under enriched conditions were more epiphytized and thus effectively exposed to lower carbon concentrations at the leaf surface than were *Vallisneria* leaves. This explanation suggests that the carbon-to-nitrogen ratio of *Halodule* leaves with a lower epiphyte load would also increase under carbon dioxide enrichment. Alternatively, responses of individual species may reflect differences in carbon metabolism between species; specifically, *Halodule* may be more effective at internal recycling of photorespired carbon dioxide and consequently less responsive to external increases. High carbon-to-nitrogen ratios may result in poorer forage for consumer organisms and decrease the decomposition rate of plant detritus, thereby slowing nutrient recycling. Integrated, long-term studies are sorely needed to predict such consequences of rising atmospheric concentrations of carbon dioxide for SAV ecosystems.

Effects of Accelerated Sea-level Rise

An increase in global temperatures would accelerate present rates of sea-level rise through thermal expansion of ocean water and melting of polar ice caps (Titus 1988). Predicted increases range from 15 to 95 cm by the year 2100 (Houghton et al. 1995). The most obvious effect of a rise in mean sea level on submersed vegetation is an increase in the depth of water overlying SAV beds. The dependence of SAV distribution, production, and long-term survival on light availability is well established (Dennison 1987; Goldsborough and Kemp 1988). Because light is attenuated exponentially through the water column, small changes in depth may greatly reduce the amount of light transmitted to rooted plants, resulting in decreased productivity and shoreward shift in plant distribution. In areas where coastal development limits the potential for shoreline migration, an increase in water depth will result in a decrease in subtidal vegetated habitat.

Another major consequence of a rise in sea level will be the inland and upstream intrusion of salt water in rivers, bays, and wetlands, subjecting coastal sites to increases in both average salinity and the peaks of salinity pulses (Titus et al. 1991). The distribution and abundance of SAV along salinity gradients has been described for many estuaries, and we can thus associate general groups of species with broad salinity zones (Stevenson and Confer 1978; Verhoeven and van Vierssen 1978; Howard-Williams and Liptrot 1980; Brock and Lane 1983). However, understanding of the mechanisms underlying these patterns is limited. Community structure at any location reflects the salinity tolerances of individual species and biotic interactions with other species. Although salinity tolerances have been determined experimentally for various North American species (Haller et al. 1974; Twilley and Barko 1990), estimates for single species vary widely, probably because of both true ecotypic variation and experimental technique. Information is lacking for many species. There is very little information on the relative importance of biotic interactions in structuring SAV communities, particularly under changing environmental constraints. Therefore, to improve our ability to predict how changes in salinity will affect SAV communities, we simultaneously evaluated the abiotic and biotic controls of submersed macrophyte responses to salinity intrusion within experimental mesocosms.

Macrophyte Responses to Salinity Intrusion

We assessed the effects of salinity on some of the most common species of SAV found in coastal waters of the southeastern United States. We selected six species representing a range of habitat types (from freshwater to brackish) and values (important wildlife food plants versus nuisance species). Our experiments were designed to determine the direct effects of salinity on community structure through physiological tolerances of individual species and the indirect effects through the potential for changing competitive hierarchies along a salinity gradient.

Abiotic Control

The first experimental series was designed to determine the tolerance of each species to salinity. We planted each species individually and, following a 3-week acclimation period, adjusted salinities to experimental levels of 0, 4, 8, or 16‰; the high end of this gradient is about half of full seawater strength. We determined the salinity tolerance of each species from measurements of growth, biomass allocation, and plant constituent concentrations after about six weeks at treatment salinities.

Species were classified as intolerant of high salinities, tolerant of high salinities, or intermediate in response. The maximum salinity at which the two intolerant species persisted was quite low (4‰ for *Hydrilla verticillata* and 8‰ for *Heteranthera dubia*). The total biomass and growth rate of these species declined steadily as salinity increased from 0‰ to the tolerance limit. The proportion of total biomass allocated to leaf material also began an early decline with increasing salinity, indicating that the decrease in growth associated with increasing salinity was indeed a stress response. In contrast, the two tolerant species *(Potamogeton pectinatus* and *Ruppia maritima)* maintained a high biomass and growth rate and a constant proportion of leaf material across the range of salinities tested, indicating physiological adaptation to high salinity. Finally, two species *(Myriophyllum spicatum* and *Vallisneria americana)* showed intermediate response. Although total biomass decreased with increasing salinity, plants persisted at the highest salinity tested. Patterns of biomass allocation suggested some degree of salinity adaptation, but growth rates at the highest salinities indicated that mortality would ultimately occur. Thus persistence at high salinity was a function of the short duration of the experiment; these species can probably withstand pulses of high salinity better than can the intolerant species, but they would be eliminated by long-term increases of 4-8‰. From these physiological tolerances we can predict the potential species composition along a gradient of mean salinities (Table 2-1).

Biotic Interactions

We designed a second experimental series to determine how these potential patterns might be altered by competitive interactions. For this series each species was grown in paired combinations at the same four test salinities. Rather than planting all pairwise combinations of species, we measured the performance of each one relative to a reference species. These relative performances we then ranked to generate a competitive hierarchy at each salinity. Using this approach we found that the relative performances of the species and the consequent order of species dominance generally remained constant from low to high salinities. Strong competitors such as *Hydrilla verticillata* and *Heteranthera*

Table 2-1. Potential changes in community composition of various species of submerged aquatic vegetation as a result of increased salinity. Given this assemblage of species, those species marked with an asterisk are expected to dominate the community.

A. Potential community composition determined from maximum salinity tolerances of individual species. An X indicates species presence at the given salinity.

	Salinity ‰			
	0	4	8	16
Hydrilla verticillata	X	X		
Heteranthera dubia	X	X	X	
Myriophyllum spicatum	X	X	X	X
Vallisneria americana	X	X	X	X
Potamogeton pectinatus	X	X	X	X
Ruppia maritima	X	X	X	X

B. Predicted community structure based on salinity tolerance and competitive performance. An X indicates species presence at a particular salinity.

	Salinity ‰			
	0	4	8	16
Hydrilla verticillata	*	X		
Heteranthera dubia	*	*	X	
Myriophyllum spicatum	*	*	X	X
Vallisneria americana	X	*	X	X
Potamogeton pectinatus	X	X	*	*
Ruppia maritima	X	X	*	*

dubia dominated at low salinities and were excluded from the high end of the salinity gradient by physiological intolerance to the abiotic conditions. Those species tolerant of high salinities, such as *Ruppia maritima* and *Potamogeton pectinatus*, were weak competitors; they were outcompeted at the low salinities and had a refuge at the stressful end of the salinity gradient. Salinity adaptation in this system thus appeared to result in a classic tradeoff between stress tolerance and competitive ability. At high salinities, information on salinity tolerance alone becomes sufficient to predict community structure.

Superimposing the effects of biotic interactions on the potential species composition as previously determined from salinity tolerances alone allows predictions for realized community structure along a salinity gradient (Table 2-1). Biotic interactions seem to play a large role in structuring the community at low salinities, and tolerance of abiotic conditions is more important at high salinities. These results are consistent with evidence from other systems in which species have shared preferences for habitat conditions, with competitive hierarchies excluding species at different distances along a stress gradient. Predictions for alterations in the salinity structure of any coastal area can be derived from physical information on local geomorphology,

watershed freshwater inputs, the volume of the tidal prism, and predicted sea-level rise. Given an existing SAV community composition and an expected change in salinity, information from this study can be used to predict changes in SAV community structure. It is important to note, however, that our experiments determined the potential for community changes following short-term salinity pulses based on competition for limiting nutrients by mature plants. More accurate predictions will require information on long-term salinity increases, the role of competition for other limiting resources such as light, and responses by other plant growth stages, particularly during propagule formation and recruitment.

Effects of Increased Storm Disturbance

An increase in the severity and frequency of tropical storms as a result of warmer tropical seas would have acute impacts on coastal SAV. Currents generated by strong winds cause erosional depressions (blowouts) that migrate through seagrass beds (Patriquin 1975). Blowouts are recolonized from seeds or vegetative branching, favoring species that can tolerate unstable mineral sediments. Thus recurrent blowouts may cause a species shift favoring colonizing species such as *Halodule wrightii* and *Syringodium filiforme* over "climax" species such as *Thalassia testudinum* (Clarke and Kirkman 1989; Williams 1990). If disturbances occur more frequently than recolonization can take place, all seagrasses may be lost from an area. Intense storm events may also result in temporary or permanent loss of seagrasses through increased water column turbidity (Davis and Carey 1981) or by complete burial (Onuf and Quammen 1983). Reduction or elimination of tidal freshwater SAV by scouring, turbidity from sediment resuspension and runoff, and burial from sedimentation has also been documented (Bilby 1977; Rybicki and Carter 1986; Johnstone and Robinson 1987).

Far less studied, but of potentially equal importance, are the chronic impacts of storm disturbance on coastal SAV. Following erosion of patches to mineral sediments by intense wind and wave disturbance, shifts in community composition can occur because of the varying resource requirements of individual species (Williams 1990). However, storm disturbances other than intense erosion events can also influence resource availability. For example, relatively small amounts of sediment deposition can cause gradual changes in the sedimentary environment across broad zones and can be a result of frequent, minor storms. By changing the availability of sediment nutrient resources, such chronic disturbance could also influence community pattern. To improve our ability to predict responses of coastal SAV to overall increases in storm disturbance, we studied the role of chronic physical disturbance in patterns of seagrass distribution and abundance in coastal Louisiana.

Responses to Overwash Disturbance

We used a combination of field observations and field experiments to relate seagrass distribution and abundance to physical factors associated with storm disturbance and to test the effects of disturbance-induced environmental conditions on observed patterns. Our investigations focused on an extensive seagrass bed in Chandeleur Sound that is protected from the Gulf of Mexico by a low-relief barrier island chain, the Chandeleur Islands. Storms regularly overwash the islands and deposit sandy, shoreface sediments in the seagrass community, but erosion and uprooting of vegetation are rare (Fig. 2-10).

From surveys of a series of 16 shore-normal transects across the seagrass bed, we were able to relate seagrass community structure to dominant environmental characteristics. We placed transects randomly within one of two disturbance regimes, in zones of frequent island overwash or in relatively protected zones behind emergent marsh. Although we found no difference in the frequency of occurrence of any species between the two disturbance regimes, we found that the average percent cover of

Thalassia was highest in protected zones whereas that of *Syringodium* was highest in overwashed zones. The nature of the sedimentary environment was related to overwash frequency; regardless of the dominant seagrass species, sediments within the overwashed zones were characterized by a higher proportion of sand and lower availability of inorganic nitrogen than were sites within the protected zones. By identifying those environmental characteristics associated with the highest percent coverage of each seagrass species, we were then able to determine the conditions contributing to patch dominance. Patches dominated by *Syringodium* were indeed associated with sandy sediments, whereas patches dominated by *Thalassia* were found in sediments of high organic content and low proportion of sand. Our subsequent growth experiments showed that *Thalassia* grows more rapidly in the relatively nutrient-rich sediments found in protected areas, whereas *Syringodium* shows no difference in growth between habitats. Presumably patches dominated by *Syringodium* are more prevalent in overwashed areas because of reduced competition from *Thalassia*.

These studies indicate that seagrass community organization can indeed be controlled in part by frequent and relatively minor overwash sediment deposition, either directly as in the case of *Thalassia* or indirectly as in the case of *Syringodium*. Therefore, by increasing deposition of sandy beach and offshore sediments in seagrass beds, a rise in the frequency of low intensity storms would alter community structure. We expect the chronic effects of increased sediment deposition from storm-generated waves to parallel the acute effects, causing an ultimate shift in community composition to early colonizing species.

Conclusions

Effects of Elevated Dissolved Inorganic Carbon

Photosynthesis

Photosynthesis was likely to increase with increased concentrations of dissolved carbon dioxide for a number of plant species and for most plant species during periods of rapid growth and/or warmer temperatures. The sole exceptions appeared to be for plants growing in environments high in dissolved carbon dioxide. The macrophyte species from the environments tested, however, seemed unlikely to increase photosynthesis in response to increased concentrations of dissolved bicarbonate and may be inhibited by such increases which raise pH and decrease available dissolved carbon dioxide. This effect may have been, in part, an experimental artifact arising from a rapid experimental increase in bicarbonate concentration and pH in plants primarily adapted to using free carbon dioxide.

Phytoplankton from saline environments, even if only brackish, did not respond to increased carbon dioxide concentrations, probably because photosynthesis was saturated by available concentrations of bicarbonate. Freshwater

Figure 2-10. The seagrass ecosystem of Chandeleur Sound, Louisiana, showing seagrass beds and areas of storm overwash.

phytoplankton did respond to increases in both dissolved carbon dioxide and dissolved bicarbonate on most occasions, except for one environment high in dissolved carbon. Even for the latter site, photosynthesis was increased on occasion.

Finally, benthic microalgal photosynthesis did not respond to increases in either dissolved carbon dioxide or dissolved bicarbonate. However, in highly autotrophic sediments in waters with low total inorganic carbon or low dissolved carbon dioxide, this community may respond as did freshwater phytoplankton.

Growth

Increased carbon dioxide did not increase production of plant biomass for either *Halodule wrightii* or *Vallisneria americana* subjected to a short-term, late-season enrichment; however, it did increase the biomass of seagrass epiphytes and did alter the allocation of macrophyte biomass, increasing the relative proportion of belowground biomass in both species. Increased carbon dioxide also increased the relative proportion of carbon to nitrogen in leaf tissues of the freshwater species. In addition, growth under increased carbon dioxide did not cause photosynthesis to acclimate to higher concentrations for either species.

Predictions for SAV Communities Under Elevated Dissolved Inorganic Carbon

Community composition will shift towards species which are less efficient users of bicarbonate, and shifts in the relative importance of primary producer groups are possible. Phytoplankton and epiphyte responses may be detrimental to both growth and survival of submersed species, particularly in eutrophic waters where nutrient limitations to algal growth are alleviated. Responses may favor SAV species whose ecological requirements are compatible with enhanced production of phytoplankton and/or epiphytes.

Benthic microalgal production is likely to be inhibited by enhanced production of phytoplankton, epiphytes, and macrophytes due to shading effects.

Shifts in the allocation of biomass to belowground plant tissues will have important consequences for other species using SAV habitats. For example, species such as wintering redhead ducks which feed primarily on belowground tissues of *Halodule wrightii* may find an expanded food base, while species such as juvenile shrimp may find a reduction in the cover they need for survival.

Increases in the relative concentration of carbon to nitrogen in plant tissues will make for poorer quality forage for grazing species such as wintering waterfowl. Decomposition processes will likely be slowed as organic matter becomes more refractory, decreasing the amount of production by higher trophic levels dependent on detrital food chains. Higher tissue/detrital carbon-to-nitrogen ratios may also alter the cycling of other critical nutrients such as nitrogen, with largely unknown effects for these

ecosystems. This alteration may also happen to phytoplankton communities, but no research has been conducted on this aspect to date. Other possible effects on macrophytes include alteration of plant morphology, increased biomass, accelerated growth, and compression of life history.

Effects of Increased Salinity Caused By Elevated Sea Level

Based on the responses of mature plants to short-term salinity increases, we conclude that macrophyte species which tolerate high salinities are generally weak competitors at lower, less physiologically stressful salinities. Species that tend to dominate the community at low salinities are excluded from waters of higher salinity by physiological intolerance to abiotic conditions.

In systems that experience a salinity increase from freshwater to oligohaline (0.5-5‰) conditions, consequent changes in SAV community structure will be highly influenced by the competitive abilities of both existing species and new recruits. Strong competitors such as *Hydrilla verticillata*, *Myriophyllum spicatum*, and *Heteranthera dubia* are predicted to dominate Gulf of Mexico systems at low salinity.

Changes in SAV community structure in mesohaline (5-18‰) systems subjected to salinity increase will be strongly governed by the salinity tolerance of existing species and new recruits. Salt-tolerant species such as *Potamogeton pectinatus* and *Ruppia maritima* will likely dominate systems at high salinity.

The ecological value of SAV systems is a function of both primary and secondary production. Therefore, although important wildlife food plants such as *Ruppia maritima* and *Potamogeton pectinatus* may actually be enhanced by salinity increase within the mesohaline range, future habitat value will depend also on responses of other trophic levels such as macroinvertebrates. In some instances a rise in salinity may eliminate nuisance species such as *Hydrilla verticillata* and *Myriophyllum spicatum*.

Effects of Increased Storm Disturbance on Seagrass Systems

Increased deposition of sandy shoreface sediments in seagrass beds results in a higher proportion of large-sized particles in the substrate and lower availability of inorganic nitrogen. Seagrass beds protected from frequent overwash deposition are dominated by *Thalassia testudinum*, a climax seagrass species with a high nitrogen demand, while *Syringodium filiforme* dominates areas subject to frequent overwash deposition, presumably because of reduced competition from *Thalassia testudinum*. Therefore, increased deposition of sandy sediments caused by increased storm disturbance will likely cause a shift in seagrass community composition to early colonizing species *(Syringodium filiforme, Halodule wrightii)* with relatively low nutrient demands.

Chapter 3:
Global Climate Change and Sea-level Rise: Estimating the Potential for Submergence of Coastal Wetlands

by

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Abstract: The ability of coastal wetlands to keep pace with sea-level rise through vertical accretion and transgression onto adjacent upslope habitats was examined for the following coastal habitats in the southeastern United States: low salt marsh, high salt marsh, brackish marsh, and mangrove forests (fringe, basin, and overwash islands). The relationship between vertical accretion and soil elevation change was determined for these wetland types along gradients of marsh type, tidal range, and subsidence. Simultaneous measures of vertical accretion and soil elevation change were used to calculate each wetland's rate of shallow subsidence (accretion minus elevation change) and to evaluate the potential for submergence of each wetland given the local rate of sea-level rise. Significant rates of shallow subsidence were measured at 7 of 12 marsh-mangrove wetlands. Four of these seven sites experienced a significant elevation deficit (elevation minus relative sea-level rise), but none of the four sites experienced a significant accretion deficit (accretion minus relative sea-level rise), indicating how misleading accretion data can be when evaluating the potential for submergence of coastal wetlands. These findings also indicated that subsurface processes occurring in the top few meters of the soil were as or more important in determining marsh elevation than surface accretionary processes for some of the marshes. Subsurface processes that likely influenced elevation included compaction, plant growth, plant decomposition, and shrink-swell from water storage. Forces driving these processes apparently included seasonal changes in water levels and aperiodic occurrences of major storms. Hence, the potential for submergence of some coastal marshes is best determined by calculating elevation deficits rather than accretion deficits.

Rates of marsh transgression onto adjacent upland forests were determined at two high salt marshes located on Pamlico Sound, North Carolina, by radiocarbon dating of basal marsh peats along transects running from the marsh into the forest. The rate of movement of the marsh edge onto adjacent forest habitat was neither gradual nor constant, but was instead punctuated. The ages of the basal marsh sediments were grouped, indicating that transgression occurred as a series of events separated by longer periods of relatively little marsh-edge movement. It is unlikely that the transgression events were initiated directly by rapid, local relative sea-level rise because the events were not synchronous between the two sites. Rather, the transgression events were likely generated by disturbance of the upland vegetation, allowing the marsh to leap forward. A likely vector for disturbance would be major storms (e.g., hurricanes) or fires, although sea-level rise is still the driving force behind the transgression. Hence, short-term rates of marsh transgression may be meaningless and may not be useful tools to predict wetland habitat change, at least for some marshes.

The findings from this study indicate that predicting the vertical buildup and migration of coastal wetlands in response to sea-level rise requires site-specific information, and also that we need to understand more about the interactions among vegetation, soil, and hydrologic processes as they relate to soil elevation in marshes and mangrove forests if we are to properly manage these resources during future increases in sea level. Specifically, we need information on shallow subsidence from additional environmental settings, the critical processes controlling elevation in each environmental setting and site, the natural forces driving the processes controlling elevation, and the influence of management processes on shallow subsidence, marsh transgression, and the potential for marsh submergence.

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Introduction

In this chapter we present a summary of the technical results of a multiyear investigation into the relationships among accretionary processes, sea-level rise, and the potential for submergence of coastal wetlands during future rises in sea level. Technical explanations of the methodologies and experimental design used in this study are provided in Boumans and Day (1993), Cahoon et al. (1995a; 1995b; 1996a; 1996b), Reed and Cahoon (1992), and Reed et al. (1995).

Global mean sea level has risen approximately 1–2 mm/year during the past 100 years (Gornitz 1995). The Intergovernmental Panel on Climate Change predicts a 50-cm rise in average global eustatic sea level by 2100, between two and five times the rise in the past century (Watson et al. 1996). The low and high estimates of change range from 15 to 95 cm (Watson et al. 1996). Latest estimates by the U. S. Environmental Protection Agency (USEPA) similarly indicate that global warming will likely raise sea level 15 cm by the year 2050 and that the present rate of eustatic sea-level rise will increase by 4.2 mm/year (two- to fourfold) by the year 2100 (Titus and Narayanan 1995). These estimates do not include sea-level rise caused by factors other than global warming (e.g., land subsidence). Areas with high local rates of subsidence, such as the Mississippi River delta, are currently experiencing relative sea-level rise rates (i.e., eustatic sea-level rise plus land subsidence) up to 10 times the global mean sea-level rise rate (Penland and Ramsey 1990; Gornitz 1995). The potential for submergence of coastal wetlands, particularly deltas, will increase under a scenario of rising relative sea level (Gornitz 1991).

In order for marshes not to become submerged as sea level rises, vertical buildup of the marsh surface will have to equal or exceed the rate of relative sea-level rise. The question arises as to how an increase in sea level will affect marsh sediment deposition, vertical accretion processes, and ultimately elevation. An increase in sea level may increase or decrease the local tide range and may also result in a phase shift of the estuary from flood- to ebb-dominated (Dyer 1995). Such changes would directly affect patterns of water circulation, suspended sediment concentrations, and marsh flooding, as well as rates of vegetation growth and, ultimately, marsh accretionary processes (Dyer 1995; Reed 1995). Also, increased global warming may increase the frequency of hurricanes (Emanuel 1987), which could influence local sediment supplies and marsh accretionary processes as well as erosion caused by wind and waves. As sea level rises, marshes may migrate landward, provided there is no barrier to movement such as a fixed structure (e.g., a building or seawall). Subsidence can vary strongly among sites: for example, being high in deltas with thick Holocene deposits and low on stable geologic formations such as ancient shields.

Hence, the potential for coastal marsh submergence is controlled more by the local environmental factors of relative sea-level rise, coastal geomorphology, sediment supply, and frequency of major storms than by the trend in eustatic mean sea level (Gornitz 1995). Therefore, predicting the potential for coastal marsh submergence caused by sea-level rise requires site-specific information and an improved understanding of the interactions among marsh vegetation, soil, and hydrological processes.

In this study, we investigated marsh accretion and elevation change in coastal marshes and mangroves selected along gradients of tidal range, subsidence, and marsh type in order to evaluate the processes controlling both vertical development of the marsh surface and transgression (horizontal movement) of the marsh surface onto adjacent uplands. The goal of this study was to improve our understanding of the relationships among marsh accretionary processes, marsh elevation changes, hydroperiod, relative sea-level rise, and the potential for coastal marsh submergence so that we could better evaluate the ability of marshes to keep pace with sea-level rise.

Vertical Buildup of the Marsh Surface

Traditionally, the potential for marsh submergence has been determined by calculating accretion deficits (Reed and Cahoon 1993). Measured rates of vertical accretion are compared directly to local rates of relative sea-level rise. If accretion is not keeping pace with sea-level rise then an accretion deficit is said to exist, and the potential for submergence of the coastal marsh is high. The accretion deficit concept assumes that surface accretion measures are a good indicator of marsh surface elevation change. We also know, however, that the marsh surface subsides because of autocompaction of the Holocene marsh deposits (Kaye and Barghoorn 1964), as reflected in the sharp decline in water content as well as consolidation over the top 1 m of the marsh substrate (Kearney and Ward 1986) and as inferred from slower accretion rates for historic (^{137}Cs and ^{210}Pb) and geologic (^{14}C) accretion methods (Reed and Cahoon 1993; Stevenson et al. 1986), and also that additional subsidence may occur through faulting and compaction of deep sediments, particularly in deltaic environments (Penland et al. 1989). Hence, the validity of the assumption that surface accretion equals elevation change should be questioned. If the increase in elevation is smaller than the vertical accretion gain because of soil subsidence, then the accretion deficit concept is underestimating the potential for coastal marsh submergence. Important questions for coastal managers include: What is the relationship between accretion and elevation change? How does this relationship vary over the range of coastal hydrogeomorphic settings? If elevation gain is slower than accretion gain, what are the important processes controlling elevation? What natural forces drive these processes? And, what are

the implications for managing coastal wetlands during periods of rising sea level?

The objectives of this part of the study were to (1) measure accretion and elevation change in marshes along gradients of marsh type, subsidence, and hydroperiod; (2) evaluate the relationship between accretion and elevation change both within and between sites; (3) evaluate the role of hydroperiod in determining marsh response to sea-level rise; and (4) evaluate the relationship between elevation change and relative sea-level rise (i.e., calculate an elevation deficit).

Experimental Approach and Terminology

In order to meet these objectives and answer these questions, it was necessary to develop a new investigative approach that simultaneously quantified vertical accretion and surface-elevation change with a level of accuracy sufficient to distinquish between the influences of surface and subsurface processes on marsh elevation. Surface accretionary processes (e.g., sediment deposition and erosion) were determined from artificial marker horizon plots established on the marsh surface (Cahoon and Turner 1989). Marsh surface-elevation change was measured relative to a subsurface datum (usually 3–5 m deep) using a sedimentation-erosion table (SET) (Boumans and Day 1993). This method of measuring elevation integrates both surface processes (e.g., deposition, erosion) and subsurface processes (e.g., compaction, shrink-swell, plant growth, decomposition) occurring over the top several meters of the soil. The difference between the two simultaneous measures gives an estimate of the impact of subsurface processes on marsh surface elevation change and of the degree to which accretion measures alone underestimate the potential for coastal marsh submergence, if at all. The influence of subsurface processes on marsh elevation has been termed "shallow subsidence." These concepts and the relationship between the two methods are graphically presented in Fig. 3-1 and explained in detail in Cahoon et al. (1995a).

Study sites were selected along gradients of marsh type, subsidence, and tidal range, primarily in the southeastern United States (Fig. 3-2). Most sites were located in saline coastal habitats of low salt marsh (Old Oyster Bayou, Bayou Chitigue, and Tijuana Slough National Wildlife Refuge [NWR]), high salt marsh (St. Marks NWR and Cedar Island NWR), or mangrove (Rookery Bay) (Fig. 3-3a,b,c). Two sites were located in brackish marsh (McFaddin NWR and Three Bayous). At Rookery Bay, measurements were made in fringe, basin, and overwash island forests. The sites from the Mississippi River delta in Louisiana represent areas of high subsidence. Bayou Chitigue is a rapidly deteriorating low salt marsh, in contrast to Old Oyster Bayou, which is a stable, healthy marsh. All other sites represent low subsidence areas. All sites are microtidal, but the tidal range at St. Marks is five times greater than for Cedar Island. The tidal range at Tijuana Slough is three
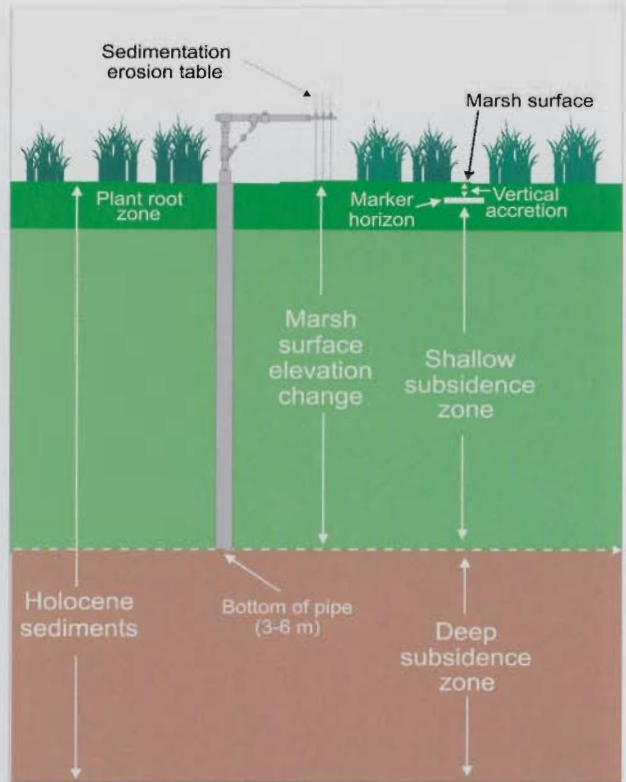
Figure 3-1. Conceptual diagram (not to scale) showing those portions of the soil profile being measured by the sedimentation-erosion table (SET) and marker horizon techniques. The boundary separating shallow and deep subsidence is defined operationally by the bottom of the SET pipe.

Figure 3-2. Location of study sites for estimating the potential for submergence of coastal wetlands.

times greater than the Louisiana marshes. Since both sediment distribution and plant growth are hydrologically mediated, hydroperiod (i.e., the frequency, depth, and duration of marsh surface flooding) was determined at each site from a local tide gauge and detailed levelling of the marsh

Fig. 3-3a. Low salt marsh dominated by *Spartina alterniflora*.

Fig. 3-3b. High salt marsh dominated by *Juncus roemerianus*.

Fig. 3-3c. Mangrove forest dominated by red mangrove, *Rhizophora mangle*.

surface (Reed and Cahoon 1992; Cahoon and Reed 1995; Cahoon et al. 1996a).

Shallow Subsidence

Comparison of annual means of vertical accretion and elevation change allowed us to calculate rates of shallow subsidence for each site (Table 3-1). Measurements were made approximately every 6 months over a 2- to 3.5-year period, and annual rates were determined from regression analyses. Vertical accretion rates at all 12 sites were significantly different from zero, with highest rates measured in low salt marsh, followed by brackish marsh, mangrove forests, and high salt marsh. In contrast, only 6 of 12 sites had rates of elevation change significantly different from zero with no apparent pattern related to wetland type. Significant shallow subsidence occurred at 7 of the 12 sites (Table 3-1), primarily in wetlands with highly organic or unstable soils.

Four of six low salt marsh and mangrove sites along the Gulf of Mexico had significant rates of shallow subsidence, ranging from 0.38 to 2.39 cm/year, with the highest rate measured at Bayou Chitigue. In contrast, Old Oyster Bayou, located near sediment-rich Atchafalaya Bay, and the basin mangrove forest at Rookery Bay had no significant shallow subsidence. The overwash islands and fringe mangrove forests at Rookery Bay, however, had significant rates of shallow subsidence of 0.38 and 0.58 mm/year. One of the islands had no significant elevation gain over the 2-year period despite significant vertical accretion.

In the southeastern United States, two high salt marshes dominated by black needlerush (*Juncus roemerianus*) had no significant elevation gain and a significant rate of shallow subsidence of nearly 3 mm/year. In contrast, two brackish marshes dominated by saltmeadow cordgrass (*Spartina patens*), one from the chenier plain and one from the delta plain along the north central Gulf of Mexico coast, had no measured shallow subsidence. In southern California, where sediment delivery to the marsh is related to erratic annual rainfall patterns and associated riverflows (Cahoon et al. 1996a), Tijuana Slough experienced a major sedimentation event associated with a major winter storm during our first sampling interval. In the low California cordgrass (*Spartina foliosa*) marsh, significant vertical accretion and elevation gain associated primarily with this event were measured, but no significant shallow subsidence occurred (Table 3-1). The high marsh, however, experienced a shallow subsidence rate of nearly 3 mm/year because of no significant gain in elevation over a 2-year period.

Significant rates of shallow subsidence indicate that, for some marshes, measures of total subsidence based on tide gauge records are underestimated by the amount of shallow subsidence occurring at depths between the tide gauge base and the marsh surface (Cahoon et al. 1995a). For example, at Bayou Chitigue, where the marsh is rapidly deteriorating, the actual rate of relative sea-level rise (RSLR) is likely greater than 3 cm/year (RSLR = 2.39 cm/year [shallow subsidence] + 1.38 cm/year [RSLR from tide gauge] = 3.77 cm/year).

Elevation Deficits

Significant rates of shallow subsidence also indicate that the potential for submergence of some coastal marshes is best determined by calculating elevation deficits rather than accretion deficits. Accretion and elevation deficits are

Table 3-1. Accretion, elevation, and shallow subsidence rates for selected coastal marshes in the United States.

Site	Dominant vegetation	Vertical accretion[a]	Change in elevation[a]	Shallow subsidence[b]	Length of record (year)
U. S. Southeastern coast					
Bayou Chitigue	*Spartina alterniflora*	2.67 ± 0.20**	0.28 ± 0.11	2.39**	3.0
Old Oyster Bayou	*Spartina alterniflora*	0.95 ± 0.19**	0.77 ± 0.24*	ns	3.0
Rookery Bay					
fringe forest	*Rhizophora mangle*	0.72 ± 0.02**	0.14 ± 0.05*	0.58**	2.5
basin forest	*Avicennia germinans*	0.60 ± 0.05**	0.37 ± 0.12*	ns	2.5
exposed island	*Rhizophora mangle*	0.63 ± 0.12**	0.25 ± 0.09*	0.38*	2.0
protected island	*Rhizophora mangle*	0.44 ± 0.03**	0.06 ± 0.11	0.38**	2.0
Cedar Island	*Juncus roemerianus*	0.37 ± 0.03**	0.08 ± 0.08	0.29**	3.5
St. Marks	*Juncus roemerianus*	0.46 ± 0.04**	0.19 ± 0.11	0.27*	3.0
McFaddin NWR	*Spartina patens*	1.11 ± 0.04**	1.26 ± 0.51	ns	2.0
Three Bayous	*Spartina patens*	0.78 ± 0.15**	1.49 ± 0.38*	ns	2.0
U. S. Pacific coast					
Tijuana Estuary					
low marsh	*Spartina foliosa*	1.31 ± 0.20**	1.96 ± 0.36**	ns	2.5
high marsh	*Salicornia subterminalis*	0.15 ± 0.01**	-0.13 ± 0.11	0.28*	2.0

[a] Vertical accretion and elevation change data are means ± 1 SE; units are cm/year. Means were calculated from regression analysis, and those rates which are significantly different from zero are indicated by an asterisk (5% = *; 1% = **).
[b] Shallow subsidence = (vertical accretion - elevation change). Shallow subsidence was calculated only for those sites where the mean vertical accretion and elevation change rates were significantly different (5% = *; 1% = **).
ns Indicates no significant difference between the rates of vertical accretion and elevation change.

calculated by comparing accretion and elevation rates with sea-level rise (Fig. 3-4). For example, data from Bayou Chitigue show how misleading accretion measures can be when used as a measurement of elevation increase (Fig. 3-4a). The accretion data indicate there is no deficit relative to sea level; indeed, there is an accretion surplus. Yet a significant elevation deficit exists. In contrast, there is no accretion or elevation deficit at Old Oyster Bayou, where the marsh surface is in equilibrium with local relative sea-level rise; the marsh is not deteriorating, and the vegetation is healthy (Cahoon et al. 1995a).

A significant rate of shallow subsidence does not automatically mean that an elevation deficit exists relative to sea level. Both black needlerush high salt marsh sites (Cedar Island and St. Marks) were in equilibrium with current rates of rise in sea level, and these marshes can be considered stable (Fig. 3-4b), despite significant shallow subsidence. Similarly, in the mangroves of south Florida, where sea-level rise estimates range from 2–4 mm/year (Maul and

Martin 1993; Wanless et al. 1994), three of the four sites were in equilibrium with the lower estimate of sea-level rise despite significantly smaller gains in elevation (compared to accretion) at three of the sites (Fig. 3-4c). Only the leeward island experienced an elevation deficit. Using the higher estimate of sea-level rise, both the leeward island and the fringe forest experienced a serious elevation deficit. Note, however, that none of the mangrove sites experienced an accretion deficit under the highest estimate of sea-level rise, again indicating how misleading accretion deficit data can be.

The infrequently flooded high marsh at Tijuana Slough, where there was significant shallow subsidence, experienced a significant elevation deficit (Fig. 3-4b). In the low marsh at Tijuana Slough, however, there was no accretion or elevation deficit (Fig. 3-4a) because a major winter storm in 1993 deposited about 32,000 metric tons of sediment, primarily in the low marsh (Cahoon et al. 1996a). This pulse of sediment ended nine years of drought, during which
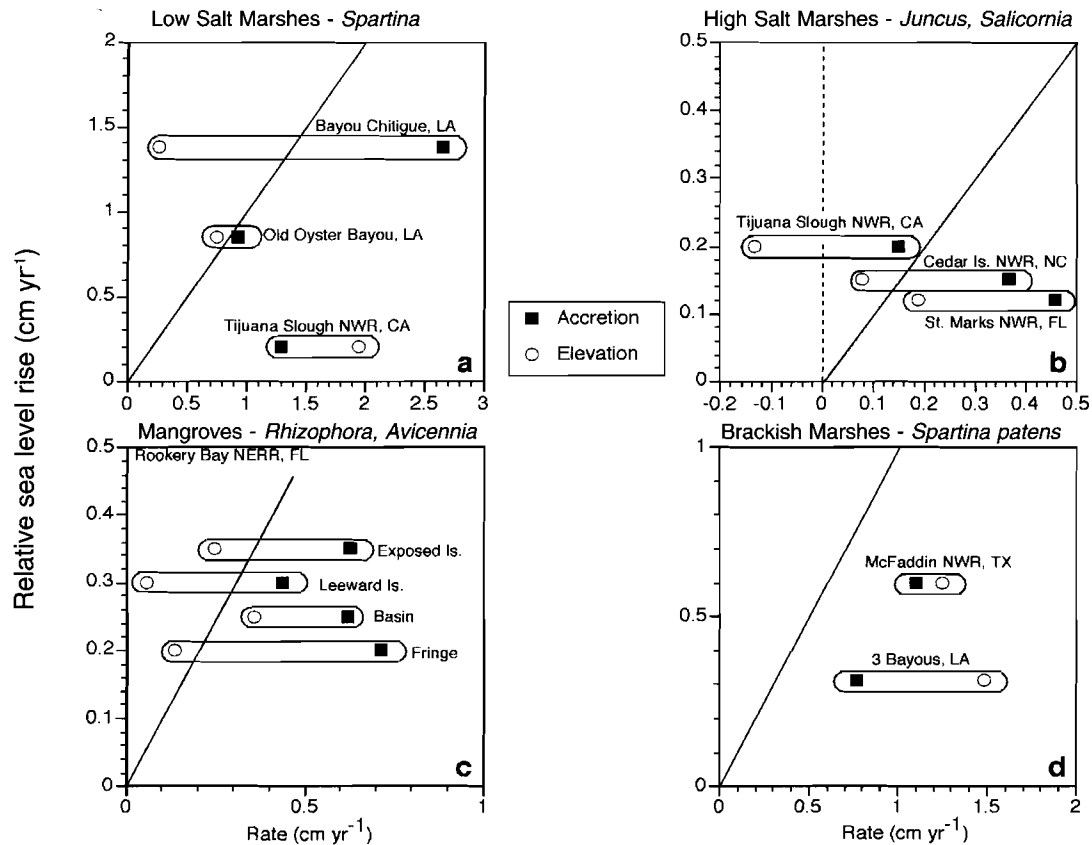
Figure 3-4. Relationship of vertical accretion and marsh surface elevation change with local relative sea-level rise for sites located in (a) low salt marsh, (b) high salt marsh, (c) mangrove forest, and (d) brackish marsh. Diagonal line indicates parity between accretion or elevation change and sea-level rise. Sea-level rise rates are from Stevenson et al. (1986) (North Carolina, northern Florida, and Texas), Baumann et al. (1984) (Old Oyster Bayou), Nyman et al. (1993) (Bayou Chitigue), Wanless et al. (1994) and Maul and Martin (1993) (southern Florida), and Roemmich (1992) (Tijuana Estuary).

time little or no sediment deposition occurred because of very limited river flow. There has been little sediment deposition since the storm. Finally, the brackish marshes on the northern Gulf of Mexico coast did not experience either shallow subsidence or an elevation deficit (Fig. 3-4d).

Processes Influencing Elevation Change

Significant rates of shallow subsidence indicate that subsurface processes can exert as strong, or stronger, an influence on marsh surface elevation as surficial processes of sediment deposition and erosion. Within-site comparisons of seasonal patterns (every 6 months) in vertical accretion and elevation change suggested that changes in marsh surface elevation are related to aperiodic soil compaction associated with hurricanes and to the changes in soil volume associated with (a) seasonal belowground plant production and decomposition cycles and (b) water storage as influenced by seasonal variations in local tide range and sea level. Hence, the controlling process is site specific and depends on the environmental setting and type of

marsh substrate (e.g., organic vs. mineral soil). Marshes with highly organic or unstable substrates were most likely to exhibit shallow subsidence.

Shallow subsidence at two sites was apparently related to compaction of shallow sediments (<5 m) during passage of a major hurricane, with the degree of compaction related to stability of the substrate. For example, in 1992, Hurricane Andrew deposited 2–3 cm of material in the smooth cordgrass (*Spartina alterniflora*) salt marshes at Bayou Chitigue and Old Oyster Bayou in the Mississippi River delta in Louisiana (Cahoon et al. 1995b). Bayou Chitigue has a weak, deteriorating mineral soil caused by stress to the vegetation (Day et al. 1994). This marsh experienced a loss in elevation despite storm-related sediment accretion, apparently as a result of sediment overburden and/or storm surge impacts (Fig. 3-5a). The loss of elevation persisted over the next 2.5 years, suggesting it was caused by reduced soil porosity and compaction of organic matter. Old Oyster Bayou has a healthy, vigorous vegetative cover and
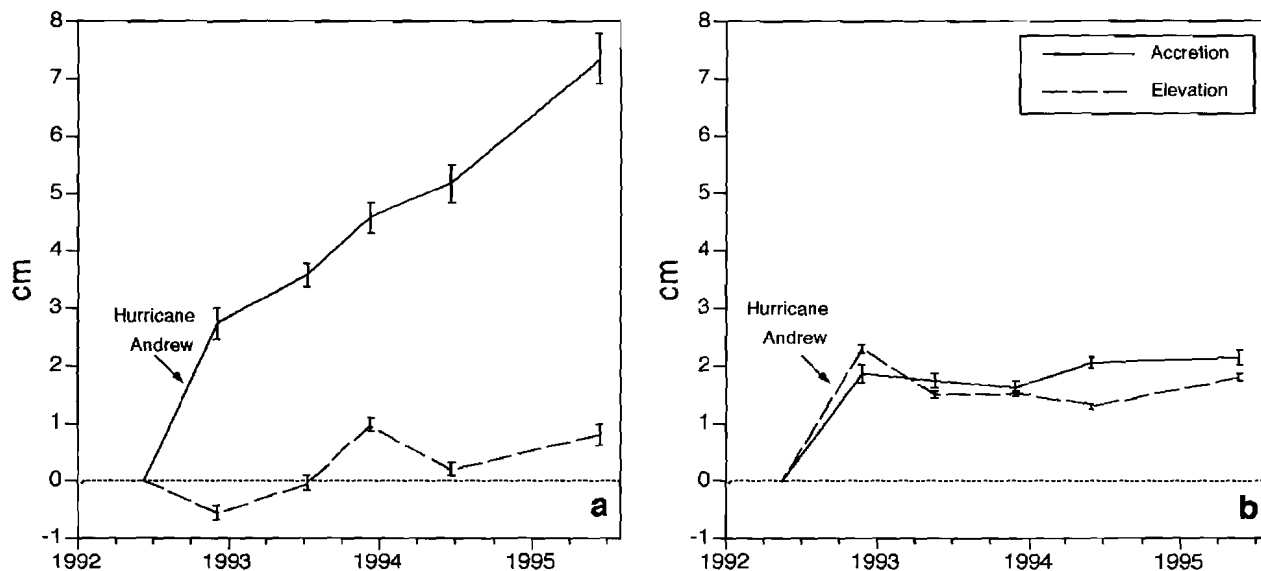
Figure 3-5. Marsh surface elevation change and vertical accretion at (a) Bayou Chitigue and (b) Old Oyster Bayou located in the delta plain of Louisiana. Separation between the two lines represents shallow subsidence.

stable soil substrate and experienced no loss of elevation (Fig. 3-5b). A similar loss of elevation related to passage of a hurricane was observed at the black needlerush marsh in North Carolina (Cedar Island NWR), which has a highly organic substrate (>60% by weight) (Fig. 3-6a). Three different hurricanes impacted this site, and each time there was a loss of elevation, even if sediment was deposited. The elevation loss was apparently related to compaction of organic matter and/or degassing of the substrate. After

the second hurricane, the marsh surface apparently rebounded, only to be compressed again by the third storm. These results suggest that some marshes with highly organic substrates are being aperiodically compacted by major storms.

At the high salt marsh dominated by black needlerush in northern Florida (St. Marks NWR), there was no discernible relationship between the patterns of vertical accretion and surface elevation change (Fig. 3-6b), indicating

Figure 3-6. Marsh surface elevation change and vertical accretion at (a) Cedar Island on the southeast Atlantic coast and (b) St. Marks on the northern gulf coast of Florida.

that elevation is controlled by subsurface processes rather than the surficial processes which influence accretion. The changes in elevation were likely not related to daily tidal flooding and associated water storage, as has been reported for low salt marshes in New England (Nuttle et al. 1990), because surface elevation did not change over a single tidal cycle when the ground water level varied from greater than 33 cm below the soil surface to 6 cm above it (Cahoon et al. 1995a). Two possible explanations for this pattern are seasonal changes in soil water storage and changes in the volume of the root zone related to a seasonal pattern of plant production (summer) and decomposition (winter) (Cahoon et al. 1995a).

The seasonal trend in elevation could be caused by changes in water storage directly related to the seasonal variation in Gulf of Mexico mean water level and/or an increase in depth of water flooding the marsh at high tide. Mean water level in the northern Gulf of Mexico averages 25 cm higher in summer (Marmer 1954), and there was a 12-cm difference in mean daily tide range between summer (88.7 cm) and winter (76.4 cm) measured by a water level gauge at the site (Reed et al. 1995). Alternatively, the seasonal variations in water levels may influence plant production and belowground decomposition processes. Increased daily tidal range during the summer creates more oxidized substrate conditions which are well suited for plant production (Steever et al. 1976; Howes et al. 1986). In addition, evapotranspiration during periods of active photosynthesis in salt marsh plants can remove significant amounts of water from the soil (Dacey and Howes 1984; Morris and Whiting 1985). During the winter, aerobic plant decomposition processes are enhanced by lower mean

water levels and plant senescence and death (Hackney and de la Cruz 1980). The combined influence of seasonal variations in both water level and plant production and decomposition may be responsible for the pattern of elevation change shown in Fig. 3-6b. In contrast, the seasonal trend was not observed in the black needlerush marsh at Cedar Island because there was no strong seasonal pattern in daily tidal range (16.8 cm in summer versus 24.1 cm in winter) and Cedar Island marsh is irregularly flooded, wind-dominated, and characterized by long, shallow flooding events (average flooding event is 47 h long and 13.7 cm deep [mean maximum depth] versus 3.5 h and 16.9 cm deep [mean maximum depth] at St. Marks; Reed et al. 1995). Finally, the data were inconclusive regarding the potential influence of major storms on elevation at St. Marks. Major storms may have increased elevation in October 1992 and July 1994 through water storage, but Hurricane Allison had no effect on elevation in June 1995.

In the mangroves of Rookery Bay, which occupy an ecological niche similar to the salt marshes at St. Marks, elevation change closely followed accretion in the basin forest (Fig. 3-7) but lagged behind accretion in the fringe (Fig. 3-7) and overwash island (Fig. 3-8) forests because of the influence of subsurface processes. The basin forest was located inland of the fringe forest and therefore was hydrologically remote. The soil of the basin forest was highly organic (58% organic content) since much of the vertical accretion was due to accumulation of leaf litter. In contrast, soils of the fringe forest were highly mineral (8% organic matter) and were exposed to continuous wave and tidal action. Consequently, the soil surface was a mosaic of small patches (<0.5 m²) of mud and bare shell.
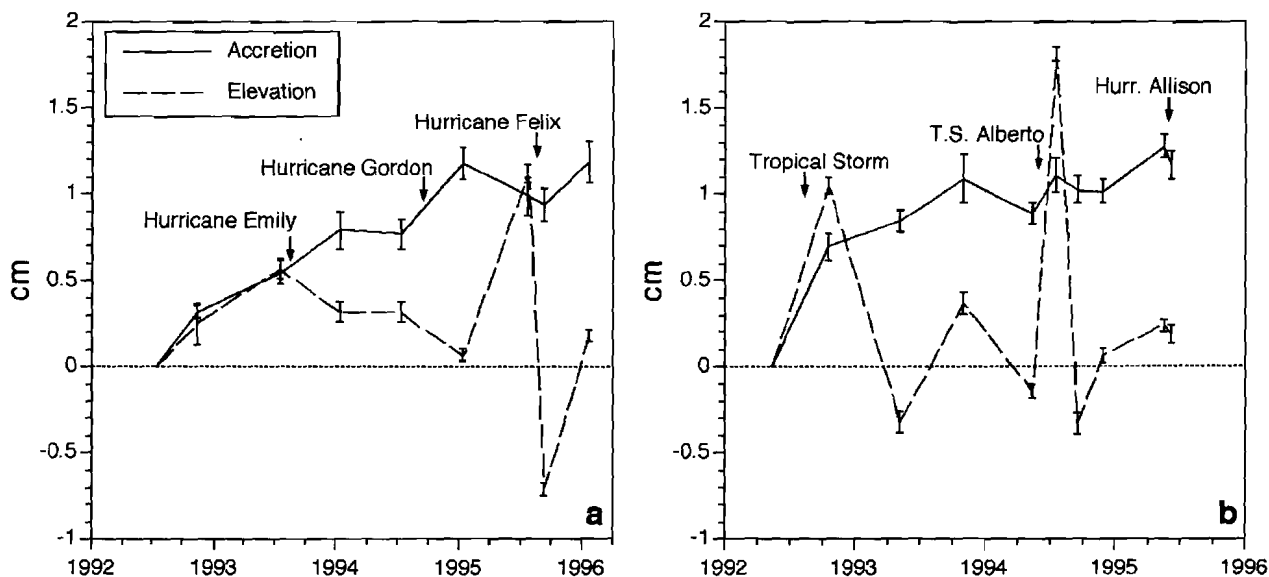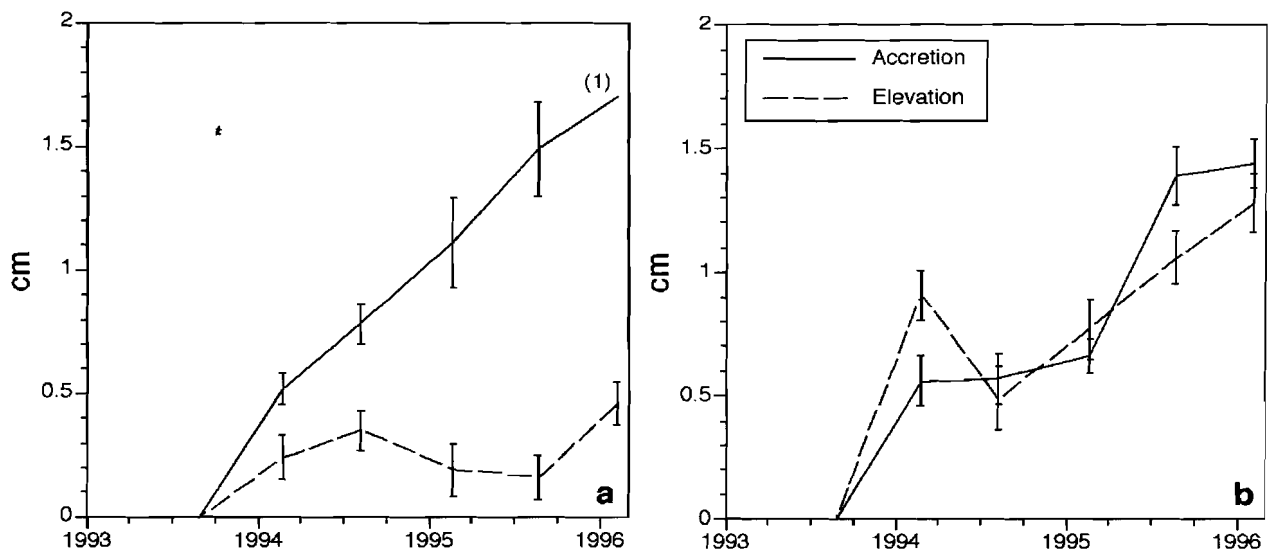

Figure 3-7. Marsh surface elevation change and vertical accretion at (a) the fringe mangrove forest and (b) the basin mangrove forest at Rookery Bay, Florida.

In the fringe forest, vertical accretion occurred wherever the loose, fine-grained mud was bound in place by filamentous algae. There were some bare shell patches where fine-grained mineral sediments did not accumulate because of wave action, although shells may continue to accumulate at this site. Since the marker horizon technique had an inherent bias toward measuring accreting surfaces to the exclusion of eroding surfaces (because those markers are lost), it likely overestimated accretion rates in the fringe forest. Erosion of the marker horizons occurred continuously over time, with only 50% of the markers remaining after 18 months and only 1 out of 21 remaining after 30 months. Hence, the slope of the accretion graph (Fig. 3-7) represents a maximum rate of accretion. On the other hand, the SET was equally likely to measure an eroding or an accreting surface and therefore provided a better estimate of overall surface elevation change. The difference between accretion and elevation (Fig. 3-7) was likely overestimated because of the bias of the accretion technique. The impact of erosion on elevation change was deduced by comparing the rate of shallow subsidence during the first 12 months, when erosion was low (Fig. 3-7), to the 2.5-year rate. The rate of shallow subsidence for the first year was 0.43 cm y^{-1}, indicating that erosion caused the remaining 1.5 cm y^{-1} loss in elevation (Table 3-1). Hence, most of the difference between accretion and elevation was apparently related to subsurface processes rather than erosion.

Two mangrove islands dominated by red mangrove (*Rhizophora mangle*), one exposed to wave fetch along most of the length of Rookery Bay and the other protected from wave action in the lee of a larger island, had substrates regularly washed by tides and firmly bound by fine roots (41% organic matter). The protected island had a

very flat topography and had no significant gain in elevation despite continuous accretion (100% of the markers recovered). The vertical buildup of the soil was apparently counterbalanced by compaction and decomposition of organic matter (i.e., shallow subsidence; Fig. 3-8). The exposed island had a raised berm on its windward shore, and there was greater variation in the accretion data compared to the protected island. This greater variability, considered with the significant gain in elevation, suggests that there may be a closer relationship between accretion and elevation for this site than our calculated rate of shallow subsidence would indicate.

In the high marsh at Tijuana Estuary, the substrate consisted primarily of coarse-grained sediments (i.e., sand) with only shallow peat development (Cahoon et al. 1996a). This site received little influx of mineral sediments even during the major flood which occurred at the beginning of the study (Fig. 3-9a). There was a small but significant elevation gain during the sampling interval which included the storm, followed by a significant and steady decline. We hypothesize that two months of freshwater river flows reduced the salinity impacts of daily tides and temporarily improved growth conditions in this sandy soil (i.e., reduced high soil salinities related to nine years of drought), which resulted in a short-term increase in belowground plant growth (Zedler et al. 1986) and a gain in elevation. When drought conditions returned, production of belowground plant material declined because of salt stress (Zedler et al. 1986) which resulted in a loss of elevation. In contrast, there was no shallow subsidence in the low marsh at Tijuana Estuary.

The rates of vertical accretion and elevation change were the same in the two brackish marshes, yet the data from
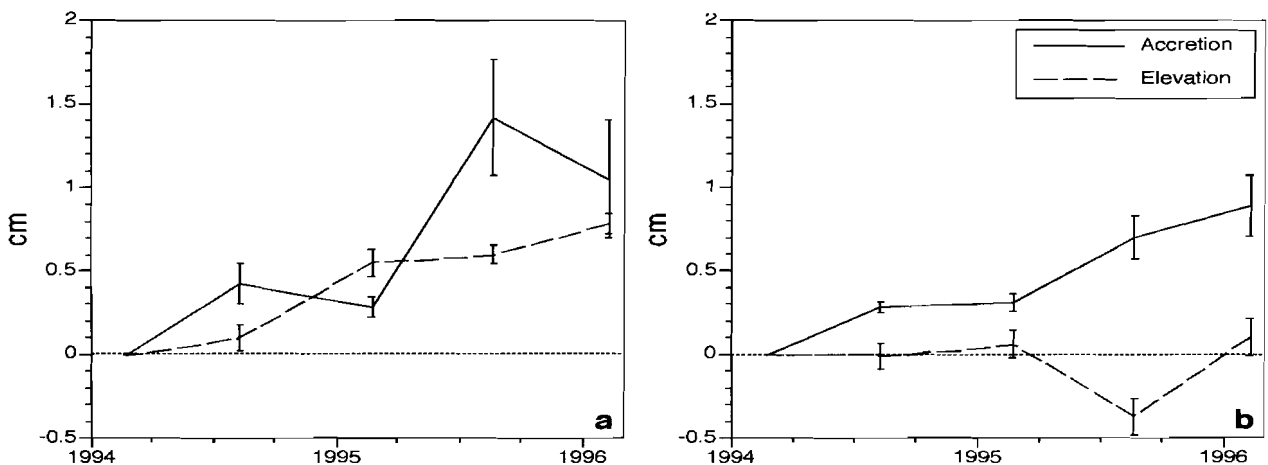

Figure 3-8. Marsh surface elevation change and vertical accretion at (a) the exposed island and (b) the protected island at Rookery Bay, Florida.
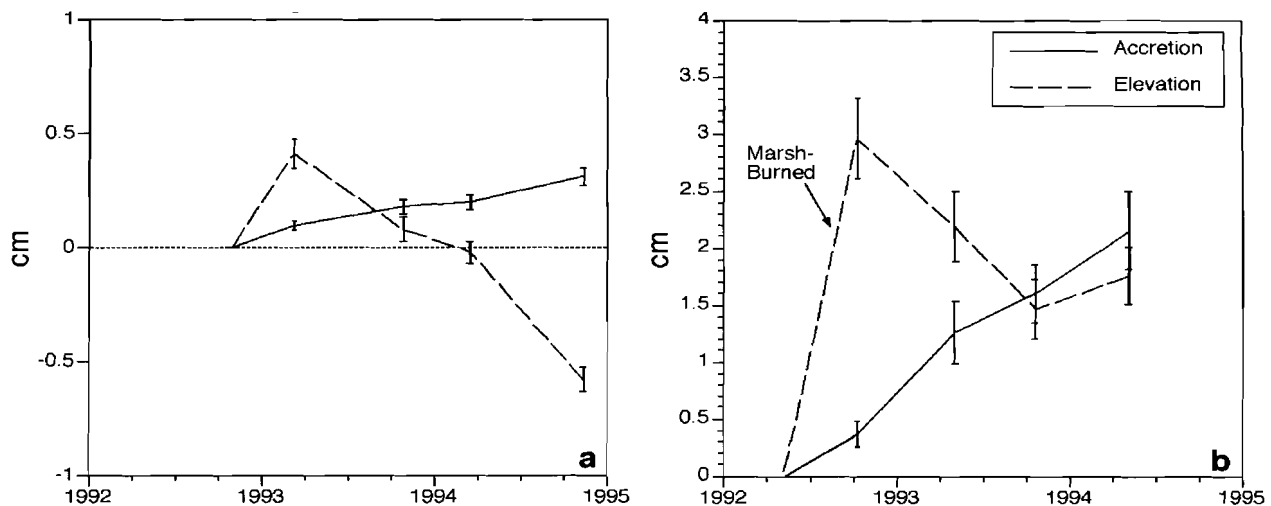
Figure 3-9. Marsh surface elevation change and vertical accretion for (a) the high marsh at Tijuana Estuary, California, and (b) the brackish *Spartina patens* marsh at McFaddin NWR on the upper Texas coast.

McFaddin NWR suggest that the management practice of burning the marsh may have influenced marsh elevation. A dramatic increase in elevation relative to accretion occurred during the first sampling interval, during which time the marsh had been burned (Fig. 3-9b). The rate of elevation change subsequently decreased until it was equal to the rate of accretion. The difference may have been related to a misinterpretation of the marsh surface because of accumulation of burned litter, or caused by an increase in soil volume associated with the rapid mineralization of nutrients and the resulting increase in growth of belowground plant parts.

Role of Hydroperiod in Vertical Accretion and Elevation Change

There was no significant relationship, either positive or negative, between vertical accretion and hydroperiod parameters (mean duration of flooding and mean maximum depth of flooding). Sites with higher duration of tidal flooding did not show increased vertical accretion, and the highest rates of accretion were at sites with relatively low duration of flooding. This pattern is in contrast to that reported by Cahoon and Reed (1995) for a single marsh in south Louisiana where there was an increase in accretion with increased flooding duration. The present analysis compares sites across the southeastern United States and across different marsh types. The sites with highest durations of flooding but only moderate levels of accretion were in brackish marshes (Three Bayous and McFaddin NWR) which are far from ready sources of sediment supply. Three Bayous is located in middle Barataria Basin, where there is no direct input of fluvial sediment. This marsh is also far from the bays in the southern part of the basin, a source of

sediments remobilized by storms (Reed 1989). Supplies of sediment to McFaddin NWR are probably dominated by rainfall input within the Sabine-Neches system, and periods of high coastal water levels will not always coincide with periods of sediment supply. In contrast, the site with highest accretion, Bayou Chitigue, is located close to an open bay area where the same events which flood the marsh surface may also introduce sediments (Reed 1989). These ideas are confirmed by an examination of vertical accretion versus mean maximal depth of flooding. Bayou Chitigue had relatively deep flooding and was supplied with sediment, which raised accretion rates. However, events which resulted in deep flooding at the other sites did not necessarily introduce sediments, as reflected by moderate levels of accretion.

Like vertical accretion, there was no significant relationship between elevation change and any of the hydrologic variables. These hydrologic analyses provide further confirmation that site-specific factors such as geomorphology, marsh type, sediment supply, and storm frequency strongly influence vertical accretion and likely control elevation change through both surface and subsurface processes.

Landward Migration of the Marsh Surface

As sea level rises, marshes, like barrier islands and other coastal environments, move landward up the coastal plain. While this fact has been generally recognized, there has been little attempt to characterize, model, or document the landward movement of the boundary between upland and marsh. In order to thoroughly understand the system-wide response of coastal wetlands to rising sea levels, and in

order to make reasonable predictions about the future of modern coastal wetlands, we must have a detailed understanding of the nature of marsh transgression, as well as of marsh accretion, erosion, and drowning.

The slope of the adjacent upland and the rates of sea-level rise and sedimentation are key factors in controlling coastal wetland transgression (migration of wetlands onto adjacent uplands). If horizontal migration of a coastal wetland is impeded by the steepness of the slope of adjacent uplands or by a barrier to marsh transgression (such as a sea wall or building), then the coastal wetland may become submerged. If the slope of the adjacent upland is gradual, then wetland expansion is possible. Although both responses of coastal marshes to sea-level rise have been observed, we know very little about the mechanism of marsh transgression. Are slope, the rate of sea-level rise, and accretion the only variables that need be considered for short-term prediction? To answer this question, a model for marsh transgression was developed based on a detailed, 2,000-year record of marsh edge movement from eastern North Carolina (Young 1995).

Experimental Approach

The investigative approach to studying past marsh transgression is straightforward. By identifying and dating the base of the modern marsh sediments in a core sample, we can determine the time at which marsh peat formation first began at the site where the core was taken. Thus, we can identify the time when the landward-moving boundary between the upland and the marsh reached the location of the particular core, although the marsh surface would have been at a slightly lower elevation. Therefore, in order to reconstruct the transgression of the marsh edge at a particular site, one can date the base of the marsh sediments in a transect of cores extending from the center of the marsh into the transition zone. By dating the base of the marsh in each core in the transect, the landward migration of the wetland margin can be observed, and the rate and nature of the marsh edge versus movement up the transgression surface (the basal unconformity) can be determined. Two marshes located on Pamlico Sound in coastal North Carolina, at Cedar Island NWR and Long Shoal River, were selected for study because (1) there was evidence of marsh transgression (i.e., dead trees standing in the marsh), and (2) there were no tidal creeks in the irregularly flooded, low energy marsh systems, hence interpretation of the cores would not be confounded by erosional unconformities caused by channel migration.

The Process of Marsh Transgression

An initial assumption in this study was that a rate for the gradual, landward movement of the upland/marsh boundary under a regime of rising sea level could be established for use in short-term marsh management. However, Fig. 3-10 illustrates that the marsh edge transgressions in both the Cedar Island and Long Shoal River sites were neither gradual nor constant. The ages of the base of the marsh sediments are grouped. Two or three consecutive cores along the transect have essentially the same basal peat age, followed by another set of cores with a much younger age. This pattern continues along the transect in both sites up to the modern upland/marsh boundary. If the basal peat dates indicate marsh initiation at each point along the transect, it is apparent that the marsh edge is moving landward in a series of relatively rapid jumps. These *transgression events* are separated by longer periods of relatively little marsh edge movement. Transgression events have occurred about every 300–350 years at both sites, and the magnitude of the jumps varies from two- to threefold.

A model of punctuated marsh transgression has been developed to explain these observations (Fig. 3-11). It is unlikely that the transgression events are initiated directly by rapid, local relative sea-level rise because the events are not synchronous between the two sites. Rather, the transgression events are likely generated by disturbance of the upland vegetation, such as by major storms (e.g., hurricanes or fires), which allows the marsh to leap forward. It is important to keep in mind that although disturbance of upland vegetation is the likely mechanism that allows transgression to occur in this model, sea-level rise is still the driving force behind the transgression. Based on this model, the process of marsh transgression can be described as follows: (a) upland vegetation delays the advance of the marsh margin, even as sea level continues to rise; (b) a disturbance impacts the upland vegetation, thus allowing the marsh margin to jump forward and strive for a new equilibrium position with the temporal position of sea level; and (c) following the transgression event, the marsh edge will move very little until the next disturbance.

Conclusions

Subsurface processes occurring in the top few meters of the soil were at least as important in determining marsh elevation than surface accretionary processes for some marshes. Elevation gain lagged behind vertical accretion at 7 of the 12 marshes we studied, indicating that subsurface processes occurring in the top few meters of the soil exerted more control over elevation than accretion. Four of these seven sites experienced a significant elevation deficit (elevation minus relative sea-level rise), but none of the four sites experienced a significant accretion deficit (accretion minus relative sea-level rise), indicating how misleading accretion data can be when evaluating the potential for submergence of coastal wetlands. Examples of subsurface processes that can influence elevation include compaction, plant growth and decomposition, and shrink-swell of the soil related to water storage. The term "shallow subsidence" is used to describe the collective effect of these processes on marsh surface elevation. Some of the
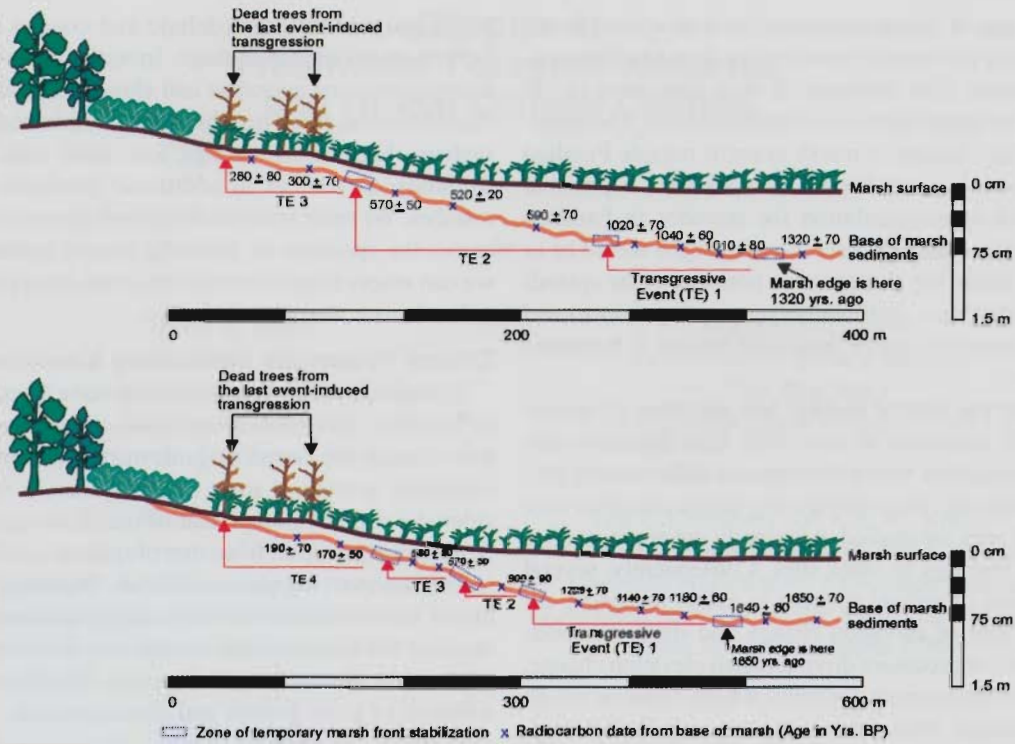
Figure 3-10. Diagram of punctuated marsh transgression event at Long Shoal River (top) and Cedar Island (bottom), North Carolina.
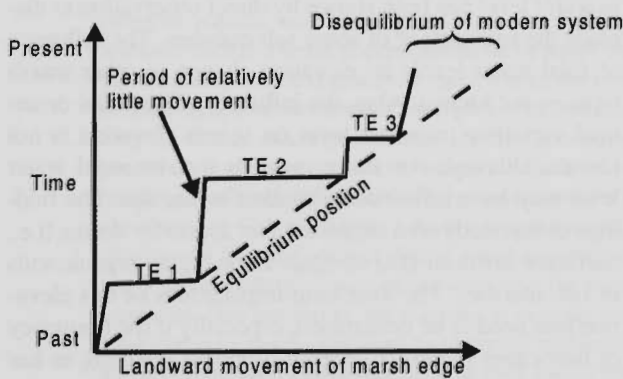
Figure 3-11. Diagram of the conceptual model for punctuated marsh transgression. TE = transgression event.

forces driving shallow subsidence apparently included seasonal changes in water levels and aperiodic occurrences of major storms. Hence, the controlling process for marsh elevation was site specific and depended on the environmental setting. Marshes with highly organic or unstable substrates were most likely to exhibit shallow subsidence.

Marsh transgression was an episodic process that was driven not only by sea-level rise but also local environmental conditions. Transgression of two marshes on Pamlico Sound, North Carolina, appears to have occurred through a process of punctuated events which were controlled by the biologic system (i.e., the biologic system influences geologic change), and therefore landward migration of the marsh was only indirectly linked to the rate of sea-level rise. The apparent trigger for a transgression event was a disturbance of the upland vegetation, such as a major storm event.

Management Implications

The potential for submergence of some coastal marshes is best determined by calculating elevation deficits rather than accretion deficits. The possible occurrence of shallow subsidence in a marsh system means that marsh managers should be calculating elevation deficits rather than accretion deficits when determining the potential for submergence of a marsh. The implication of these findings is that the potential for coastal marsh submergence is being underestimated for some marshes, especially in the Mississippi delta.

Measures of total subsidence based on tide gauge records are underestimated by the amount of shallow subsidence.

Short-term rates of marsh transgression may be meaningless and may not be useful tools to predict wetland

habitat change. If marsh transgression is an episodic process driven by infrequent events rather than a continuous, gradual process, then estimates of short-term rates (<100 years) may be meaningless as a predictive tool. The applicability of this finding to marsh systems outside Pamlico Sound, however, is not known. Nevertheless, a possible management recommendation for marshes in Pamlico Sound which are about to become submerged would be to artificially release the transgression potential at the upland/marsh boundary (i.e., artificially create a disturbance) and allow the marsh to move landward before it becomes submerged.

Predicting the vertical buildup and migration of coastal wetlands in response to sea-level rise requires site-specific information. Given the apparent differences in processes and driving forces influencing marsh elevation over the range of sites we studied, it is clearly not appropriate to extrapolate findings to other sites. Consequently, several issues become of critical concern to marsh managers, including the rate of elevation change and shallow subsidence, the critical processes driving marsh elevation change, and current management practices which enhance marsh elevation change. Managers must also consider how current management practices influence the potential for submergence of a marsh; whether transgression of the marsh is occurring, and if so, if it occurs through a series of punctuated events or a gradual process; and how he/she can facilitate marsh transgression. We recommend that marsh managers employ management techniques that will enhance marsh elevation and minimize the potential for marsh submergence.

Future Research

The findings from this study indicate that we need to understand more about the interactions among vegetation, soil, and hydrologic processes as they relate to soil elevation in marshes and mangrove forests. Specifically, we need information on (1) shallow subsidence at additional environmental settings, (2) the critical processes controlling elevation in each environmental setting and site, (3) the natural forces driving those processes, and (4) the influence of management processes on shallow subsidence, marsh transgression, and the potential for marsh submergence.

Additional Environmental Settings

The site-specific nature of the relationship between accretion and elevation change, and the driving forces affecting that relationship, indicate that it is not appropriate to extrapolate findings of our study to other sites. The 12 sites we investigated represent a limited range of marsh types (tidal salt and brackish marsh, mangrove forest) and

physiographic settings (deltaic and coastal fringe), all located in microtidal settings. Investigations of the relationship between accretion and elevation need to be conducted in tidal fresh marshes, river-dominated mangrove systems, backbarrier settings, and meso- and macrotidal wetlands, as well as in additional brackish and saline marshes. We must establish long-term elevation data bases across the spectrum of federally owned wetlands so that we can assess their vulnerability to sea-level rise and provide advance warning of change.

Critical Processes Controlling Elevation

Numerous subsurface processes have been suggested or identified as causes of elevation change, but few have been directly measured. Organic matter content of the soil, especially growth of roots and rhizomes, is widely considered a primary component of marsh elevation change. Separating its impact from that of mineral sediment deposition, however, has proven difficult. Shrinking and swelling of the soil related to water storage has been shown to displace the marsh surface in some salt marshes. Soil compaction also decreases soil elevation. But the relative contribution of plant growth and decomposition, water storage, and compaction to marsh soil elevation change has not been determined.

Natural Driving Forces

Hydrologic events on daily, seasonal, or annual time scales can influence marsh soil elevation. Tidal variation in water level has been shown by direct observation to displace the soil surface of some salt marshes. The influence of tidal water levels on elevation change in other marsh types is not known. Also, the influence of seasonal or annual variations in water level on marsh elevation is not known, although our study suggests that seasonal water level may have influenced elevation at one site. The findings of this study also suggested that aperiodic storms (i.e., hurricane storm surges) compacted the highly organic soils of two marshes. The long-term implications of this elevation loss need to be determined, especially if the frequency of hurricanes increases because of global warming as has been predicted (Emanuel 1987).

Influence of Management Practices

Common wetland management and restoration practices include burning, hydrologic manipulations, sediment introduction (including dredged material disposal), and controlled and uncontrolled river diversions. A considerable portion of the several million acres of federally owned wetlands has been managed by at least one of these methods. There are few data available, however, on the impact of these management practices on wetland soil elevation. In addition, research is needed to evaluate the feasibility of artificially inducing a marsh transgression event.

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
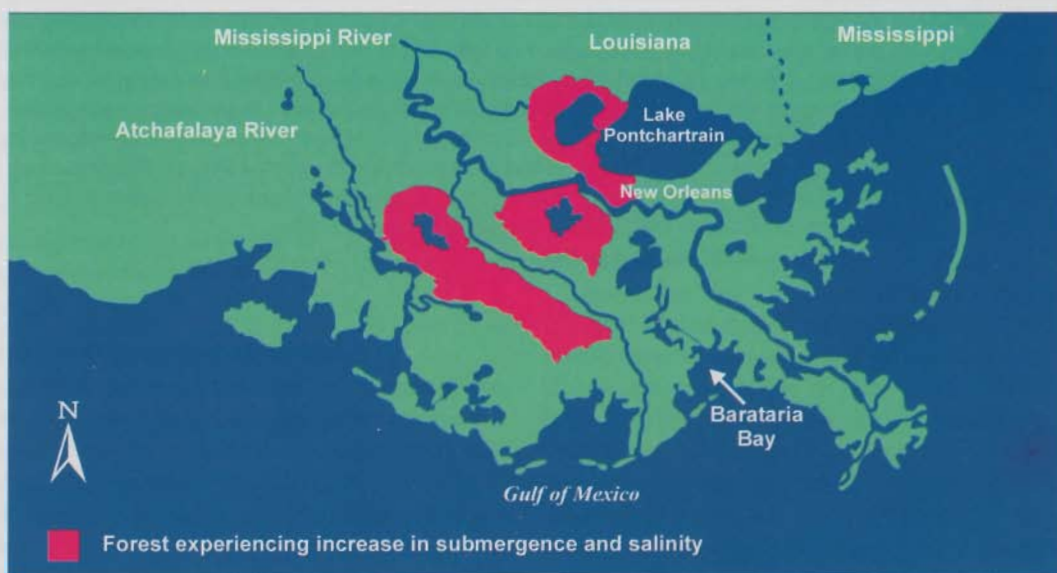

Figure 4-1. Louisiana gulf coast forests currently experiencing increased flooding or saltwater intrusion or both. Source: Modified from Pezeshki et al. 1990.

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
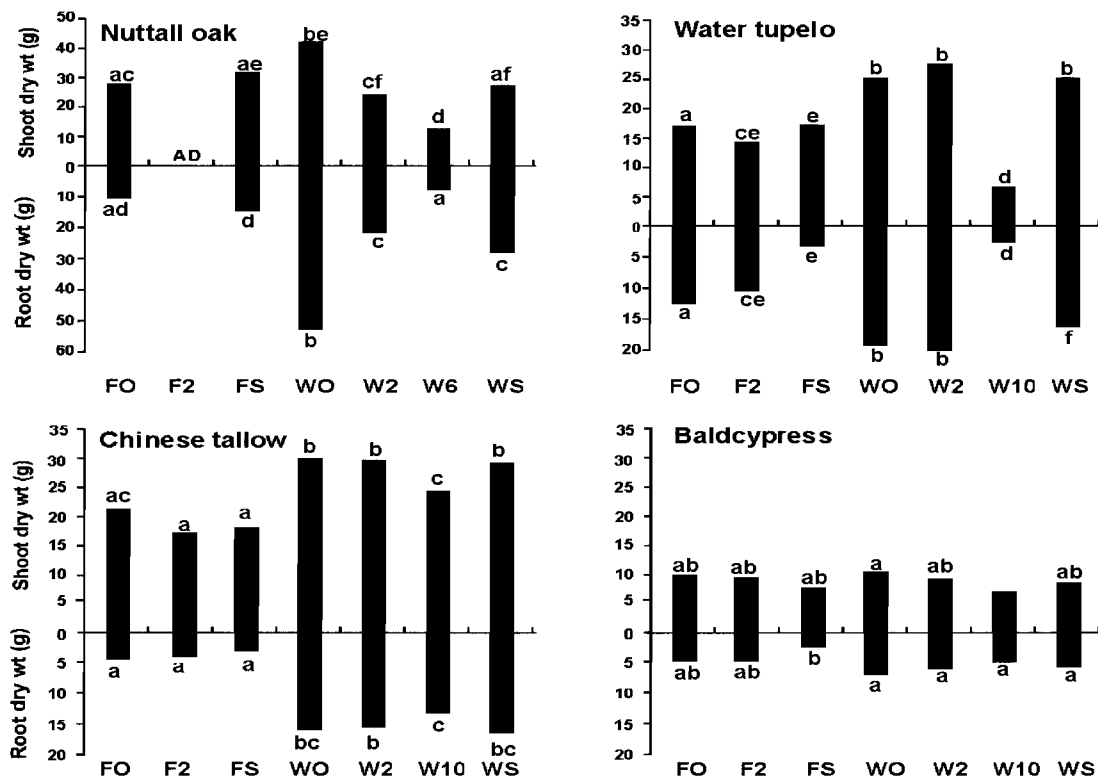
Figure 4-2. Effects of flooding and salinity on shoot and root biomass of Nuttall oak, baldcypress, water tupelo, and Chinese tallow (±SE). F indicates flooded (water levels were maintained at about 5 cm above the soil surface), and W indicates well-watered (seedlings were watered regularly but without 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 salt-water 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

by
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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.

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

Species	Flood tolerance[1]	Salinity tolerance Low-level+flooding[2]	Salinity tolerance 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.
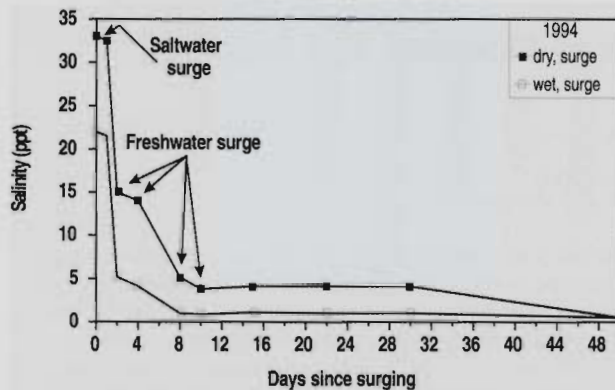
Figure 4-3. Salinity levels in surge tanks after flooding with saltwater and subsequent freshwater additions (the "storm surge" treatment referred to in the text). Source: Conner 1995.

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.
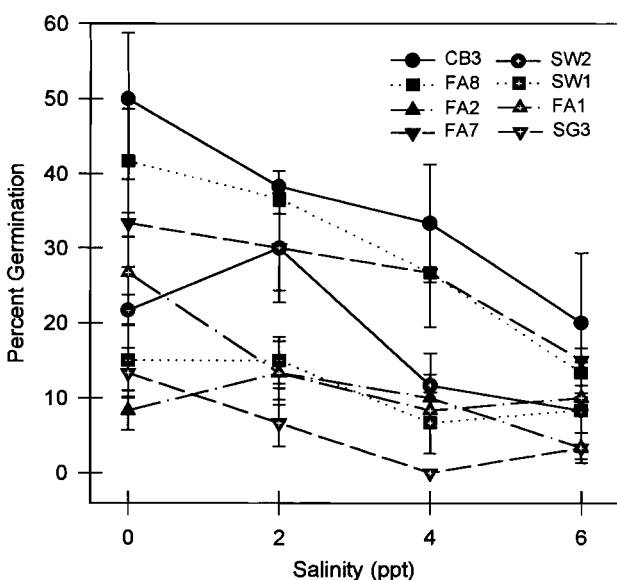

Figure 4-6. Intraspecific variation in baldcypress seed germination at four soil salinity concentrations. Families SW1 and SW2 represent the two freshwater source collections. Source: after Krauss et al. 1998 (permission to reproduce granted to authors by Kluwer Academic Publishers, Inc.).

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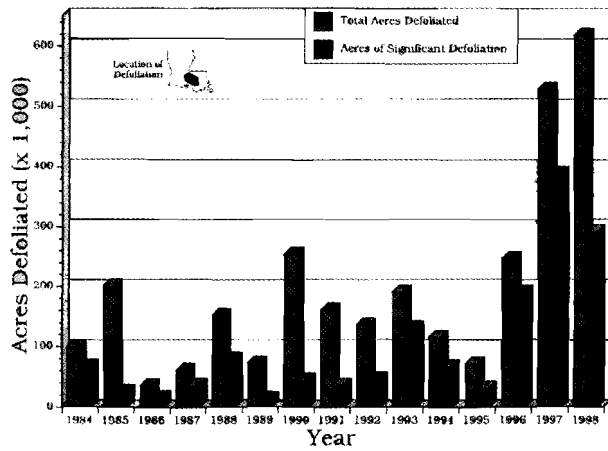
Figure 4-8. Amount of defoliation (acres) by fruittree leafroller. Source: Goyer, unpublished data.

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.
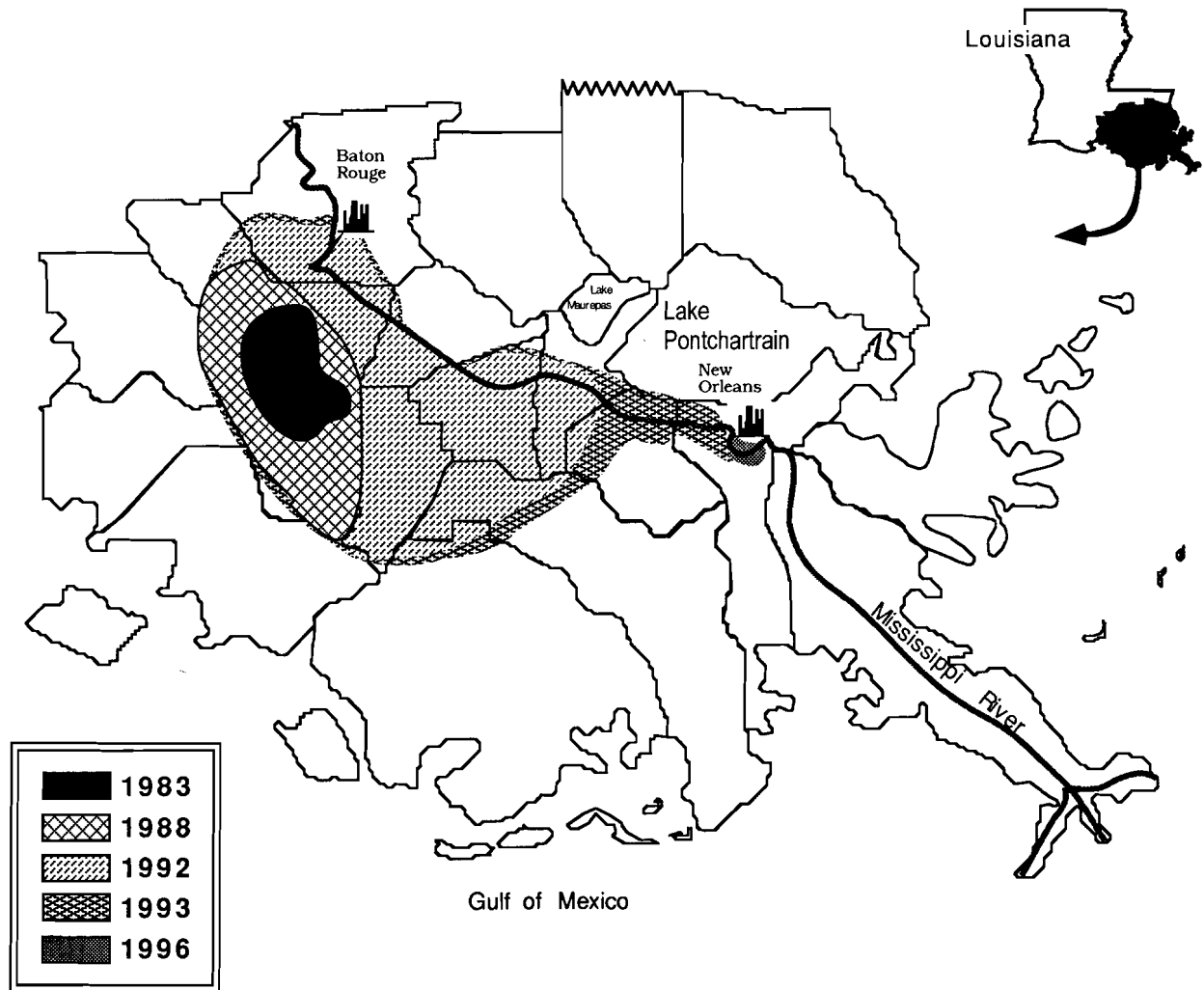
Figure 4-9. Extent of fruittree leafroller defoliation in 1983, 1988, 1992, 1993, and 1996. Source: Goyer, unpublished data.
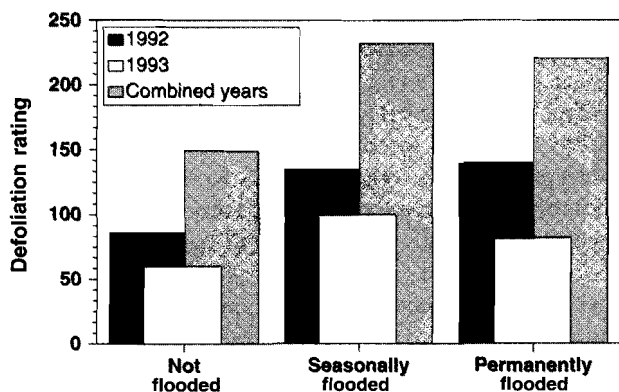
Figure 4-10. Baldcypress defoliation rating for three hydrological regimes, Bayou Chevreuil, Louisiana. Source: Goyer and Chambers 1997.
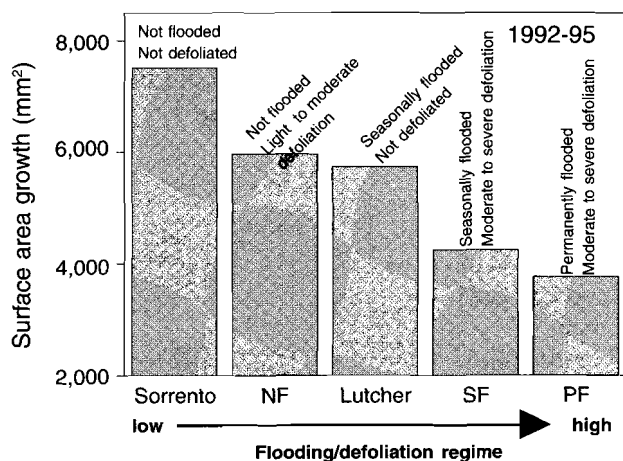
Figure 4-11. Surface area growth of baldcypress as influenced by flooding and insect herbivory (after data from Goyer 1996; Table 4-3).

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.

Chapter 5:
Sensitivity of Gulf Coast Forests to Climate Change

by

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Abstract: Data from a long-term study of vegetation and tree demography were used to investigate potential effects of climate change on a major forested region of the United States, the Coastal Plain of the Southeast. Study sites included dry, mesic, and wet sites in the Big Thicket of east Texas that are representative of important vegetation types on the Coastal Plain. Results indicated spatial and temporal variability in species importance and stand turnover rates related to history of human disturbance, history of natural disturbance, and site conditions. Investigation of within-stand patterns related to shade-tolerance, a central element of the theory of forest dynamics, reinforced the idea that shade tolerance and tradeoffs relating to it are central to our understanding of the mechanisms controlling forest variation in time and space. Analyses of tree-ring chronologies indicated that species range boundaries are not set by climatic limitations on individual growth. On the other hand, analyses of seedling demography, sapling and tree growth, and tree rings indicated short-term variations that suggest sensitivity of the forests to long-term climate change. Comparing effects of disturbance on stand dynamics with effects of climate variation on individual growth, our analyses suggest that climate change would have a stronger and more direct effect through changes in frequency and intensity of hurricanes, floods, and droughts than through changes in relative growth performance among species. Because of high stand turnover rates, possible responses would be rapid. While the responses noted here are not as dramatic as we had previously seen, they do have important implications for managers of both natural area preserves and commercial timberlands.

Introduction

Forests of the Coastal Plain region of the southeastern United States are among the most productive in North America and form the basis of a large timber and wood products industry. In addition, unmanaged forests in parks and preserves are important biologically and for conservation (e.g., Marks and Harcombe 1981; Bridges and Orzell 1989; Ware et al. 1993). Understanding potential effects of climate change on Coastal Plain forests is therefore critical from both economic and biological perspectives (see also Morse et al. 1995).

Existing long-term studies are particularly useful for understanding potential impacts of climate change on forests for three reasons. First, long-term studies initiated prior to climate changes provide invaluable baseline data on forest variability under existing climatic conditions. Without such data, distinguishing long-term changes in forests caused by climate change from short-term fluctuations caused by disturbance or climatic anomalies may be impossible. Second, long-term studies provide an opportunity to directly observe effects on forests of short-term climate fluctuations and related disturbance phenomena, such as fires and hurricanes. We can then use these observations of actual forest change as the basis for inferences about sensitivity to longer term climate and disturbance changes in the future. Finally, long-term studies may provide critical data for testing and refining predictions about climate change effects made using simulation models.

In this report, we summarize the results of 20 years of forest dynamics study in the Big Thicket region of southeast Texas. Our study is unique in the amount of detailed data that have been collected on woody plant growth and population changes on the same sites over a long time period. A second unique feature of the study is the simultaneous accumulation of a variety of environmental data (e.g., drought, light, flooding) with which to interpret the woody plant population data. Also, the location of the study in the Big Thicket is highly advantageous for global change research. The forests of the Big Thicket are typical of a large biogeographic region on the Coastal Plain of the southeastern United States which spans the area from east Texas to the Carolinas; many of the results presented here apply to the region as a whole. Also, the study area is close to the southwestern range limit of most of the eastern forest trees. If forests change in response to shifts in global climate, the changes will likely occur first at the range limits; our long-term study is therefore in an excellent position to detect early indications of possible long-term shifts in species composition and demographic processes.

The Big Thicket is at the western edge of the Southern Mixed Hardwoods region (Küchler 1964) or the Southeastern Evergreen Forest described by Braun (1950). Recent biogeographic studies place the Big Thicket in the Coastal Plains and Flatwoods Ecoregion, Western Gulf Section, Subsection 231Fb (Southwest Flatwoods; Keys et al. 1995). The climate is humid subtropical with an average annual rainfall of 1,341 mm/yr (National Climatic Data Center 1994) evenly distributed throughout the year. Average annual temperature is 20.4° C; mean monthly temperature exceeds 10° C for all months. The growing season is long, from March to November, with approximately 240 consecutive frost-free days. Physically, it is mostly within the drainage of the Neches River 50–100 km inland from the Gulf of Mexico and about 75 km west of the Louisiana border.

As in most of the Coastal Plain, plant communities of the Big Thicket area have been altered by humans. Exclusion of fire has converted large portions of upland habitats that were formerly longleaf pine savannas or woodlands (i.e., open forests with a grassy understory) to closed forest (Harcombe et al. 1993; Ware et al. 1993). Furthermore, logging, which reached its peak in the early 20th century, may have left remnant stands somewhat enriched with shade-intolerant species, such as loblolly pine (*Pinus taeda*), water oak (*Quercus nigra*), and sweetgum (*Liquidambar styraciflua*). Bottomland areas have also been logged, but species composition and forest structure over large areas do not appear greatly different than in remnant old-growth forests from other parts of the Coastal Plain (e.g., Congaree Swamp National Monument, South Carolina).

Long-term Study Sites

Much of our work has focused on three permanent study plots. These three sites represent the major dry, mesic, and wet forest communities of the Coastal Plain of the southeastern United States (Marks and Harcombe 1981; Christensen 1988; Harcombe et al. 1993; Ware et al. 1993). Sites were selected to be as undisturbed as possible, in order to study natural patterns of forest dynamics rather than responses to logging. Although this objective was not entirely achieved and may not be possible in the current landscape, the mesic and wet sites probably do not differ greatly from old-growth forest in most ecologically meaningful parameters.

The dry site is a low sandy ridge southeast of Warren, Texas, adjacent to a floodplain in the Turkey Creek Unit of the Big Thicket National Preserve. The vegetation type is Oak-Hickory-Pine (Küchler 1964) or Upper Slope Pine Oak (Marks and Harcombe 1981). The dominant hardwoods, post oak (*Quercus stellata*), southern red oak (*Quercus falcata*), and black hickory (*Carya texana*), form a relatively open canopy 15–20 m tall below emergent longleaf pine (*Pinus palustris*), loblolly pine, and shortleaf pine (*Pinus echinata*; Table 5-1). Red maple (*Acer rubrum*) and sweetgum are minor canopy components that tend to occur in moist microhabitats, especially along the

Table 5-1. Basal area (m²/ha) and annualized percent change in basal area for the three study sites. Annual percent change in basal area (BA) is the difference between current and initial basal area divided by the initial basal area and the number of years since the initial basal area reading (e.g., annual percent change in BA for Neches Bottom=[BA94-BA80]/[BA80*(94-80)]).

Species	Turkey Creek (Dry) BA 1993	Turkey Creek (Dry) Annual % change in BA	Wier Woods (Mesic) BA 1995	Wier Woods (Mesic) Annual % change in BA	Neches Bottom (Wet) BA 1994	Neches Bottom (Wet) Annual % change in BA
Longleaf pine	6.069	0.02	-	-	-	-
Post oak	5.14	0.00	-	-	-	-
Southern red oak	4.91	0.01	0.11	0.00	-	-
Shortleaf pine	1.94	0.01	0.04	-0.02	-	-
Yaupon	0.71	1.07	0.05	0.09	-	-
Flowering dogwood	0.19	-0.02	0.21	0.02	-	-
Bluejack oak	0.05	-0.06	-	-	-	-
Hickory	1.54	0.03	-	-	-	-
Loblolly pine	4.31	0.04	11.90	0.01	-	-
White oak	0.15	0.04	3.65	-0.01	-	-
American holly	0.22	1.52	2.45	0.04	0.62	-0.02
Upland laurel oak	0.13	0.00	1.40	-0.01	-	-
Laurel oak	-	-	-	-	0.35	0.06
Southern magnolia	0.05	-	5.06	0.01	-	-
American beech	-	-	3.15	-0.02	-	-
White-bay magnolia	-	-	0.39	0.02	-	-
Blackgum	0.04	1.47	1.34	0.01	0.99	0.01
Sweetgum	0.87	0.05	1.54	0.01	6.74	0.01
Red maple	0.03	0.51	0.79	0.01	2.56	0.00
Water oak	-	-	2.08	-0.03	2.90	0.03
Swamp chestnut oak	-	-	0.08	0.01	3.09	0.01
American hornbeam	-	-	0.05	-0.02	2.76	-0.04
Baldcypress	-	-	-	-	1.72	0.03
Swamp blackgum	-	-	-	-	1.61	0.00
Overcup oak	-	-	-	-	1.36	0.02
Water hickory	-	-	-	-	0.85	-0.01
American elm	-	-	-	-	0.66	-0.02
Other	0.53		0.54		1.84	
Total	**26.88**		**34.83**		**28.05**	

edges of the study plot. The understory is a moderately dense mixture of tree saplings and shrubs; flowering dogwood (*Cornus florida*) and yaupon (*Ilex vomitoria*) are particularly abundant, and saplings of most tree species are common. The soil is sandy. The site was logged in 1930, but many trees of considerable age remained on the site so the stand is not strongly even-aged (Harcombe et al. 1993; Kaiser 1995). Prior to 1930, the site probably burned relatively frequently, judging from the widespread presence of charcoal on stumps and the importance of longleaf pine, a fire-adapted species, in the overstory. Nevertheless, hardwoods probably contributed 30–40% of stand basal area.

Stand basal area increased from 21.7 m²/ha in 1982 to 26.2 m²/ha in 1993, a compound rate of increase of 1.7% per year. Though all major species increased in absolute basal area (Table 5-1), there was a slight decrease in relative dominance for three of the four major species (longleaf pine, post oak, and southern red oak) and an increase in

relative dominance and diversity (14 new species) of minor species (Kaiser 1995). These trends suggest successional recovery from the 1930 logging event in a system in which fire frequency is much lower than it was prior to logging. The dramatic difference in species composition between the prelogging forest and the forest today illustrates the magnitude of the effect of fire on the pre-Anglo landscape.

The mesic site is located in Wier Woods Preserve (The Nature Conservancy) near Lumberton, Texas, about 16 km north of Beaumont. Forests of this type have been called Southern Mixed Hardwood Forest (Quarterman and Keever 1962), Beech-Magnolia-Holly (Delcourt and Delcourt 1977), or Lower Slope Hardwood Pine (Marks and Harcombe 1981). The closed canopy of tall trees (25–40 m) is dominated by loblolly pine, water oak, American beech (*Fagus grandifolia*), southern magnolia (*Magnolia grandiflora*), and white oak (*Quercus alba*). Red maple,

sweetgum, and black gum (*Nyssa sylvatica*) are abundant as small to medium stems but are infrequent as large trees. American holly (*Ilex opaca*), flowering dogwood, and yaupon are important understory species. The soil is loamy. The forest was logged for pine once in about 1910 and there appears to have been no further human modification of the stand (Glitzenstein et al. 1986).

Hurricane Bonnie passed over Wier Woods on June 26, 1986. Winds at that time were estimated at 120 km/hr (Neumann et al. 1993; Doyle and Girod 1997). Tree-ring analyses (Glitzenstein et al. 1986) suggested earlier episodes of canopy opening in 1810, 1855, and, to a lesser extent, in the mid-1960's. The latter episode may have been caused by Hurricane Carla in 1961. The great Galveston Hurricane of 1900 (Bray 1901) may have contributed to canopy disturbance in the early 1900's, but this effect was difficult to separate from the effects of logging disturbance.

Basal area has varied between 33.7 m²/ha and 35.1 m²/ha during the 16-year period of the study. Changes in individual species (Table 5-1) reflect a variety of causes. Loblolly pine is increasing in basal area because postlogging recruits have reached their stage of maximum growth; however, it is a shade-intolerant species which is not regenerating in the stand and therefore seems destined to decline in the absence of future major canopy opening. American holly, the other strongly increasing species, is a shade-tolerant midstory species which is responding to light increases as the postlogging canopy becomes more heterogeneous. Water oak and American beech showed the most significant declines. Water oak is a relatively shade-intolerant, somewhat short-lived species that might be expected to decline from a postlogging position of dominance. In contrast, American beech is a shade-tolerant species of mature forests and seems to be declining for reasons unrelated to stand development. Possible explanations include a long-delayed reaction to drought in the 1980's or increased pathogen invasions due to structural damage by Hurricane Bonnie.

The wet site is on the floodplain of the Neches River, near Evadale, Texas, in the Neches Bottom Unit of the Big Thicket National Preserve. The Neches River drains approximately 26,000 km² of the humid forested region of southeast Texas. The study stand is a mature example of Southern Floodplain Forest (Küchler 1964) or River Floodplain Forest (Marks and Harcombe 1981). On the flats, widely spaced, large individuals of sweetgum, swamp chestnut oak (*Quercus michauxii*), water oak, and red maple dominate the somewhat open overstory above a dense midcanopy layer of American hornbeam (*Carpinus caroliniana*). Under intact canopies, the shrub layer is open, with only a single important species, possumhaw (*Ilex decidua*). In canopy openings, density of tree saplings (Hall 1993) or herbs (Mohler 1979) can reach very high levels. Baldcypress (*Taxodium distichum*) and water tupelo (*Nyssa*

aquatica) are commonly found in the sloughs. The transition between slough and flat vegetation is relatively abrupt. Baldcypress was removed along the sloughs early in the century, but there is no strong evidence for subsequent logging; the stand appears unevenly aged, with oldest individuals originating before 1800.

Distributions of seedlings, saplings, and trees on this stand are all related to elevation (Streng et al. 1989; Hall 1993; Hall and Harcombe 1997; R.G. Knox, Goddard Space Flight Center, Greenbelt, Maryland, unpublished data). Saplings also showed a strong tendency to occur in patches (Hall 1993). The soil is very deep, somewhat poorly drained, very slowly permeable acidic clay. During most of the year, available water is ample and, during winter and spring, the water table is high, at a depth of only 30–60 cm most years. Maximum flooding during the forest long-term study occurred in 1989 and 1992 (Fig. 5-1; Hall 1993).

Total basal area fluctuated between 28.1 m²/ha in 1980 and 29.1 m²/ha in 1989, followed by a 5% decline to 27.7 m²/ha in 1994. However, there were trends in several important species. Sweetgum, water oak, swamp chestnut oak, baldcypress, and overcup oak (*Quercus lyrata*) increased, while American holly, American elm (*Ulmus americana*), and water hickory (*Carya aquatica*) decreased. More notably, American hornbeam, a very important midstory species, has been declining since the study began, with a particularly precipitous drop of nearly 50% after 1989 due to flood-related mortality.

One of the strongest indications of potential direct effects of climate change on composition at this site was the strong effect of the severe drought in 1980 on seedling composition, recruitment, and mortality at the wet site (Streng et al. 1989). Timing of mortality within the 1980
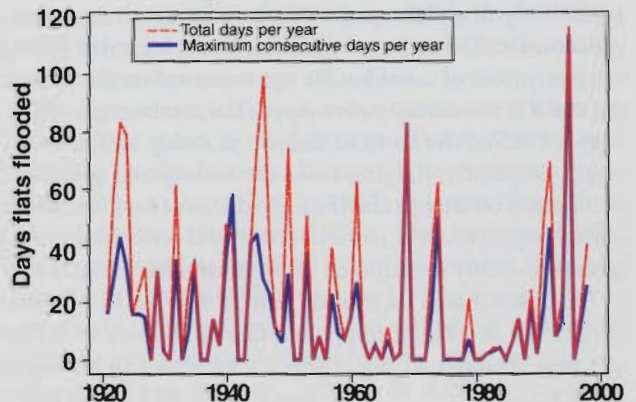

Figure 5-1. Total and maximum consecutive days flooded for the flats at the wet study site, 1920-90.

growing season was closely correlated with the intensity of drought stress as measured by predawn leaf water potential measurements. Mortality of larger-seeded species, especially oaks, was less affected than was mortality of lighter-seeded trees such as sweetgum and American hornbeam. This difference in mortality suggests that prolonged dry periods may select against the lighter-seeded trees, leading to increased dominance by oaks.

Cross-site Comparisons

Each of the three intensive study sites has a unique history which must be understood if information of general significance regarding mechanisms of forest dynamics and causes of forest change is to be extracted from these and other case studies. Furthermore, each site is a single, unreplicated representative of its habitat type. Therefore, caution must be exercised in interpreting the results; attempts to extract generalizations must be made, but these generalizations should serve only as hypotheses for further testing. We compare and contrast patterns in mortality, sapling dynamics, and stand turnover to elucidate mechanisms of forest dynamics and factors influencing

forest change. Knowledge of these mechanisms and factors can form the basis for predictions about global change effects.

Mortality

At the dry site, mortality loss varied by a factor of three over the period of record (Fig. 5-2), averaging about 0.22 m^2/ha per year (0.9% of live basal area). There were no obvious trends or event-related peaks, except that understory trees showed slightly elevated mortality between 1987 and 1993, probably owing to increased canopy density. Much of the year-to-year variation in overall mortality was related to chance death of large trees. Turnover time, the time it would take to replace all the live basal area if new growth were equal to mortality, was 108 years.

At the mesic site, average mortality loss was higher (0.55 m^2/ha per year; 1.5% of live basal area) and more variable (eightfold difference between maximum and minimum). Highest mortality (1.59 m^2/ha; 4.3% of live basal area) was associated with Hurricane Bonnie (Fig. 5-2), which hit the stand in 1986 (the hurricane actually occurred in 1986, but since it occurred after the mortality survey for that year,
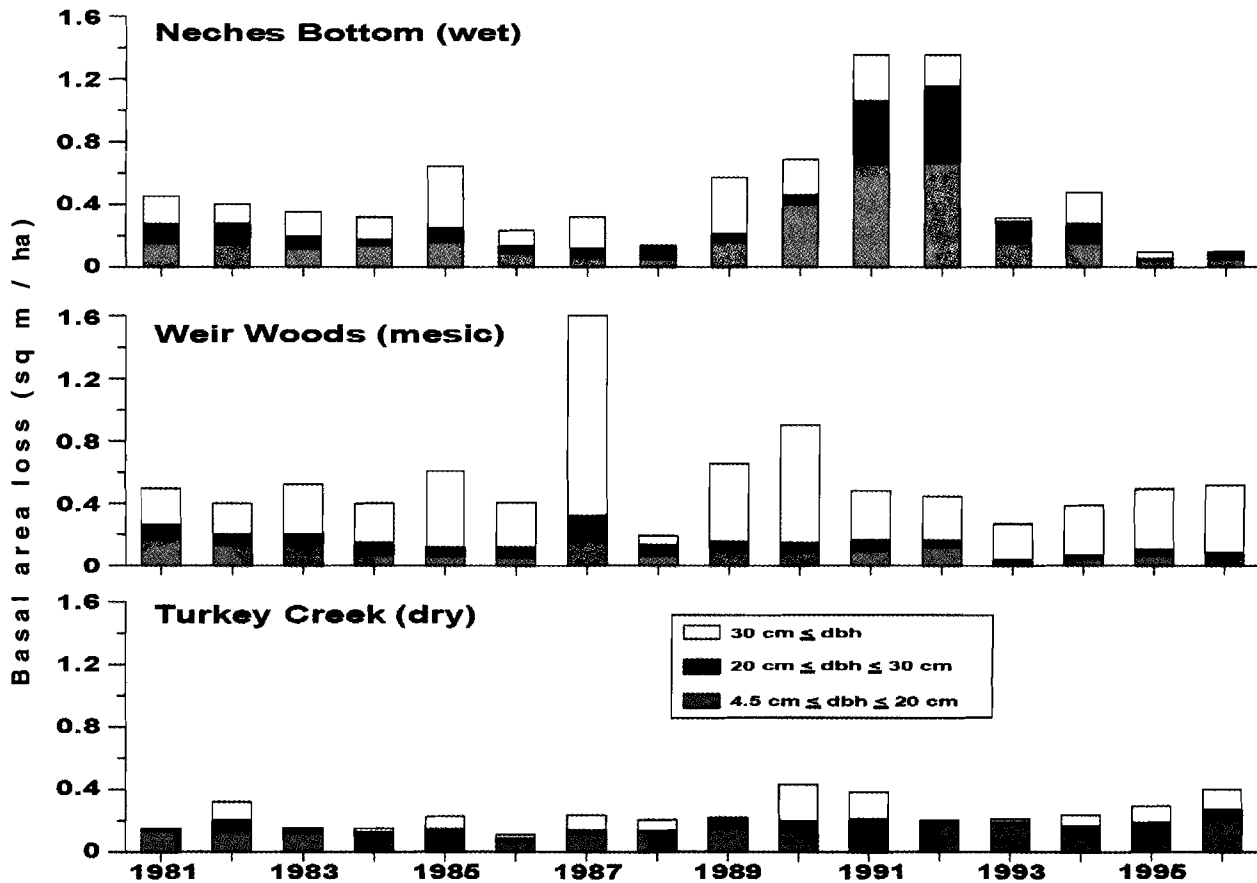

Figure 5-2. Basal area loss by size class for all sites, 1980-96.

the mortality increase is reflected in the 1987 data). Post-hurricane mortality was low in the year following the hurricane; such reductions have been attributed to reduced competition (Waring and Schlesinger 1987). Mortality then showed a mean peak; others have postulated that such peaks are caused by slow death of damaged trees (Putz and Sharitz 1991). To quantify the role of hurricanes, we calculated the overall average basal area loss in nonhurricane years (0.49 m²/ha per year) and called that normal, or background, mortality. Subtracting that average from the average of all years gave the amount of mortality attributable to the hurricane (0.06 m²/ha per year), approximately one-eighth of the total mortality. Thus, turnover time was reduced by the hurricane from 69 years for normal mortality alone to 64 years overall. When we consider the likelihood that not all hurricanes will hit this stand and the likely variability of hurricanes, the hurricane effect on stand structure and turnover reported here is probably a high estimate (Bill 1995).

At the wet site, average annual mortality was very high (0.58 m²/ha per year; 2.1% of live basal area) and intermediate in level of variation (sixfold difference between maximum and minimum). This site may have the highest turnover rate ever reported for a well-developed, mature forest stand in the eastern United States. To quantify the role of flooding, we calculated the overall average basal area loss in nonflood years (0.38 m²/ha per year) and called that normal, or background, mortality. Subtracting that value from the average over all years gave the amount of mortality attributable to flooding (0.19 m²/ha per year), approximately one-third of the total mortality. Thus, flooding substantially reduced stand turnover time from 131 years for normal mortality alone to 77 years for all sources of mortality. This estimate of the flood effect must be considered tentative due to the relatively short duration of the record.

There were four cases of a strong species decline in basal area at the three sites (Table 5-1) owing to relatively high mortality over a short period. The most interesting case involves American hornbeam (wet site); considering that there have been many floods of similar magnitude and duration over the 100-year period of record, the high death following the 1989 flood is somewhat puzzling. The explanation may lie in alterations of the flow regime caused by construction of dams 50–80 km north of the study site in 1951 and 1965. Those dams substantially increased the average number of years between long growing-season floods (Streng 1986; Hall 1993; Hall and Harcombe 1997). A consequence of this reduced flooding could have been expansion of the American hornbeam population beginning in the 1950's, at least partly in formerly flood-prone areas. Thus, the population may have been much larger and much more susceptible to a long-duration growing-season flood like that of 1989 because of the long period of low growing-season flooding. The implication is

that the altered flow regime has made both mortality and population expansion more variable.

Of the other species showing declines, two species may be declining due to successional change. At the dry site, increasing overstory density is probably causing the suppression and death of bluejack oak (*Quercus incana*), a short, slow-growing, shade-intolerant species. At the mesic site, the decline in water oak, a mid-successional, relatively shade-intolerant species, could possibly be explained in terms of the relatively synchronous death of the 70-year-old postlogging cohort. However, there is little evidence for this kind of synchrony in mixed forests of North America, and others have reported greater longevity for this species (Burns and Honkala 1990), so the successional interpretation must be considered tentative. One species, American beech (mesic site), demonstrated a marked decline for no clear reason. Since it is a dominant species on the mesic site and on similar sites across the southeastern United States, its decline warrants additional investigation.

At the stand level, several observations can be made. First, mortality rates were higher and basal area turnover times were lower at the mesic and wet sites than at the dry site. This difference presumably reflects the higher productivity at sites where moisture and nutrients are less limiting. Second, there were fairly large differences between the sites in distribution of mortality among the classes of diameter at breast height (dbh; Fig. 5-2). At the dry site, only 24% of the basal area loss occurred in trees greater than 30 cm dbh, compared to 69% at the mesic site and 39% at the wet site. These differences in composition of mortality probably reflect differences among sites in stand structure (smaller average dbh at the dry site, for example, or the importance of a small tree, American hornbeam, at the wet site) and disturbance regime (higher mortality of large trees in the hurricane-impacted stand). Third, the magnitude of year-to-year variation was fairly low; mortality varied by a factor of three at the dry site, eight at the mesic site, and six at the wet site. Fourth, the two observed stand-level perturbations, the hurricane at mesic site and the floods at the wet site, had strong effects on the mortality patterns. In the case of flooding, this effect was spread over several years; for the hurricane, mortality was much more strongly concentrated, as might have been expected. Although basal area loss was high in disturbance years, it was low in comparison to background mortality when each was averaged over the whole period of record. The fact that the hurricane disturbed only one of the three stands, all of which were in or near its path, is a useful reminder of the high variability in space and time of major climatic perturbations.

Interpretation of the mortality records for the three sites involves three kinds of explanation: species- or stand-level trends related to postlogging successional processes (dry and mesic sites), species- or stand-level trends related to

particular perturbations (mesic and wet sites), and normal or background mortality. Identification of these processes makes detection of future changes in mortality that might be related to climate change possible; long-term records which allow comparisons between species and between sites, such as the ones accumulated in this study, provide the baseline for detection of effects of global change. Also, the quantitative data reported here allow us to make some assessment of the potential for change. For example, the high rates of natural turnover indicate that these forests will respond rapidly to climate change, and if hurricanes and floods increase in frequency and intensity as a result of global warming, forest turnover rate may be even more rapid. If higher mortality is not offset by higher growth, standing biomass of the forests may decline.

Sapling and Seedling Dynamics

At the dry site, saplings have been declining (Fig. 5-3), owing largely to a decline in loblolly pine following a pulse of recruitment in the 1970's. The recruitment pulse is attributed to reduction in competition by a ground fire or selective logging (Harcombe et al. 1993). In contrast to the overall decline, five species poorly represented in the overstory but typical of mesic sites (southern magnolia, sweetgum, American holly, red maple, and upland laurel oak [Quercus laurifolia]) showed peak densities in the 1980's as small saplings (Fig. 5-3). As these saplings grew larger, they moved into the large sapling class, which leveled off recently (Fig 5-3). Trends for seedlings (woody stems less than 50 cm tall) were similar to those for saplings, showing declines in dry-site species and increases in mesic species. The greatest declines were experienced by species typical of open, longleaf pine savannas or woodlands, including longleaf pine, bluejack oak, and deerberry (Vaccinium stamineum; Table 5-2). Seedlings of canopy trees typical of somewhat less frequently burned oak-hickory woodlands and dry sites (post oak, southern red oak, mockernut hickory [Carya alba], and black hickory) also declined but not quite as precipitously. In contrast, seedlings of mesic species showed dramatic increases (e.g., yaupon, which increased fourfold).

At the mesic site, sapling density has increased gradually over the period of record (Fig. 5-3); southern magnolia accounts for much of the increase. This increase may be partly attributable to an increase in canopy heterogeneity in the postlogging forest as a consequence of larger mean dbh of dying canopy trees (Bill 1995). There was no strong increase in small saplings in the years following Hurricane Bonnie, in marked contrast to the response observed for Hurricane Kate at Woodyard Hammock in Florida (W.J. Platt, Louisiana State University, unpublished data) and to our own reconstructions of recruitment pulses at the mesic site following earlier periods of enhanced canopy opening (Glitzenstein et al. 1986). Nevertheless, Hurricane Bonnie

appears to have promoted recruitment of three species, Chinese tallow (Sapium sebiferum), loblolly pine, and white oak (Fig. 5-3). The first is an exotic invader, the second is a native light-demanding species, and the third is a common tree of intermediate shade tolerance in mesic forests that has shown low recruitment in recent years (Harcombe and Marks 1983; Glitzenstein et al. 1986; Bill 1995).

At the wet site, sapling populations showed dramatic change as well (Fig. 5-3). Small saplings increased by a factor of five to a peak in 1989, declined, and then began to increase again following the pulse of midstory American hornbeam death. Large saplings began to increase somewhat later and were still increasing in 1995. Most of the increases were concentrated in a few species: sweetgum, water oak, and American hornbeam for the small saplings and sweetgum, water oak, Chinese tallow, and laurel oak for the large saplings (Fig. 5-3). The increase in Chinese tallow is of particular interest since it is an exotic gap invader. It increased by a factor of 30 between 1981 and 1995. It should be noted, however, that the increase in the native dominants, sweetgum (27x) and water oak (16x) was also dramatic.

These increases in saplings at the wet site may be due to a change in the long-term flood pattern (Fig. 5-1); the period 1975–89 was the longest period of low flooding observed since recording began in 1921. The implication is that frequency of long-duration floods strongly controls sapling recruitment in floodplains by limiting regeneration to infrequent flood-free intervals and to areas of high light availability in gaps. These large-scale temporal patterns are superimposed on year-to-year variation in seedlings (Streng et al. 1989) and saplings (Hall 1993) caused by flooding. Our results suggest that human action has altered the hydrologic regime such that overall structure of the forest will shift towards an increasingly dense shrub layer and possibly towards greater importance of slower-growing, relatively shade-tolerant species in the postdam era when flood frequency is lower. Since upland species (e.g., American beech, sweetbay [Magnolia virginiana], and loblolly pine) are known to occur on levees and other natural high spots in the river floodplain, they may begin to increase as well; such species would be excluded by a normal flood regime (see Jones et al. 1994).

At all three sites, increases in sapling numbers are tied to disturbances in the recent past. At two of the sites (dry and mesic), the disturbance was superimposed upon a pattern of stand recovery from prior logging. Human action appears to have changed natural processes more at the dry site (altered fire regime) and the wet site (altered flood regime) than at the mesic site. Nevertheless, because the disturbances were characteristic for the sites (i.e., fire at the dry site, flooding at the wet site, and a hurricane at the mesic site), some general interpretation is warranted. Most important, fire and flood are similar in that they affect
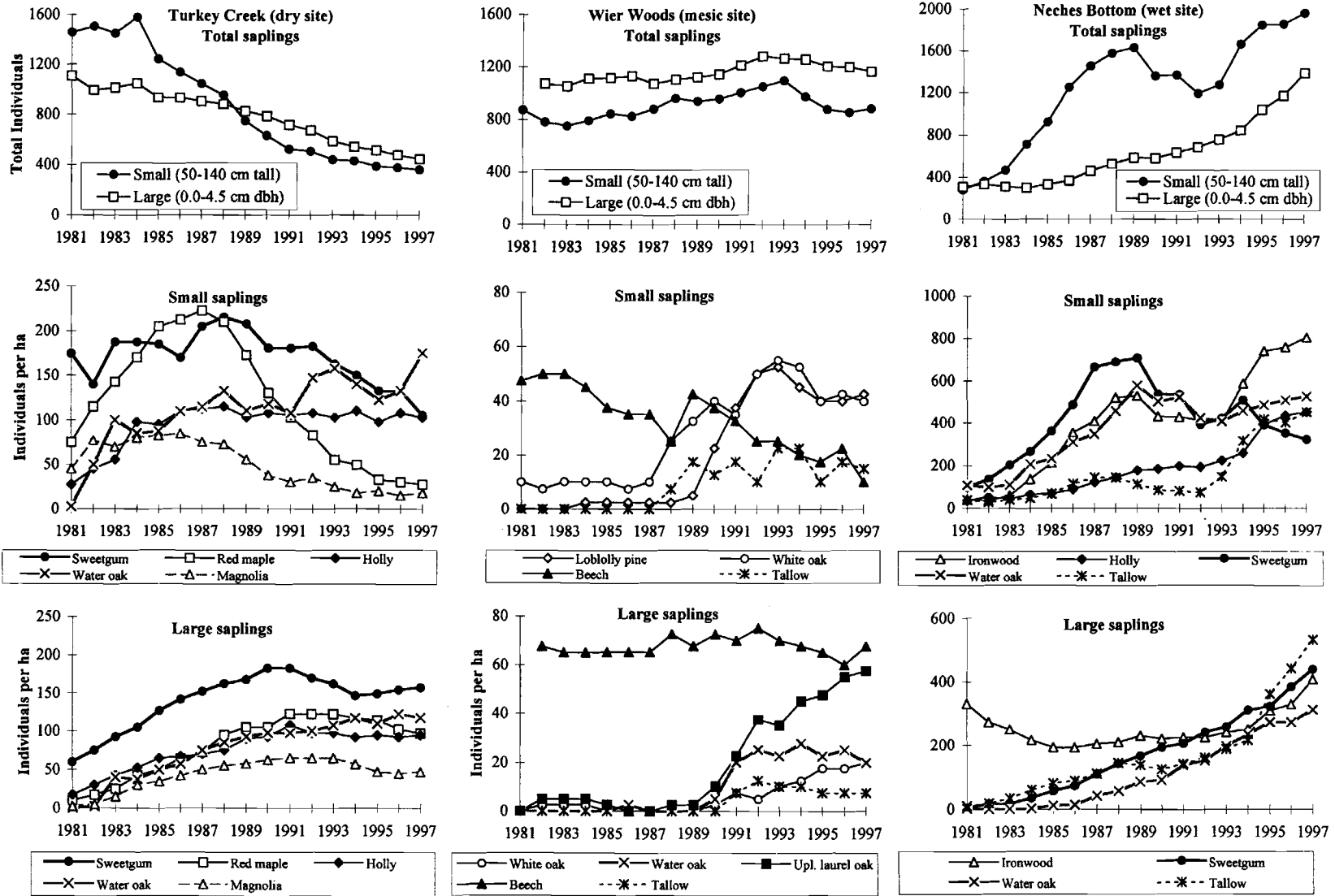
Figure 5-3. Total saplings and density of saplings of selected species at three study sites, 1981-97. Small saplings are individuals between 50 and 140 cm in height. Large saplings are individuals between 0.4 and 4.5 cm dbh.

Table 5-2: Changes over time in relative densities of greater than 1-year-old woody seedlings (stems less than 50 cm tall) in 100 1 m by 1 m plots at the dry study site. All species having 5 or more stems in any census period are listed.

A. Shade-intolerant species adapted to frequent fire

	1980	1981	1982	1983	1984	1995
Wax myrtle	0.6	0.7	1.0	1.0	0.8	0.2
Longleaf pine	7.1	5.1	3.6	2.8	2.5	0.0
Shortleaf pine	1.7	1.5	1.4	1.2	0.9	0.2
Bluejack oak	3.7	4.3	4.2	3.3	2.1	0.2
Blackjack oak	0.4	0.6	0.6	0.6	0.7	0.0
Deerberry	8.8	9.1	9.3	9.0	6.2	2.6

B. Somewhat less shade-intolerant species adapted to occasional fire

	1980	1981	1982	1983	1984	1995
Hickory	2.7	2.8	2.9	2.8	2.4	1.2
Flowering dogwood	6.4	5.6	4.7	5.4	4.4	4.2
Loblolly pine	17.1	13.8	9.1	8.7	27.1	7.7
Southern red oak	4.1	4.7	3.9	4.1	3.6	2.9
Post oak	16.1	13.2	16.2	14.1	9.9	5.6
Sassafras	9.5	9.9	10.5	10.8	9.4	4.4
Farkleberry	0.1	0.0	0.1	0.3	0.2	1.0

C. Shade tolerant, mostly fire-intolerant species

	1980	1981	1982	1983	1984	1995
Red maple	2.7	3.5	3.3	3.2	3.3	3.9
American holly	1.1	1.3	1.1	1.4	1.3	2.9
Yaupon	9.8	16.2	20.8	22.1	16.1	41.2
Sweetgum	0.9	0.7	1.3	1.2	1.4	1.3
Southern magnolia	0.4	0.4	0.7	0.6	0.5	0.9
Red bay	0.9	0.9	0.7	1.2	1.4	3.4
White oak	0.0	0.0	0.0	0.0	0.0	1.0
Upland laurel oak	0.4	0.4	0.6	0.8	0.7	1.3
Carolina buckthorn	0.0	0.0	0.0	0.0	0.0	4.5
Total Individuals	**704**	**681**	**718**	**780**	**920**	**68**

saplings more strongly than they affect trees, given the relatively high frequency and low intensity of these events in habitats like these in the southeastern United States.

The immediate consequence of intervals without fire or flood was a substantial pulse of recruitment at the two sites. At the dry site, however, the most successful recruits were not current site dominants; this implies future successional change. At the wet site, the recruits were of the dominant species, which implies compositional stability. The difference may be that successional replacement is prevented by soil anoxia for much of the winter at the wet site, which kills seedlings of mesic species, whereas summer drought at the dry site is not so extreme as to kill seedlings of the mesic species. Alternatively, such differences may have to do with dispersal distance (Schmeda and Ellner 1984). The dry site is in a topographically complex upland with mesic

habitats nearby that are a ready source of seeds, whereas the wet site is in a large, homogeneous river bottomland, which is at some distance from a source of seeds of mesic species.

In contrast to the wet and the dry sites, the mesic site showed only modest fluctuations in sapling populations, in spite of the hurricane. This lesser response to disturbance is surely related in part to the relatively minor level of damage inflicted by the hurricane, but it may also be influenced by the nature of the mesic upland system. Since neither fire nor flood is commonly part of these systems, a dense and diverse shrub-sapling layer is characteristically present, which will respond to perturbations by accelerated growth of preexisting individuals in newly formed gaps rather than by recruitment of a new cohort. Even in the absence of a dense shrub-sapling layer, stand-opening

events would not necessarily change conditions in ways that would favor species from either wetter or drier habitats like the long-term changes in fire and flooding at the other two sites. If hurricanes were to become more frequent or more severe because of global warming, such a regime would favor mobile, fecund species like loblolly pine or the shade-intolerant, fast-growing species of the wet sites (sweetgum, water oak) and would undoubtedly reverse the successional decline in loblolly pine and water oak that seems imminent for this stand.

The invasion of an exotic woody species, Chinese tallow, illustrates the strong effect of edaphic conditions in determining invasion potential; Chinese tallow is virtually absent from the dry site, probably because the species is highly moisture-demanding. The Chinese tallow invasion also illustrates the effect of stand structure on the invasibility of a system. Compared to the mesic site, the wet site experienced invasion much earlier because of the open understory; invasion of the mesic site began only after canopy disruption by the hurricane.

Aside from the effects of perturbations, there were predictable differences in overall rates of seedling and sapling recruitment at the three sites. Seedling appearance rates were highest at the wet site, intermediate at the mesic site, and lowest at the dry site, presumably because of a combination of higher fecundity of individuals where moisture is less limiting, as well as higher germination and early survival rates in moister soils. In contrast, small sapling recruitment was highest at the wet site, intermediate at the dry site (but only because of a strong pine pulse), and lowest at the mesic site. The low small sapling recruitment at the mesic site may be attributed to heavy shade from the dense shrub-sapling layer.

These trends imply that the response of vegetation on contrasting sites to climate change would vary because of differences in recruitment. Since many factors are involved in the recruitment process (distance to potential source trees and differences in fecundity, vagility, viability, and seedling survivorship), not to mention other processes, the nature of the response could be difficult to predict, especially since some of the factors might change in offsetting ways, while other changes would be additive or multiplicative. However, the trends we observed in saplings suggest that the net result may be a reduction in the degree of compositional variation across the landscape.

Overall Stand Dynamics and Vegetation Response Time

Only modest changes in tree basal area, density, and species composition were observed at the three sites; these changes were mostly explainable in terms of successional change following logging or alterations in flood or fire regimes. In contrast, the sapling and seedling layers varied more, apparently in response to recent disturbances, which suggests strong sensitivity to global warming by way of its effect on the disturbance regime. For the dry stand, autogenic succession is the dominant process, particularly in the subcanopy strata. Nevertheless, the stand may well be sensitive to climate change since the successional process could be accelerated by increased storm activity which could kill canopy trees and thereby accelerate succession to a mesic, less fire-dependent community type (Glitzenstein and Harcombe 1988; Liu et al. 1997). On the other hand, succession could be reversed by increased drought severity; drought could kill mesic juveniles directly via water stress or indirectly via increased fire frequency (e.g., Glitzenstein et al. 1995). The indirect effects could equal or exceed the magnitude of the direct effects.

For the mesic stand, which may be close to a long-term steady state, the effect of the hurricane on recruitment indicates that the stand will also be sensitive to a changing climate. In such communities, one likely effect of global warming would be to increase the disturbance rate and thereby to maintain the importance of loblolly pine, water oak, and white oak, as well as promote invasion by exotic woody species like Chinese tallow. If the decline in American beech is somehow related to global warming, the response of sites like this one may be much greater.

In the wet forest, global change effects are harder to predict, since they might involve increases in frequency and intensity of both floods and droughts. It seems likely that the flooding effect would prevail, however, possibly reversing the changes set in motion by human alteration of the hydrologic regime.

Vegetation can respond to climate either by changes in local abundance caused primarily by differential effects of climate on growth and regeneration (Type A response) or by changes in range limits (Type B response; Webb 1986). Our monitoring results apply to the Type A response related to regeneration. Melillo et al. (1996) cite four forest studies reporting response times of 30–150 years (MacDonald et al. 1993; Mayle and Cwynar 1995; Gear and Huntley 1991; Zackrisson et al. 1995). Campbell and McAndrews (1993) cite a successional response in Ontario of dieback with a slow response time of several centuries due to tree longevity. In our study, the response times reported are short (turnover times of 69–108 years) because of relatively short life spans, rapid recruitment, and high growth rates. Because of the similarity of vegetation across the southeastern United States, these response times probably apply to similar stands throughout the region. If a climate change effect were primarily to alter the competitive balance among species by differentially changing growth or recruitment rates, we would expect a slow, gradual vegetation response. Alternatively, if climate change primarily affected the disturbance regime a much more rapid response

would be predicted, involving shifts in species composition (greatest shifts on dry sites, intermediate shifts on mesic sites, low shifts on wet sites). These results, based on field data, support the suggestion that southern forests are sensitive to climate change (Urban and Shugart 1990), but it is too early to speculate on the magnitude of the impact.

Pattern and Process

In addition to the general picture of stand dynamics and the relationship to the flood regime that has developed as part of the long-term study, we have analyzed the fine-scale temporal and spatial patterns of stand dynamics. One element of this analysis (Hall and Harcombe 1998) examines the interaction of flooding and light availability in determining spatial patterns of tree saplings.

Flood and Shade Tolerance

Continuum theory suggests that species will be assorted along an environmental gradient in an order which reflects their realized niches with respect to the varying environmental condition. Where two gradients are present, the expectation is that direct gradient ordination techniques will recover the ordering of species on both. Many authors have assessed either flood tolerance (Teskey and Hinckley 1977; McKnight et al. 1981; Wharton et al. 1982; Mitsch and Gosselink 1986) or shade tolerance (McKnight et al. 1981; Burns and Honkala 1990) for most of the dominant tree species found at the wet site. Thus, at least for those two variables, it is possible to create a model of expectations representing a null hypothesis for the ordering of major tree species along these two gradients.

We took hemispherical photos at the centers of each of 100 20- by 20-m plots in the stand to estimate light availability using SOLARCALC (Chazdon and Field 1987a,b), which is a computerized version of the Anderson (1964) method. Soil texture and nutrients were measured for 100 points across the stand. Values for all environmental variables were estimated for each plot using block kriging (GEO-EAS; Englund and Sparks 1988).

We conducted correspondence analysis (CA), a form of indirect gradient analysis (Hill 1974), on mean sapling abundance over 10 years from 15 randomly located permanent plots. There were 19 species of woody saplings found in the plots. The mean number of individuals of each species in each plot was the response variable. The CA was used to determine the total amount of variation which could be explained by unconstrained ordination techniques. We determined the number of stable axes using a scaled rank variance (SRV) statistic (Knox and Peet 1989). Canonical correspondence analysis (CCA; Ter Braak 1987; Ter Braak and Prentice 1988), a form of direct gradient analysis, was then used to examine the portion of variation in species composition that could be explained by changes

in the environmental variables. There were eight environmental variables available for use in the model either to constrain the axes or as covariables: elevation, weighted percent sky, percent sand, percent clay, available phosphorus, available iron, available calcium, and available nitrate.

For the indirect gradient analysis (CA), the first four axes accounted for 75% of the total variation. Axis 1 was correlated with elevation ($r = -0.95$), while Axis 2 was correlated with percent sky ($r = -0.76$). Monte-Carlo tests (Ter Braak 1987) showed that both correlations were significant ($p = 0.01$ and $p = 0.02$, respectively).

Comparison of first axis ranking of species with flood tolerance rankings obtained from the literature shows substantial agreement, indicating that elevation is a surrogate for flood tolerance.

In contrast, comparison of second axis ranking with species shade tolerance rankings obtained from the literature shows little correspondence between position on the light gradient and species shade-tolerance rankings. Several of the most shade-tolerant species (American holly, water-elm [*Planera aquatica*], and American elm) are placed on the high light end of the light gradient. There are at least two possible explanations for this discrepancy. First, there is some disagreement in the literature about the shade tolerance of the species listed here (especially laurel oak). However, it is unlikely that significant disagreement extends to all species, especially those considered most shade tolerant. Second, there may be interactions for some species between shade tolerance and other environmental variables such as flooding or moisture availability.

Our data indicate the existence of such interactions: species were assorted across a gradient of canopy openness, but not in accordance with their shade tolerance. The interactions acted to limit the success of at least some shade-tolerant species in the highly stressful floodplain environment with both frequent flooding and shade. These interactions can be illustrated using a matrix to compare shade-tolerance rankings to position on the light gradient (Table 5-3). The null expectation would be that species should fall primarily along a single diagonal. However, many species were shifted away from the diagonal. Apparently, flood tolerance may allow persistence of some species under lower light conditions than normal, while flood intolerance may limit some normally shade-tolerant species to higher light conditions where growth is fast enough to allow escape from the flooding hazard (Fulton 1991). The movement of almost all of the shade-tolerant species to higher light conditions suggests that it is difficult to survive both flooding and low light conditions.

Our results support the conclusions of Menges and Waller (1983) that the combination of flooding and low light is so severe that few species can adapt to it. This conclusion may explain the sparse understory, which is characteristic of most southern floodplain forests (Wharton

Table 5-3. Light gradient position of Neches Bottom species compared to expected shade tolerance (from Hall and Harcombe 1998).

Shade tolerance (Predicted position)	Light Gradient Position (Actual Position)		
	Low	Intermediate	High
Tolerant	Hackberry	Red maple American hornbeam	American holly Water elm American elm
Intermediate	Carolina ash Sycamore Blackgum Baldcypress	Laurel oak Water hickory Overcup oak Basket oak	
Intolerant			Water oak Sweetgum Cherrybark oak

et al. 1982), as well as the dominance of shade-intolerant species (e.g., sweetgum and water oak) noted in this study. Jones et al. (1995) also suggested that flooding prevents successful replacement of shade-intolerant species by shade-tolerant species. Our results further indicate that light is important in determining within-stand patterns of plant occurrence, as shown previously for herbs (Menges and Waller 1983) and tree seedlings (Streng et al. 1989; Jones and Sharitz 1990; Jones et al. 1995). Species were assorted across a gradient of light availability, but the basis for this assorting was not shade tolerance alone. Instead, the ordering may reflect species-specific tradeoffs between light requirements and flood tolerance.

Growth Responses

One of the goals of this research was to determine whether sapling growth showed year-to-year variation that might be related to variation in annual rainfall or temperature. The rationale was that strong response to variation in these climate variables at this time scale would be presumptive evidence that forests of the region would be sensitive to climate change occurring over decades. In this section, we report the results from an analysis of sapling growth at the three study sites from 1980–1994 and the results of a more detailed study of the wet site from 1980–1989 (Hall 1993) for small saplings (50 cm tall to less than 140 cm tall) and large saplings (greater than 0.0 cm dbh to less than 4.5 cm dbh). The climatic variable selected for initial screening was the Palmer Drought Severity Index (PDSI) from Cook et al. (1997).

The overall rate of sapling growth varied significantly among sites (pairwise median test); median growth was 5 cm per year at the wet site, 3 cm per year at the mesic site, and 2 cm per year at the dry site. There was no apparent correlation of the annual growth values pooled across sites with annual PDSI (Pearson product-moment correlation

coefficient, r = -0.05), but there was an obvious temporal trend. On the provisional assumption that this trend was related to stand dynamics processes, a nonlinear curve was fitted to the series and residual deviation from this curve was calculated. The residual values had a much higher, though nonsignificant, correlation with PDSI (r = 0.34, p = 0.22). Examination of a graph of pooled residual growth and PDSI (Fig. 5-4) suggests that sapling growth might be related to PDSI, though other sources of variation are also present. When the sites were examined separately (Fig. 5-5), the relationship was stronger: growth residuals at the wet and dry sites were correlated (r = 0.58, p = 0.02), which strongly supports the suggestion of a climate signal. The intersite correlation appears to have been stronger early in the 15-year period when drought was a factor. Later in the period, some deterioration in the climate relationship seems
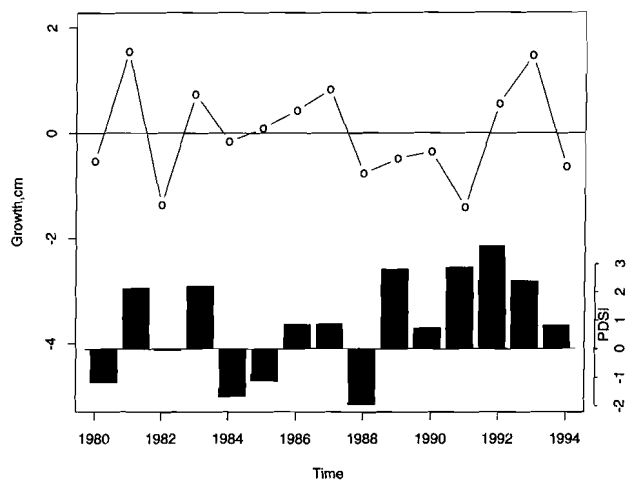

Figure 5-4. Pooled residual sapling growth for three study sites compared to Palmer Drought Severity Index, 1980-93.
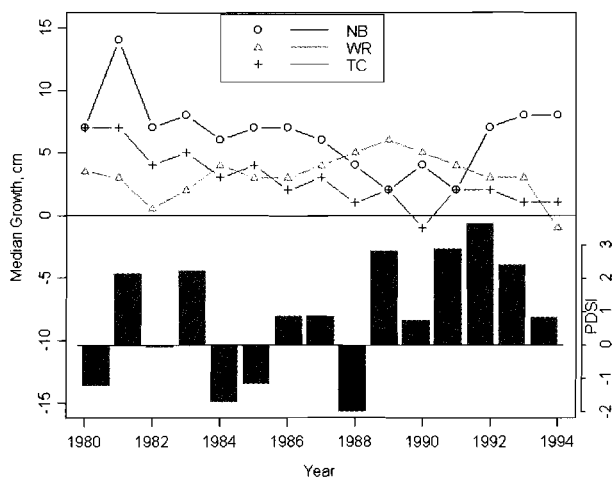
Figure 5-5. Comparison of median residual sapling growth by site with Palmer Drought Severity Index, 1980-93.

to have occurred. One cause of this deterioration was flooding at the wet site which caused saplings there to do poorly. The two lowest-growth years at the wet site (1989 and 1991) were among the worst flooding years and followed relatively dry years (Fig. 5-6). The strength of the wet site–dry site correlation increased when analysis was repeated using only the species found at all three sites (r = 0.70, p = 0.004). It is clear from the analysis that the mesic site was different from the other two sites in its response to climate, possibly because growth there responded more to processes like the hurricane than to annual variation in drought severity.

Additional analysis of data from the wet site showed that severe flooding reduced small sapling height increment; the lowest height increment year occurred in 1989, the year
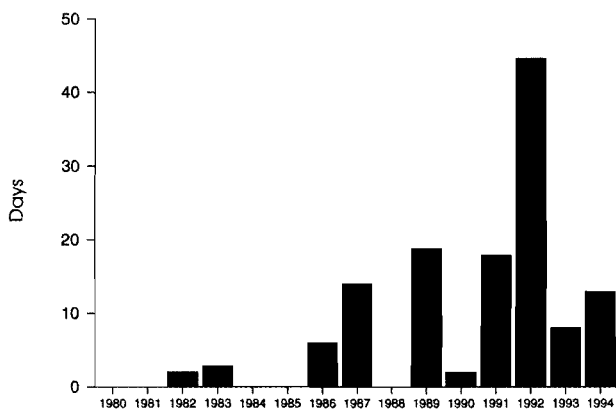

Figure 5-6. Maximum consecutively flooded growing-season days for flats at wet site, 1980-94.

of major growing-season flooding. However, there appeared to be both a seasonal effect and thresholds related to sapling size and length of flooding (Hall 1993). The impact of dormant-season flooding was less severe.

There were a few interesting differences among species in median small sapling height growth (Fig. 5-7). Water hickory and American elm exhibited net height growth of below or near zero. This negative net growth suggests that most individuals of these species were not succeeding in the plots, at least over the last 10 years. The rest of the species showed positive median height growth, indicating that most individuals which made it to the sapling size class were succeeding over the period of observation. Chinese tallow, an exotic invader, grew 23 cm per year, more than three times median height growth pooled over all species and years and more than twice the median height growth rate of the next-ranked species (red maple: 9 cm; Median test, T = 19.57, p < 0.001). Differences among the native species were minimal, except that there was a breakpoint between the faster growing oaks and American holly and the slower growing species. It is surprising that the native species did not show more differences in height growth rates, though this result is consistent with the earlier report that tree seedling growth rates differed very little among species (Streng et al. 1989).

Large saplings also showed variation among species in median diameter growth (Fig. 5-8). Again, Chinese tallow grew significantly faster than all the other species (Median test, T = 34.22, p < 0.001). Large saplings of cherrybark oak (*Quercus pagoda*) and water hickory exhibited greater growth than one might expect, considering their low growth as small saplings; in contrast, red maple and American hornbeam seemed to do relatively worse as large saplings.

To determine whether growth was faster in and around canopy gaps, we compared sapling growth between the randomly placed permanent sapling plots and plots containing sapling patches related to canopy gaps. Median height growth for small saplings in patch plots was 1 cm more than the 7 cm per year found for the random plots (Median test, T = 7.9512, p = 0.005); large saplings in or around canopy gaps also grew significantly better (Median test, T = 35.11, p < 0.001). All but two species showed higher growth in the gap-related patches, either as small or large saplings. Thus, gaps appear to be important to the success of saplings.

We used stepwise linear least-squares regression to model growth as a function of several site variables (percent sand, percent clay, relative elevation, and weighted percent sky; details on estimation of environmental variables can be found in Hall 1993). The following predictor variables were also included in the analysis: size of the individual at the beginning of the period of growth, species-specific growth ranking, total density of individuals
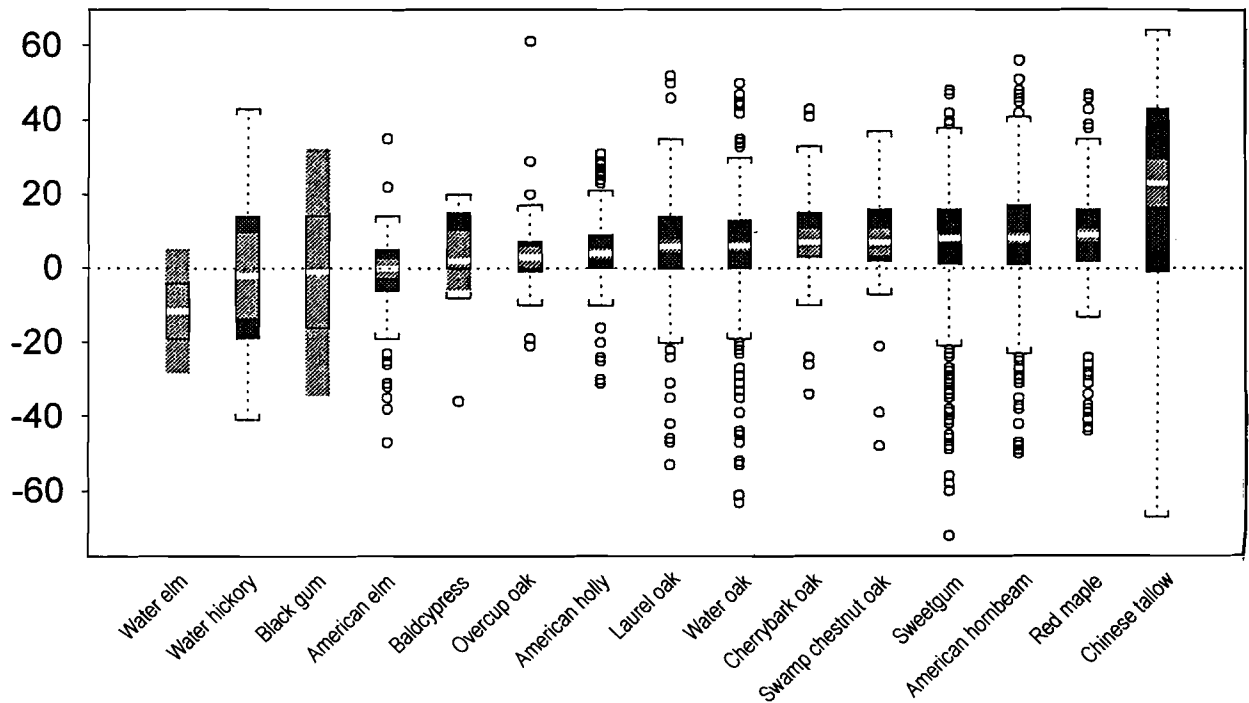
Figure 5-7. Box plots of median height growth of small saplings by species at wet site (from Hall 1993). For each boxplot, the white bar represents the median, the light gray bar represents the 95% confidence interval, the dark gray bar and the black outlined box represent the interquartile range, the brackets or whiskers represent 1.5 times the interquartile range, and the empty circles represent outlying data points.

in the quadrat during the year, and days flooded during the year. This mix of variables constant in time (the environmental variables and species-specific growth ranking), variables which change depending on which year the individuals grew into the plots (days flooded, density), and variables which are specific to the individual plant (size) may present some pseudoreplication problems, but it is not clear how one might reduce degrees of freedom or correct reported significance levels for this problem. With this caveat, we proceed as if reported significance levels were approximately correct.

The results are significant and slopes of the relationships are, for the most part, as expected. Height growth increased with individual size, varied among species, declined with the density of other saplings in the same plot, was greater in gaps than under the canopy, and was lower at higher elevations. This latter relationship is the opposite of what one would expect if the primary effects of elevation were associated with flooding or soil waterlogging at low elevations and may indicate that, in years without lengthy flooding, sapling growth is strongly limited at high elevations where moisture stress would be highest.

In addition to the general linear modeling, we used a generalized additive model (GAM) (Hastie and Tibshirani 1986), keeping the significant predictors from the previous analysis as linear (days flooded and percent clay) and specifying that smoothed curves be fit to the variables which showed no linear relationship (percent sky and percent sand). Intuitively, a GAM can be understood as an extension of a general linear model wherein the effects are not limited to being linear. In this analysis, the variables of days flooded, percent sky, and percent clay were significant, while percent sand was not. The most interesting and interpretable result of the GAM is that it allowed a nonlinear effect of flooding duration on growth to emerge. Growth appeared to decline until the duration of flooding was about 6 months; beyond that, growth was already maximally suppressed. The other two nonlinear relationships with weighted percent sky and percent clay had the expected sign (growth increased with increasing percent sky and with increasing percent clay), but the nonlinearities probably represent interaction effects for which we did not test.
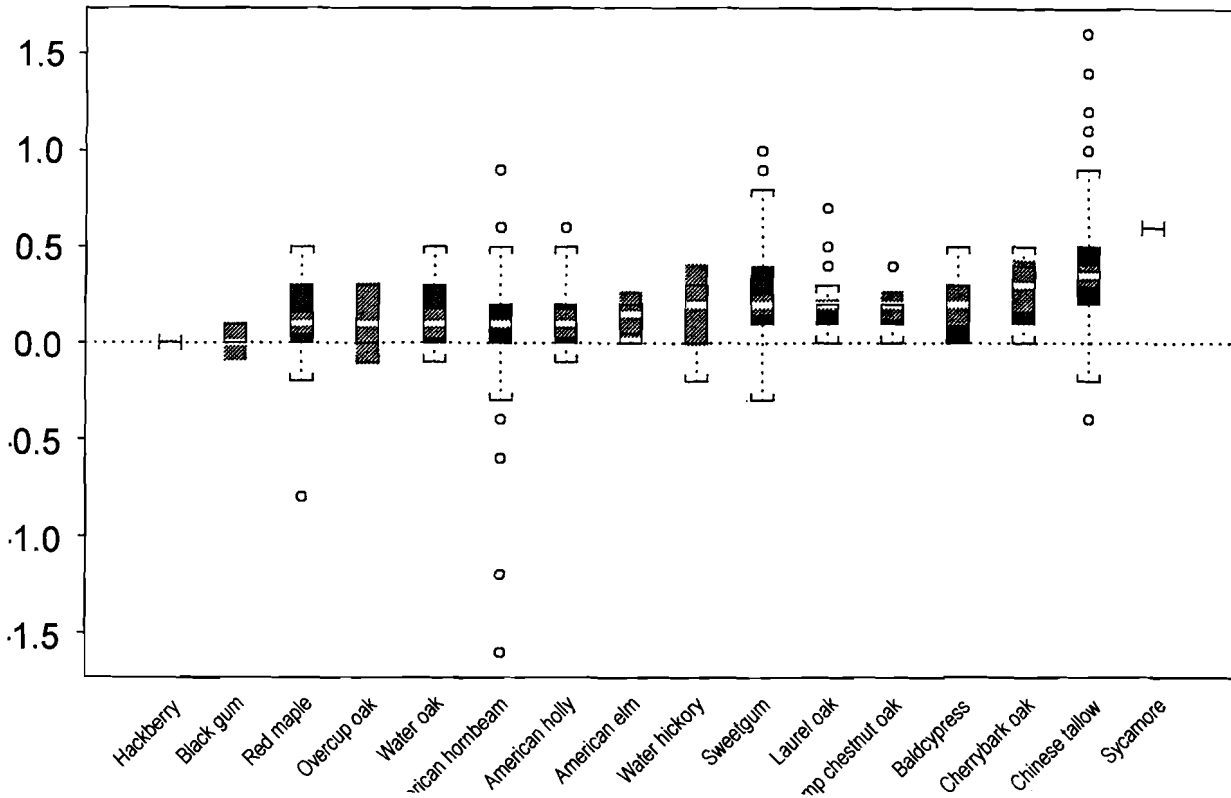
Figure 5-8. Box plots of median dbh growth of large saplings by species at the wet site (From Hall 1993). See Fig. 5-7 for explanation of box plots.

Tree Ring Analysis Along a Climatic Gradient

Attempts to model and predict effects of climate change on forests typically require assumptions about the relationship of tree growth to climate (Shugart 1984; Solomon 1986; T.W. Doyle, National Wetlands Research Center, Lafayette, Louisiana, personal communication). Unfortunately, such assumptions often have little empirical or theoretical basis and may, in fact, be grossly inaccurate (Shugart 1984; Graumlich 1989; Cook and Cole 1991). The science of dendrochronology can greatly increase our understanding of tree growth-climate relationships and thereby improve model predictions (Graumlich 1989; Cook and Cole 1991). In this section, we describe the results of a study of tree-ring growth along a climate gradient in an area which crosses the range boundaries (as defined by Little 1971) of many of the important tree species of the southeastern United States.

The tree-ring study area is defined by a rectangular region in eastern Texas and western Louisiana extending from 28° to 32°N and from 92° to 98°W (Fig. 5-9). In terms of the original vegetation, it extends from a zone of longleaf

pine dominance in eastern Texas, through a zone originally dominated by shortleaf pine, loblolly pine, oaks, and hickory, across an area dominated mostly by oak and
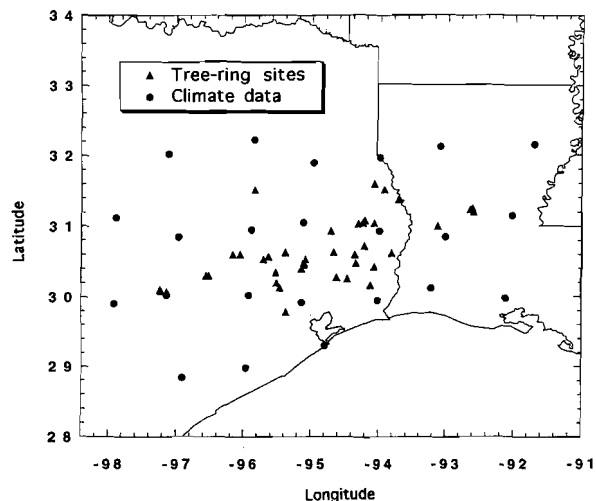

Figure 5-9. Tree-ring site locations in the Big Thicket region.

hickory, and, finally, across a narrow band of blackland prairie (Tharp 1926, 1939; Bridges and Orzell 1989). The western end is at Bastrop State Park, site of a disjunct stand of loblolly pine and eastern oaks. This site marks the approximate western limit of what is generally recognized as Eastern Deciduous Forest (Braun 1950; Greller 1989). The Big Thicket lies within the east Texas part of the study area.

The study area is characterized by a progressive east-west reduction in precipitation and an associated increase in temperature (Fig. 5-10), which probably accounts for the strong variation in forest vegetation (Tharp 1926; Greller 1989). For the winter season, this gradient is almost purely east-west, with essentially no trend from south to north. In contrast, the summer rainfall surface is more complex, with a clear south-north decline in rainfall. In all likelihood, the summer rainfall pattern is complicated by intrusions of warm and moist convective air masses from the Gulf of Mexico that dry out as they penetrate progressively northward. This mode of moisture delivery is likely to be much less frequent during the cooler winter months. Winter maximum temperature shows a general trend towards warmer conditions from east to west and cooler conditions from south to north, but there is also considerable local variation. In contrast, summer temperature shows

only a general tendency for warmer conditions from east to west. However, most of this gradient follows a uniform steep increase in maximum temperatures west of 95°W longitude. The pronounced dip in the surface is due to the extreme coastal grid point shown in Fig. 5-9. Presumably, relatively cool sea breezes contribute to this anomaly.

These climate gradients might affect the forests of the Big Thicket region in two ways. First, precipitation ought to become increasingly limiting to tree growth from east to west. In this sense, winter may be the most critical season because it is the time when precipitation is most effective in recharging soil moisture reservoirs. In contrast, much of the summer rainfall will evaporate and will not recharge the soil reservoir. Second, the trend towards warmer summer maximum temperatures from east to west will result in higher potential evaporation demand on the trees and more frequent periods of internal moisture stress. The steep temperature increase might also be significant if a threshold effect on evapotranspiration demand is crossed for some tree species.

For this project, 104 annual tree-ring chronologies were developed from 16 tree species (Table 5-4) growing on 38 sites distributed across the region (Fig. 5-9). Ten to twelve trees of a given species were sampled per site, with one increment core extracted per tree. The criteria for selecting
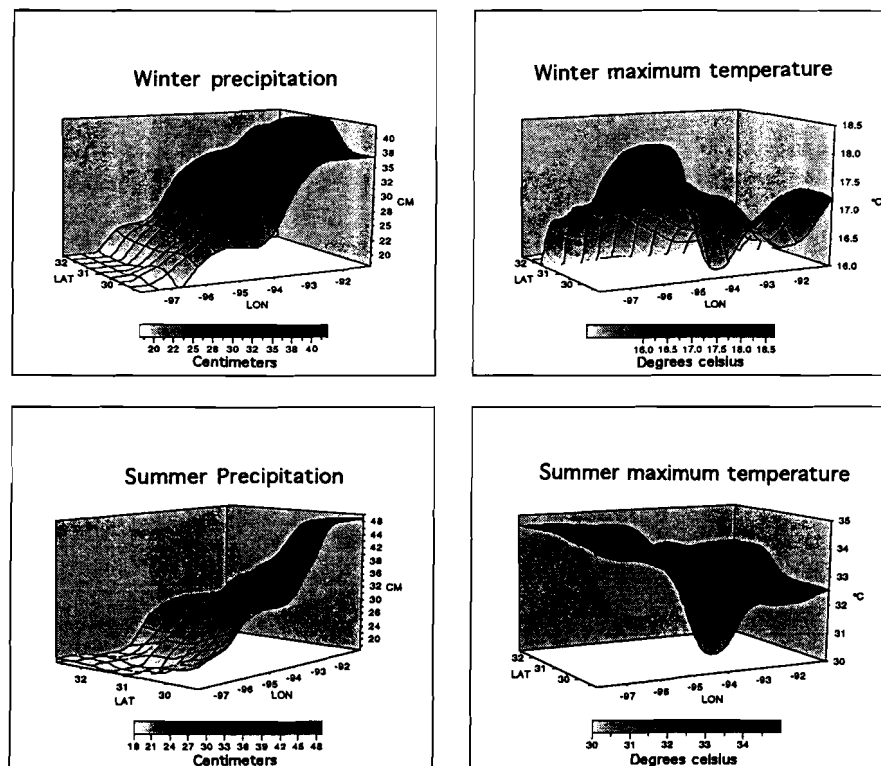

Figure 5-10. Surface maps of precipitation and maximum temperature over the Big Thicket region.

Table 5-4. Species and basic taxonomy of the 104 tree-ring chronologies.

Tree taxonomy	Latin name	Number
Family Pinaceae		
Genus *Pinus*		
Loblolly pine	*Pinus taeda*	20
Longleaf pine	*Pinus palustris*	7
Shortleaf pine	*Pinus echinata*	6
Family Taxodiaceae		
Genus *Taxodium*		
Baldcypress	*Taxodium distichum*	1
Family Fagaceae		
Genus *Quercus*		
Subgenus *Leucobalanus*		
White oak	*Quercus alba*	11
Swamp chestnut oak	*Quercus michauxii*	5
Post oak	*Quercus stellata*	4
Overcup oak	*Quercus lyrata*	3
Subgenus *Erythrobalanus*		
Southern red oak	*Quercus falcata*	10
Water oak	*Quercus nigra*	18
Willow oak	*Quercus phellos*	4
Laurel oak	*Quercus laurifolia*	1
Shumard oak	*Quercus shumardii*	1
Blackjack oak	*Quercus marilandica*	3
Bluejack oak	*Quercus incana*	1
Genus *Fagus*		
American beech	*Fagus grandifolia*	9

sampling sites were the existence of trees 50 or more years in age of the species needed for the transect in a given general location. Soils, site hydrology, slope aspect, and disturbance history were not considered in the selection of sites. Therefore, while the site selection scheme used here was not statistically random, neither was it biased towards anything but stand age and transect location. Purely random site selection might well have missed important sites at the western range limits of some species. The annual tree-ring chronologies were developed using standard dendrochronological procedures (Fritts 1976; Cook and Kairiukstis 1990). For each species collection at each site, the ring-width series were checked for cross-dating and overall quality using the computer program COFECHA (Holmes 1982).

A common modeling assumption is that climatic limitations to tree growth can be inferred from conditions at range limits (Shugart 1984). Thus, if a range limit for a particular species is characterized by a certain number of drought days or degree days, it is assumed that these conditions represent the physiological limits beyond which the tree cannot grow. If this assumption is correct, trees at the edge of their range should be growing very slowly indeed. As one moves away from the range limit, however, climate improves and the growth of the species in question should increase.

The above assumptions, commonly used in models, have not been conclusively tested (but see Prentice et al. 1991; Bonan and Sirois 1992). Here, we test whether tree growth at range limits is exceptionally limited. In addition, we test for an effect of distance from range limit on growth. Because model assumptions pertain to potential growth in the absence of competition, we use maximum growth in our analyses rather than average growth. We define maximum growth as the single largest growth ring observed for any individual of a species at a site. Analyses are limited to species with five or more sites.

The assumption that maximum potential tree growth is strongly restricted at range limits is not supported. For four species, maximum growth rates near range limits actually exceeded rangewide means (Table 5-5). For three species, American beech, loblolly pine, and shortleaf pine, the range limit values were somewhat depressed compared to the rangewide means for those species. However, even in those cases, it is hard to argue that a potential diameter growth rate of almost 10 mm per year indicates serious climatic stress. The assumption that maximum growth increases with distance from the edge of the range is also not supported (Table 5-5), except in the case of shortleaf pine. Because these data suggest minimal climatic limitation on tree growth at sites close to the range limits of species, it seems likely that climate effects on seedling establishment may be the critical limiting factor, a conclusion which is consistent with studies of southwestern oaks (Neilson and Wullstein 1983). Clearly, additional experiments to test this hypothesis are warranted.

The 104 annual tree-ring chronologies range from 37 to 739 years in length. From this overall set, we selected for analysis 99 chronologies that covered the common time

Table 5-5. Relationship of maximum ring growth to longitude (°W) for tree species sampled at greater than five sites (n = number of samples; r = Pearson product-moment correlation coefficient; P = Probability level).

Species	Correlation statistics			Growth at range limit (mm)	Percent of mean of all sites
	n	r	P		
American beech	9	-.28	.47	7.06	79.7
Shortleaf pine	6	-.86	.03	7.05	80.2
Longleaf pine	9	-.21	.57	8.80	95.4
Loblolly pine	20	-.33	.16	8.83	64.4
White oak	11	.22	.51	10.67	114.1
Southern red oak	9	.02	.95	10.36	111.9
Swamp chestnut oak	5	.46	.44	11.18	103.4
Water oak	17	.39	.12	18.40	134.6

period 1941–1993. Principal components analysis (PCA), a form of multivariate analysis (Cooley and Lohnes 1971; Richman 1986), was employed as a first step in testing for patterns in the tree-ring data. Principal components analysis and other ordination techniques are commonly used by vegetation scientists to test for patterns in species associations or plant community relationships in vegetation data. The PCA described herein is analagous, except that the input data are annual tree ring increments rather than measurements of species abundance. Thus, the results reveal similarities and differences among tree species in their responses to climate. Though PCA is a common multivariate technique, it has never before been employed in tree-ring analysis because the appropriate data set has never before been assembled.

For input data, we used tree-ring indices which sequentially removed sources of extraneous variation to focus on year-to-year variability in growth due to climate. Construction of these indices involves two steps (Cook 1985; Fritts and Swetnam 1989). First, long-term, relatively inflexible trend lines are fitted to the individual tree-ring widths and deviations from these fitted lines (residuals) are preserved for analysis. This technique effectively removes gradual changes in growth due either to intrinsic properties of trees (i.e., all other factors being equal, younger trees grow faster than older trees) or to long-term trends in biotic or abiotic environment (e.g., growth of trees into canopy gaps; see Glitzenstein et al. 1986). These gradual trends, while ecologically interesting, tend to obscure short-term growth responses related to climate.

The second step in construction of a tree-ring index is autoregressive modeling of the residuals. Autoregression (Box and Jenkins 1976) is analogous to ordinary multiple regression, except that the predictor variables are prior years in a time series. This technique controls for physiological effects which may carry over from one year to the next, blurring the influence of climate in any given year (Cook 1985). Autoregressions yield a second set of residuals, which are the final tree-ring indices used in the PCA.

The results of the PCA of annual tree-rings revealed a previously unsuspected pattern, which we call the phylogenetic effect. It is illustrated by examining the loadings of species' scores on the different PCA factors (Fig. 5-11). Each PCA factor can be thought of as an independent source of variation in the tree-ring data, analogous to axes
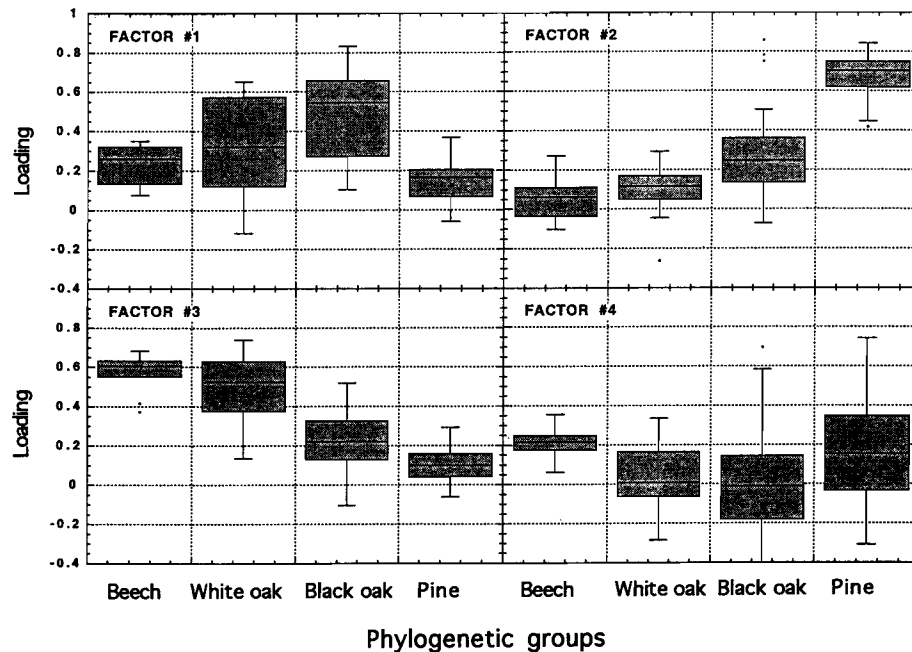

Figure 5-11. Varimax rotated factor loadings for each phylogenetic group on each principal components analysis (PCA) factor. Each of the four sections corresponds to one of the PCA factors. Within each section there is a box plot of the factor loadings for all chronologies (species x sites) within each phylogenetic group (beech, white oak, black oak, pine; see text for further definitions of phylogenetic groups). Each box plot consists of a median value (horizontal line within shaded area), a box containing all measurements from the 25th to the 75th percentiles of all values, and whiskers showing 5th and 95th percentiles.

in an ordination analysis. For Factor 1, scores for the black oak (*Erythrobalanus*) subgenus are highest (median = 0.54), followed by species of the white oak (*Leucobalanus*) subgenus (median = 0.32), American beech (median = 0.26), and pines (median = 0.17). Consequently, we call Factor 1 the black oak factor, even though the overlap between the black oaks and white oaks loadings indicates some similarity between the oak subgenera. This overlap is much reduced on Factor 2, which shows the strongest phylogenetic separation. Because pine species load well above the other groups (median = 0.70), we call Factor 2 the pine factor. The beech and white oak chronologies are separate from the black oak and pine chronologies on Factor 3, so we call this the beech/white oak factor. No particular phylogenetic group is segregated on Factor 4, and median loadings for all taxonomic groups are low. Factor 4 does have some chronologies that load very highly, however, especially in pines and black oaks. These variations suggest that there may be local, site-related explanations for this factor.

These results suggest that growth responses of species to climatic variation are determined primarily by evolutionary rather than ecological relationships. We might have expected *a priori* that factor loadings would reflect similarities among species with similar site requirements, that dry site white oaks would load with dry site black oaks and dry site pines. The lack of clustering has two important implications for predicting climate effects on forests. First, shifts in seasonal distribution of precipitation might be expected to produce similar compositional changes across a range of sites. The second implication of the phylogenetic effect for climate change predictions concerns the use of tree-ring indices in stand dynamics modeling (Cook and Cole 1991). The existence of phylogenetically homogenous groupings should greatly simplify the task of modifying these models to reflect climate effects on tree growth.

The differences we found between the oak subgenera in tree-ring growth are consistent with patterns described by Mohler (1990) from vegetation analysis. He demonstrated a tendency for species in the black oak subgenus to occur on the same sites with species in the white oak subgenus, whereas species within the same subgenera were less likely to occur on the same sites. Mohler argued that his results indicated evolutionary differences between the two subgenera that promote coexistence of species pairs by minimizing interspecific competition. Our tree-ring results suggest that differences in responses to climate may be one factor contributing to that coexistence.

In addition to demonstrating the phylogenetic effect, PCA factor loadings of species groups, when plotted versus longitude, show variation with longitude for the two oak subgenera but not for the pine group as a whole or for American beech (Fig. 5-12). There are, however,

longitudinal trends among pine species (Fig. 5-13). The exact causes of the east-west trends have not yet been identified. The absence of these trends in analysis of the raw ring-width data presented may be due to masking by the larger and more direct effects of competition and disturbance. Nevertheless, the fact that there are annual increment growth differences among species and species groups in climate response across a climate gradient indicates that climatic change could shift competitive relationships and thereby promote forest change.

Conclusion

The results of our long-term studies reveal that Big Thicket forests are highly variable. Each of the three long-term study plots has undergone shifts in tree species composition during 16–20 years of monitoring. At the dry study site, the changes were relatively easily interpreted in terms of two common regional phenomena: postlogging recovery and fire exclusion. Effects of climatic changes on sites such as this will probably involve interactions between climate and fire regimes. Changes in global climate are likely to influence both within-season timing and intensity of fires, even under managed conditions, thus affecting forest composition. If fire continues to be excluded from this system, predicted increases in regional drought may aid preserve managers by retarding the invasion of mesic, shade-tolerant species into formerly fire-maintained upland habitats.

Our study of a wet forest revealed disturbing long-term trends in woody plant species composition, particularly in the smaller size classes. Changes in flow patterns from the construction of two upstream dams appear to be favoring species of lower flood tolerance and altering the characteristic spatial structure of bottomland forests. Human intervention in the form of altered river flows has increased the variability of the system and may be predisposing this system to uncharacteristic increases of certain tree populations. Changes in regional climate will no doubt further increase this variability by increasing the frequency and intensity of both floods and droughts. An understanding of this variability may be crucial to the success of postharvest regeneration in commercial forestry operations.

At the mesic site, we had an opportunity to directly observe the effects of a hurricane. Even though it caused only a small rise in mortality of canopy trees, this storm had an important impact on forest regeneration processes. Long intervals between canopy opening events gradually reduce understory trees and shrubs, providing opportunities for regeneration of canopy species. Consequently, increasing frequency of large storms may maintain uncharacteristically dense shrub populations, with detrimental consequences for canopy tree regeneration. This suppression of tree regeneration, coupled with higher storm-related mortality could result in a decline in the standing biomass
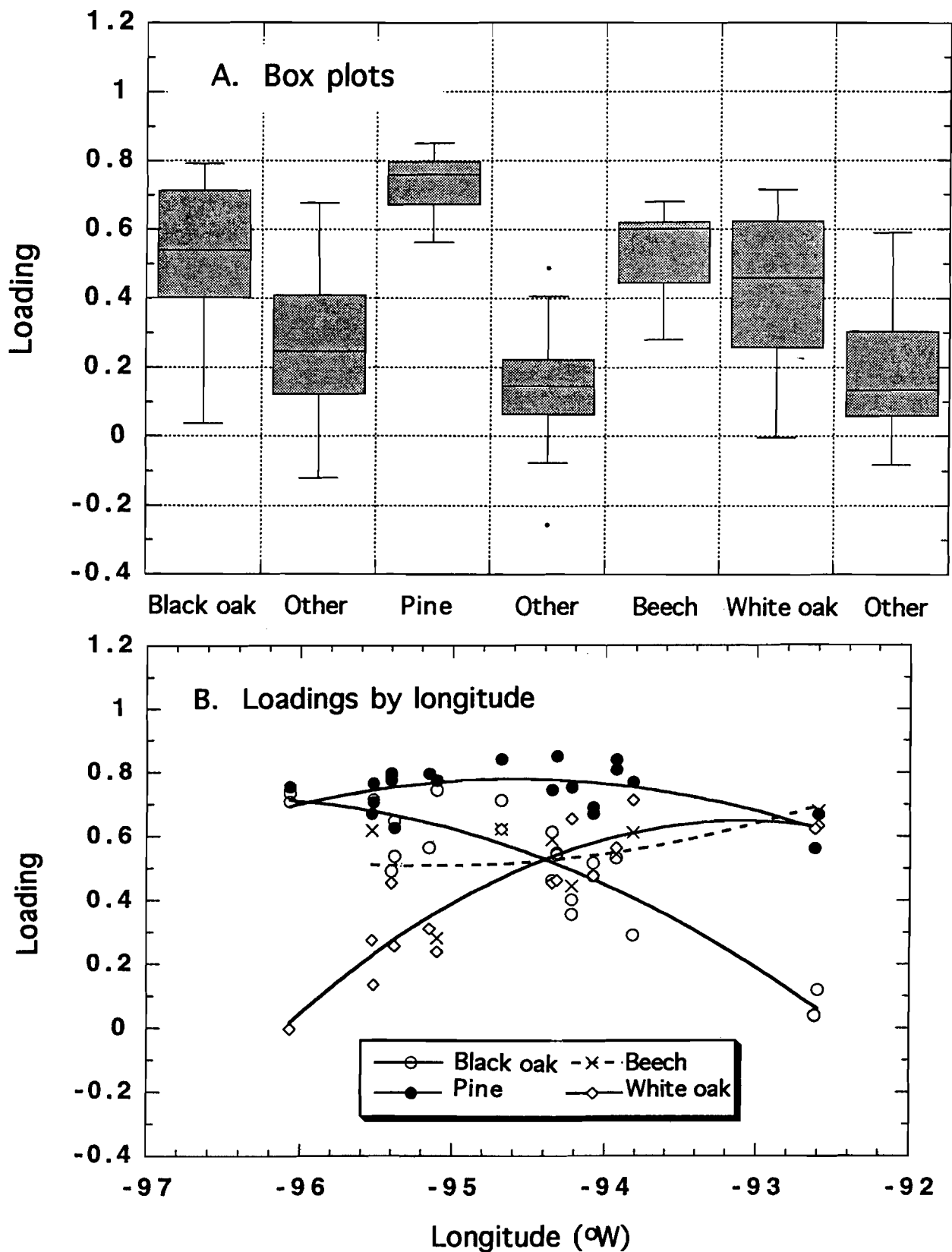
Figure 5-12. Varimax factor loadings for each of the four phylogenetic groups. Black oak loadings are Factor 1 values for the oak subgenus *Erythrobalanus*, pine loadings are Factor 2 values for pine species, beech loadings are Factor 3 values for American beech, and White oak loadings are Factor 3 values for the subgenus *Leucobalanus*.
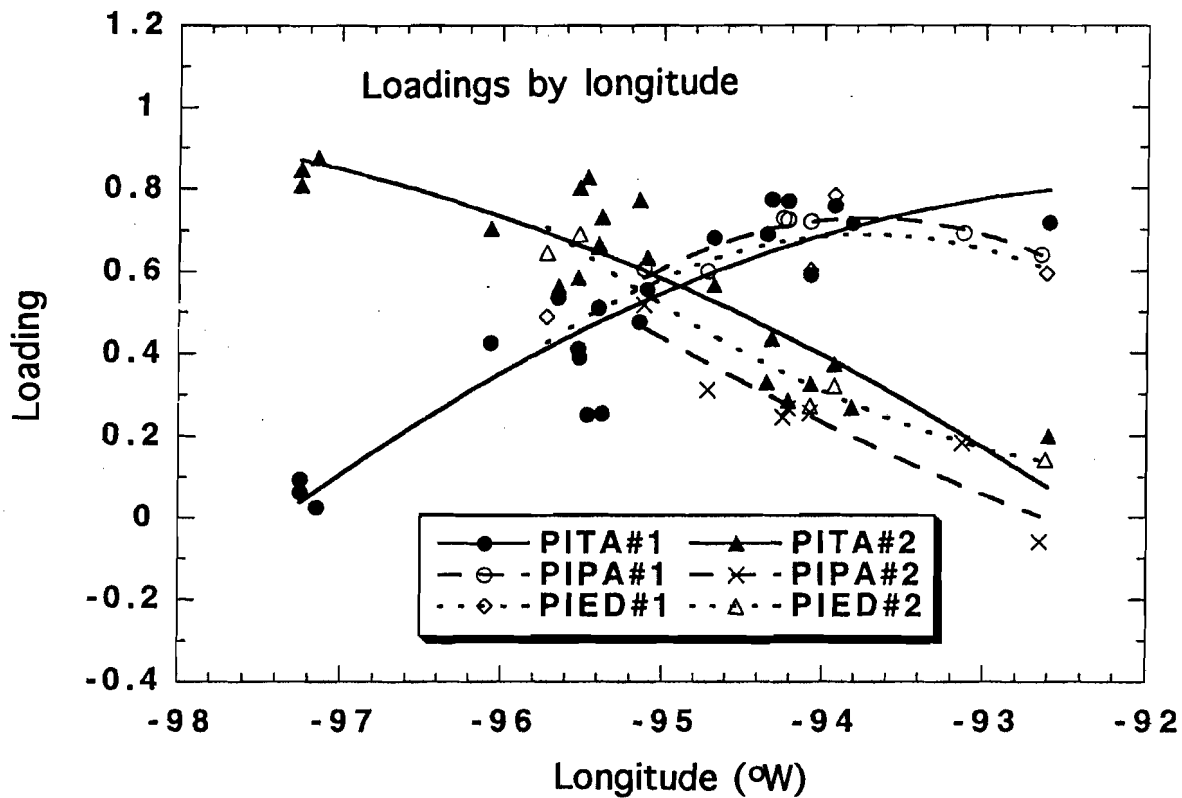
Figure 5-13. Varimax loadings by longitude for pine chronologies.

(i.e., the carbon storage capacity) of southern upland forests resulting in increased emissions of CO_2 to the atmosphere.

An important direct effect of climate is its influence on tree growth. The emerging conclusion is that present day climate variation does produce detectable effects on tree and sapling growth. However, these effects are small and therefore may be secondary to indirect effects of climate change on forests by way of increased frequency and intensity of disturbance. A surprising result from the tree ring study suggests that this conclusion applies even close to the southwestern range limit of the tree species and thus implies that climate effects on seedling regeneration may be more important in limiting the ranges of these trees than climate effects on growth.

Direct effects of climate on recruitment and mortality were not detected, though we did find that drought strongly increased seedling mortality in the wet forest (Streng et al. 1989). The absence of effects on trees may be the result of masking by gradual death of trees, by multiple influences on tree death and decline (Harcombe 1987; though see Clinton et al. 1993), or by indirect disturbance effects. Continued collection of these important data over the next

10–20 years will allow more definitive tests of direct climate effects on tree recruitment and mortality. Again, evidence from the long-term monitoring and statistical analysis of patterns of growth and mortality indicates that climate change will have a stronger effect on forest dynamics indirectly by way of more frequent or more intense disturbance than by way of more direct effects on individual growth or average mortality rates related to an increase in temperature or a change in regional moisture balance.

All forest processes vary on a variety of temporal and spatial scales. Growth and survivorship of different tree size classes depend on climatic conditions, soil factors, and competitive relations within the stand. Recruitment depends on the availability of seed sources, light conditions in the understory, subtle differences in microsites, and weather events. In this project, we are documenting many of these dependencies. The variety of influences, both internal and external to the system, makes it difficult to assess the effect of changes in boundary conditions such as climate on dynamics at the system level. The mechanistic approach to forest dynamics seeks a unified framework of constant relationships and parameters within which

community responses can be predicted and explained. One way to embody this framework is within a simulation model.

Current forest dynamics theory and modeling derived from it are based on the responses of individual trees: how they grow and complete their life-cycles in response to variations in the local environment and how they affect their local environment. Early gap models (Shugart 1984) assumed a direct relationship between range limits of taxa and the growth rates of adult trees that is not supported by available data (Prentice et al. 1991; Bonan and Sirois 1992). Our sites include several taxa growing very close to their range limits for which growth rates are as high as any recorded in the interiors of the geographic ranges. Another error of early gap models is the assumption that the phenomenon of shade tolerance is driven entirely by the ability to grow in the shade. Our data, in conjunction with results from other studies (Hall 1993; Kobe et al. 1995), indicate that the ability to survive suppression is at least as important as growth in determining shade tolerance.

Hence, the results reported here not only identify specific climatic effects on particular life stages or processes, but they also clarify forest dynamics theory, which will lead to better models. The results also reinforce the rationale for modeling: the complexity of the system and of the interactions makes it very difficult to make clear or precise predictions, except that many processes and interactions will be influenced by climate change. In followup studies, improved understanding of the mechanisms of forest dynamics should be incorporated into improved simulation models that will allow well-founded extrapolations of the effects of climate change. Such models will make it possible to quantitatively determine whether the responses noted here will result in the magnitude of change previously suggested (Urban and Shugart 1990; Nielson et al. 1991).

Chapter 6:
Modeling Global Change Effects
on Coastal Forests

by

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Abstract: Predictions about global climate change include increases in the intensity of tropical storms, to which the low-lying Gulf of Mexico and South Atlantic coasts are particularly vulnerable. The direct damage from wind and surge force associated with tropical hurricanes can be sufficient to alter coastal forest structure and diversity. Landscape simulation models were developed to evaluate the impacts of increasing water levels and disturbance associated with global climate change on mangrove forests of the Everglades, Florida. A hindcast simulation for 1886–1989 indicates that the periodicity and trajectories of a few major hurricanes accounted for most of the impact on the forest structure of modern day mangrove forests across south Florida. As hurricane intensity increases over the next century, model projections suggest that future mangrove forests are likely to be diminished in average height and will contain a higher proportion of red mangroves. In the Big Bend area of northwest Florida, land elevation and water depth are key factors controlling habitat type. A digital elevation model of the area was constructed to track the process and pattern of coastal inundation over space and time for the low, mid, and high sea-level rise projections of the Intergovernmental Panel on Climate Change. The three sea-level scenarios indicated that major portions of this coastal zone will be permanently inundated over the next century, bringing about a combined migration and loss of some habitats. Results show that there is a large land base that will be quickly converted from coastal saltwater and freshwater marsh to open water and from coastal pine forest to emergent marsh, on a scale approaching the land loss that has been experienced in south Louisiana, 65–90 km^2 per year.

Introduction

In this chapter I present a summary of an investigation into the effects of Hurricane Andrew on mangrove forests in southwest Florida and how the results of the study were used to develop computer simulation models that demonstrate the impacts of the expected increases in water levels and disturbance associated with global climate change.

The southeastern coastal region is composed of vast areas of wetland habitat for wildlife and other economically important coastal resources such as shellfish. Located on the interface between sea and land, these wetland habitats are especially vulnerable to sea-level rise and to drought and flooding aggravated by large-scale climatic shifts (Giorgi et al. 1994; Intergovernmental Panel on Climate Change 1995b). Coastal wetlands along the South Atlantic and Gulf of Mexico coasts are especially sensitive because these ecosystems exist in a dynamic equilibrium between subsidence and accretion. This equilibrium is already being threatened by sea-level rise (Stevenson et al. 1986). In some coastal areas, accretion is insufficient to balance sea-level rise, resulting in increased flooding, saltwater intrusion into freshwater wetlands, and mechanical erosion (Stevenson et al. 1986).

Dramatic losses of the emergent marsh and forested wetlands of coastal Louisiana in recent decades may serve as a precursor of climate change impacts, though other human-induced causes also may be at fault. Increased tropical storm activity may also accompany global warming as a function of higher sea temperatures: the kinetic energy of tropical storms and hurricanes is fueled from the heat exchange in warm tropical waters, and therefore an increase in seawater temperature can be expected to increase the probability of greater storm intensities (Emanuel 1987). Any increase in storm intensity will impose direct and indirect loss of wetland function.

The goal of this study was to develop a suite of spatial simulation models to predict the impacts of global climate change on the coastal wetlands of the Gulf Coast region. Computer simulation models can help benefit field and laboratory studies by providing a comprehensive means of integrating knowledge of natural systems into a holistic framework. Their greatest use is demonstrated in addressing problems that are spatially and temporally extensive and dynamic, such as global climate change. Simulation models can be particularly useful in evaluating variable or long-term environmental impacts that otherwise cannot be tested reliably with experimental methods. The same holds true for spatial models designed to account for multiscale processes and phenomena that interact to control ecosystem structure and function. Applications of this study included the coastal habitats of St. Marks National Wildlife Refuge, Florida, and mangrove-marsh of Everglades National Park, Florida, and adjoining Federal lands. Field studies were conducted to fill in knowledge gaps regarding species and community response to fire and hurricanes. Spatial simulation models were applied to predict habitat loss and change under given sea-level rise projections and hurricane disturbance regimes.

Mangroves

Mangrove ecosystems are at their most northern limit along the South Atlantic coastline of Florida and in isolated refugia of the gulf coast of Louisiana and Texas. These are marine-based forests which are specially adapted to colonize and to persist in saline intertidal waters. Three species are common to the United States, black mangrove (*Avicennia germinans*), white mangrove (*Laguncularia racemosa*), and red mangrove (*Rhizophora mangle*). Black mangrove is the most cold tolerant of the three species, though its susceptibility to frost and freeze damage prevents it from reaching full maturity in the northern extent of its range. Mangroves, which are highly productive ecosystems and provide valued habitat for fisheries and shorebirds, are susceptible to lightning and hurricane disturbance, both of which occur with great frequency in south Florida. The degree to which mangroves can tolerate prolonged flooding and extreme saline conditions is not known, though evidence suggests that high water episodes from above-normal rainfall may be responsible for recent die-offs. Sea-level rise from climate change will undoubtedly allow mangroves to encroach inland depending on the resiliency of emergent wetland types and assuming that the prevailing vegetation can keep pace with the rate of coastal inundation.

Experimental and Field Studies Supplement Modeling Applications

Field and experimental studies were conducted as part of this study to improve our understanding of mangrove species tolerance and community zonation and to aid modeling trials for study sites in north and south Florida. Permanent plots and greenhouse experiments were instituted to determine the growth habits and ecology of mangrove species following hurricane disturbance. Field sites also were established along the northern gulf coast to calibrate the impact of fire and hurricanes on the growth and succession of pine flatwood/marsh systems.

Hurricane Effects on South Florida Mangrove Communities

Mangrove ecosystems predominate the coastal areas about the lower Florida peninsula where hurricanes are common. Tropical storm frequency along any given stretch has been estimated at one major event every 5–10 years. Numerous field studies have documented the susceptibility and vulnerability of Neotropical mangrove species and

systems to hurricane disturbance (Craighead and Gilbert 1962; Stoddart 1963; Craighead 1964, 1971; Roth 1992; Wunderle et al. 1992; Smith et al. 1994). More recent investigations by Doyle et al. (1994, 1995) of Hurricane Andrew in 1992 on south Florida mangroves explained the varying degrees of windthrow and mortality relative to hurricane intensity, path, and direction. Global climate change forecasts suggest that these coastal forests will be among the ecosystems most immediately threatened by projected increases in sea level, salinity, and hurricanes. The interactive effects of environmental conditions that prevail in these forests and the changes that are likely to occur in a global warming climate may lead to major shifts in forest composition, structure, and function of mangrove ecosystems. For my study, a hurricane model, HURASIM, and a mangrove forest model, MANGRO, were combined in a spatially distributed landscape application to review the impact of hurricanes over the last century on forest structure of mangrove communities across south Florida. This integrated landscape modeling approach offered the ability to evaluate the temporal and spatial variability of hurricane disturbance over the last century and on the local and regional scale.

Population Studies

Forest inventories were conducted before and after the passage of Hurricane Andrew in 1992 to assess and monitor the effects of hurricanes and climate change on mangrove forests. Remote videography was taken at low altitude by helicopter over mangrove forests along the southwestern coast of Florida to derive a coastwide assessment of damage extent and pattern. Coastal and inland transects which were perpendicular to the hurricane path were flown within the forest boundary of mangrove extent over Ten Thousand Islands National Wildlife Refuge and Everglades National Park. Continuous video footage was taken along these transects with recorded voice transmissions of coordinate location, altitude, flight speed, bearing, and other pertinent observations of ground damage on the tape. A separate global positioning system (GPS) unit tracked exact helicopter movement along with the video. Video analysis involved both visual and image analysis protocols to assess the degree of damage, windfall orientation, and canopy height of the forest below. A systematic sampling approach was employed to preselect video frames for analysis and georeferencing.

The degree of forest damage increases within the eyepath of storms with a skewed distribution of damage that is lesser on the backside of storms compared to the forwardside for the same distance from storm center (Fig. 6-1). The results of this study demonstrate the utility of videography in capturing time- and space-dependent responses (i.e., site impact and recovery) and in increasing the overall scale and area of assessment for large phenomena such as hurricanes. Similarities and differences
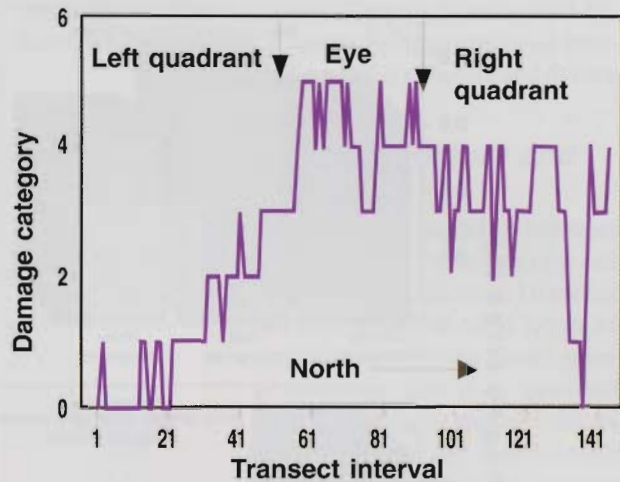

Figure 6-1. Mangrove forest damage assessment of coastal transect based on visual interpretation of canopy damage category across hurricane impacted zone of Everglades National Park and Ten Thousand Islands National Wildlife Refuge of south Florida.

between the inland and coastal transects showed the general pattern of the eyetrack where winds were highest and the circulation pattern of hurricane winds. Aerial videography proved to be an efficient and timely means to document large-scale hurricane damage and may likewise help to monitor ecosystem recovery in the coming years.

Additional field studies were also conducted to obtain mangrove growth and stand structure data for model development. Over 20 fixed plots have been established in Everglades National Park and adjoining USFWS refuges and state lands. Over 2,000 mangrove trees have been stem-mapped and measured. Field assessments of damage to mangrove forests from Hurricane Andrew have been analyzed and published (Doyle et al. 1995). Permanent field sites were established to assess the extent of forest damage and to monitor the rate and process of forest recovery after Hurricane Andrew moved across the lower Florida peninsula. It was found that canopy trees suffered the highest mortality, particularly for sites within and immediately north of the storm's eyewall. The type and extent of site damage, windthrow, branch loss, and defoliation generally decreased exponentially with increasing distance from the storm path. Right quadrant impacts were greater than left quadrant effects for the same given distance from storm center. Stand exposure, both horizontally and vertically, increased the propensity and probability of forest damage, and accounted for much of the local variability. Slight species differences were found where white mangrove exceeded black mangrove and red mangrove in damage potential under similar wind conditions (Fig. 6-2). Azimuths of downed trees were strongly correlated with predicted
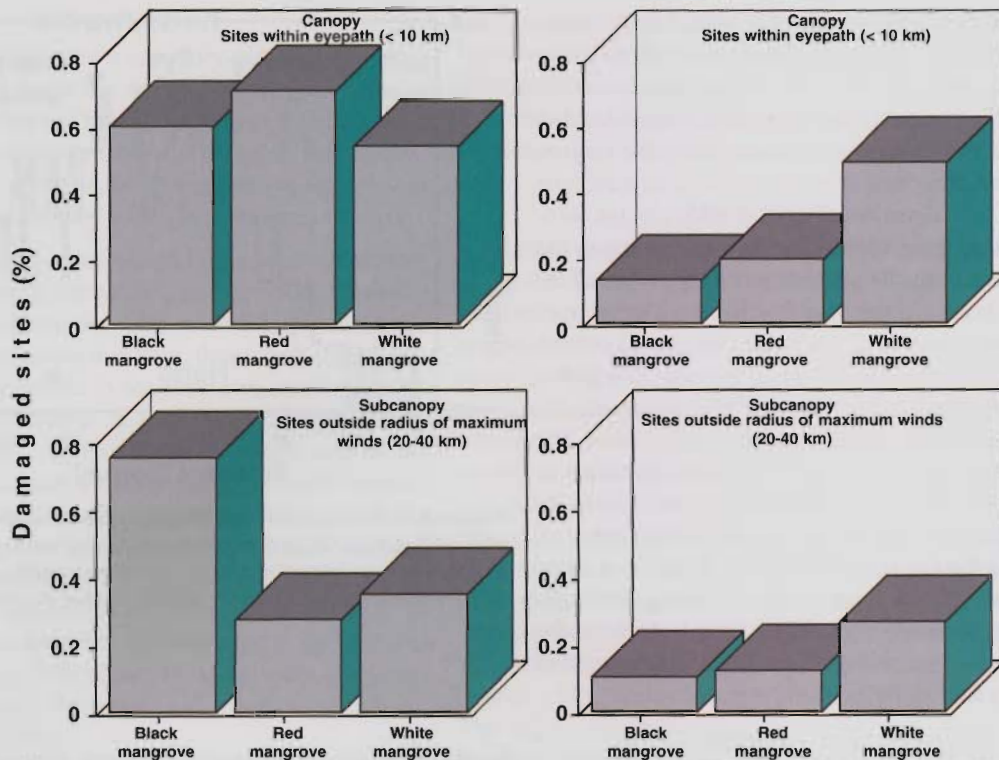
Figure 6-2. Proportion of severely damaged stems by species and crown class for sites within the eyepath and outside the radius of maximum winds.

windspeed and vectors based on a simulation of Hurricane Andrew (Fig. 6-3). Lateral branch loss and leaf defoliation on sites without windthrow damage indicated a degree of crown thinning and light penetration equal to treefall gaps under normally intact forest conditions. Measurements of photosynthetically active radiation (PAR) attenuation through mangrove canopies differentially impacted by hurricane winds of estimated force offer a means to calibrate actual wind damage probabilities on mangrove forests (Fig. 6-4).

Little has been documented about the adventitious sprouting habits of mangrove species and how mangrove communities regenerate following disturbance. Hurricane Andrew ravaged the mangrove communities of south Florida and left extensive tracts of downed trees. A field study was conducted in the Ten Thousand Island region of the northern Everglades to determine the process and rate of mangrove regeneration in blowdown sites. Seedlings and stem sprouts of black, white, and red mangroves were measured for diameter, height, and node development from two sites of comparable species and structural composition. Nodes were counted, and the length and diameter of internodes were recorded. Sampled trees included stump and bole sprouts of downed and damaged black mangrove and white mangrove which coppiced prolifically in contrast to red mangrove. Stump sprouts were on
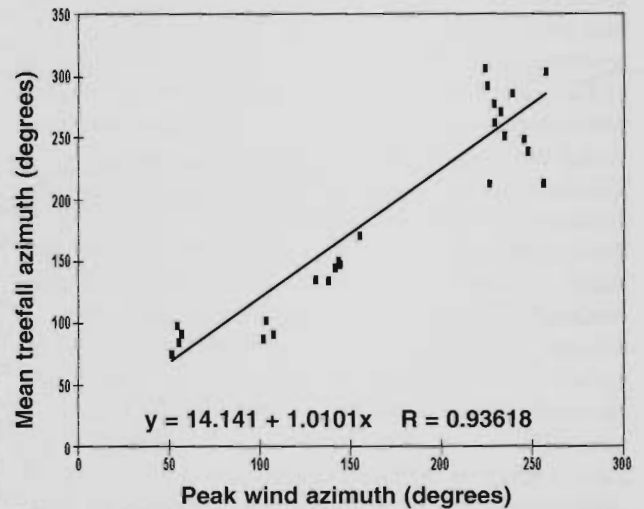

Figure 6-3. Scatter diagram and regression of actual mean treefall azimuths by site and predicted wind angle at peak hurricane wind speeds from the HURASIM simulation for all sample sites.

average more than twice the shoot size, height, and diameter compared with surrounding bole sprouts and seedlings. Patterns of node development demonstrated synchronous elongation within species and differences in node counts between species. Site, storm, and stem conditions
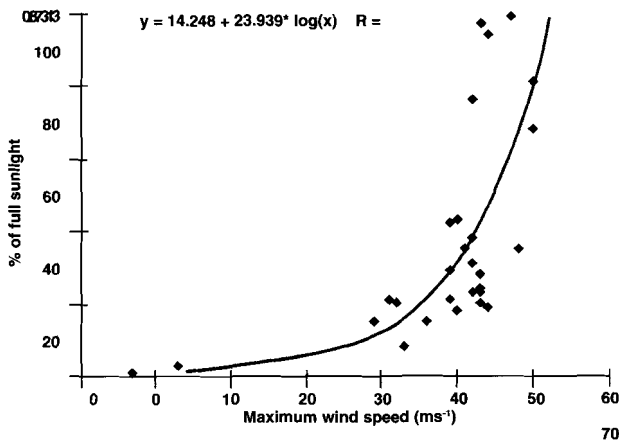
Figure 6-4. Scatter diagram and curvilinear fit of percent light (PAR) penetrating the residual forest canopy and maximum predicted wind speed from the HURASIM simulation for all sample sites.

may account for varying degrees of coppice success and seedling responses. The findings suggest that different rates of forest recovery might be expected depending on the prevalence of stump sprouting.

Modeling Climate Change Applications for the Gulf Coast Region

Wetland systems are likely to experience dramatic changes as a consequence of elevated carbon dioxide and associated environmental effects of climate change. Every level of biotic organization from the individual to the biome has a unique set of scalar and temporal properties and processes that ultimately influence structure and composition. It is this complex mix of controlling factors operating at different space and time scales that confounds efforts to identify unifying concepts and methods for classifying and analyzing natural systems. Experimental studies are limited by design to addressing questions at a single space or time scale. Simulation models, on the other hand, offer the potential to integrate across spatial and temporal scales. Elucidating the impact of climate change on wetland systems requires both the explicit consideration of the many spatial and temporal scales at which system responses occur and also the incorporation of those links and feedbacks between these scales as can be expressed with the development of computer simulation models.

For this study, a hurricane simulation model, HURASIM, was developed and applied to correlate estimated wind speeds and vectors of past hurricanes with field data (Doyle and Girod 1997). Model output was also used as input to a landscape simulation of south Florida mangroves. MANGRO, a mangrove community dynamics model, has been developed to simulate the birth, growth, and death of mangrove tree species on a square hectare forest plot. A

landscape simulation model of south Florida (SELVA-MANGRO) was applied to test the importance of hurricanes in controlling mangrove forest structure and dynamics (Doyle and Girod 1997).

Simulating Hurricane History and Impact

HURASIM is a spatial simulation model of hurricane structure and circulation intended for reconstructing estimated windforce and vectors of past hurricanes. Using historic tracking and meteorological data of dated North Atlantic tropical storms from 1886 to 1990, the model generates a matrix of storm characteristics (i.e., quadrant, windspeed, and direction) within discrete spatial units and time intervals specified by the user for any specific storm or set of storms. HURASIM recreates the spatial structure of past hurricanes based on a tangential wind function, inflow angle offset, forward speed, and radius of maximum winds. Data input for the model includes tracking information of storm position, latitude and longitude, and maximum sustained wind speed every six hours or less. The model offers a suite of mathematical functions and parameter sets for the tangential wind profile taken from other hurricane studies (Harris 1963; Bretschneiger and Tamaye 1976; Neumann 1987; Kjerfve et al. 1986; Boose et al. 1994). The radius of maximum winds is determined from the reported maximum sustained wind input and a set of empirical equations. HURASIM model output from Hurricane Andrew was correlated with field data to construct data tables of damage probabilities by site and species and to determine critical windspeeds and vectors of tree mortality and injury. HURASIM has also been applied to reconstruct probable windfields of past hurricanes for remote field locations and correlated with tree ring growth patterns and direction of leaning trees and downed logs (Doyle and Gorham 1996). HURASIM has also been used to construct landscape templates of past hurricane activity that are linked with landscape simulation models of coastal habitat.

MANGRO Forest Model

MANGRO is a spatially explicit stand simulation model constructed for Neotropical mangrove forests composed of black mangrove, white mangrove, and red mangrove. This individual-based model is composed of a species-specific set of biological functions predicting the growth, establishment, and death of individual trees. MANGRO predicts the tree and gap replacement process of natural forest succession as influenced by stand structure and environmental conditions. The position of each tree is explicitly defined on a planar coordinate system with a default stand area of 1 ha (100 m per side). Stand configuration was based on intact forest conditions with no edge effects. Canopy structure is modeled as a three-dimensional process of crown height, width, and depth in relation to

Figure 6-4 on page 71 should appear as follows:

$Y = 14.248 + 23.939 * \log(x)$ $R = 0.87313$
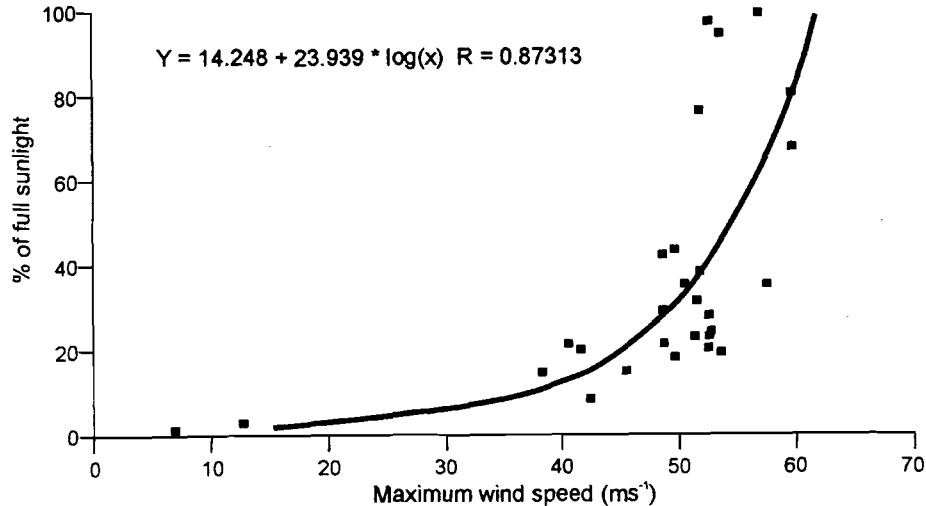
sun angle and shading by neighboring trees. Tree growth was based on growth potential for a given tree size reduced by the degree of light available to the individual tree and species response to shade. Mortality is modeled as a self-thinning process dictated by prolonged suppression, senescence, and disturbance factors, primarily hurricanes.

Hierarchial Integration of MANGROVE and HURASIM for South Florida Landscape

Both MANGRO and HURASIM were projected onto a compartmentalized landscape of south Florida at a scale equal to a 7.5 minute quadrangle. Forty-one cells of an uneven matrix design were identified across the lower peninsula of Florida, which contains mangrove habitat. Each cell represented an intact forest condition approximated by an independent simulation of the MANGRO model. Initial forest conditions were set with a normally distributed population of mature mangrove trees approximating a mean stand diameter of 50 cm and a mean stand age of 125 years. Seedling ingrowth was maintained stochastically at 1 plant per square meter every year to maintain a fully stocked stand for continuous recruitment. Equal probability was given to seedling recruitment by any species for any land area. Tree growth was constrained by size and light availability. A logistic growth function was constructed with observed data and generalized for all species taken from Craighead (1971) and Doyle et al. (1995). Stand data from 10-, 30-, and 60-year-old stands were used to approximate an empirical growth curve (Doyle and Girod 1997). Light availability was calculated for the crown zone and height of each tree as a function of light penetration through the canopies of taller neighbors. Light attenuation was calculated with Beer's Law based on a maximum leaf area index of 5.5. Growth was limited by shade tolerance (red mangrove having more shade tolerance than black mangrove, which in turn has more than white mangrove) based on a set of light response curves constructed from a concurrent experimental study (Doyle and Girod 1997). Sea-level and salinity conditions were assumed to be optimum for this simulation for all quadrangles whether seaward or not. Mortality was modeled as a stochastic process of age, suppression, and hurricane impact derived from damage probability curves developed from observed data of the effects of Hurricane Andrew in 1992 (Doyle et al. 1994, 1995) (Fig. 6-5). If in any given year of the simulation a predicted hurricane windforce exceeded 30 m/s, a probability was derived based on windspeed from which a percentage of the standing crop or trees were stochastically removed from the forest simulation. Trees that failed to maintain 30% of potential growth accumulated an increasing probability of death by suppression such that less than 1% were likely to survive 10 years.
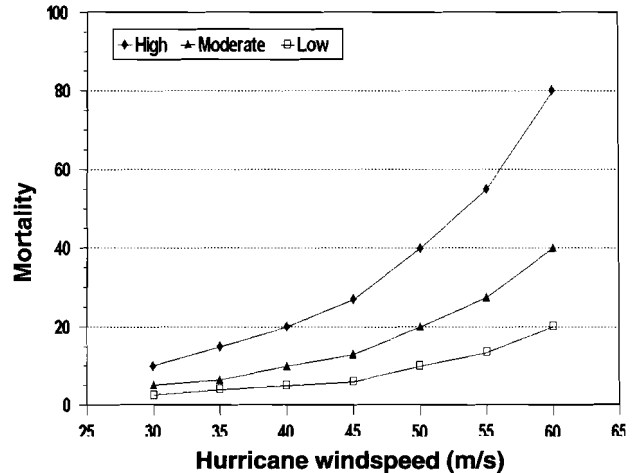

Figure 6-5. Damage probability curves calibrated from field observations showing the percentage of mangrove trees killed at given predicted wind speeds under expected hurricane impact (moderate) and for extreme (high) and nominal (low) impact scenarios.

Hindcast Simulations of Hurricane Tracks and Mangrove Community Response

Four treatment effects were implemented in this study, including a no-hurricane simulation contrasted with a low, moderate, and high mortality effect that increases with corresponding increases in windspeed (Fig. 6-5). A hindcast simulation for 1886 through 1989 was achieved by passing hurricane and site specific information from the HURASIM model to the associated MANGRO simulation for common cells. A cumulative assessment of hurricane impact was achieved by averaging stand attributes and size for the entire simulated landscape and time interval from 1890 to 1989. Simulations of hurricane tracks and history for south Florida showed that storm frequency and intensity varied across the landscape (Doyle and Girod 1997). Hurricane frequencies by quadrangle for the period of record showed that the number of storms with winds exceeding 30 m/s were more numerous on the Atlantic side than the gulf side of Florida's lower peninsula (Fig. 6-6). The southwest coast of Florida has endured stronger storms on record than the gulf and Atlantic coasts to the north. The combined layering of hurricane impact showed that there are portions of the south Florida landscape that have received more frequent and more intense storm activity than other portions.

Hindcast simulations of actual hurricane tracks and conditions seem to account for the structural composition of modern day mangrove forests across south Florida. The periodicity of major storms every 30 years in this century may be the most important factor controlling mangrove
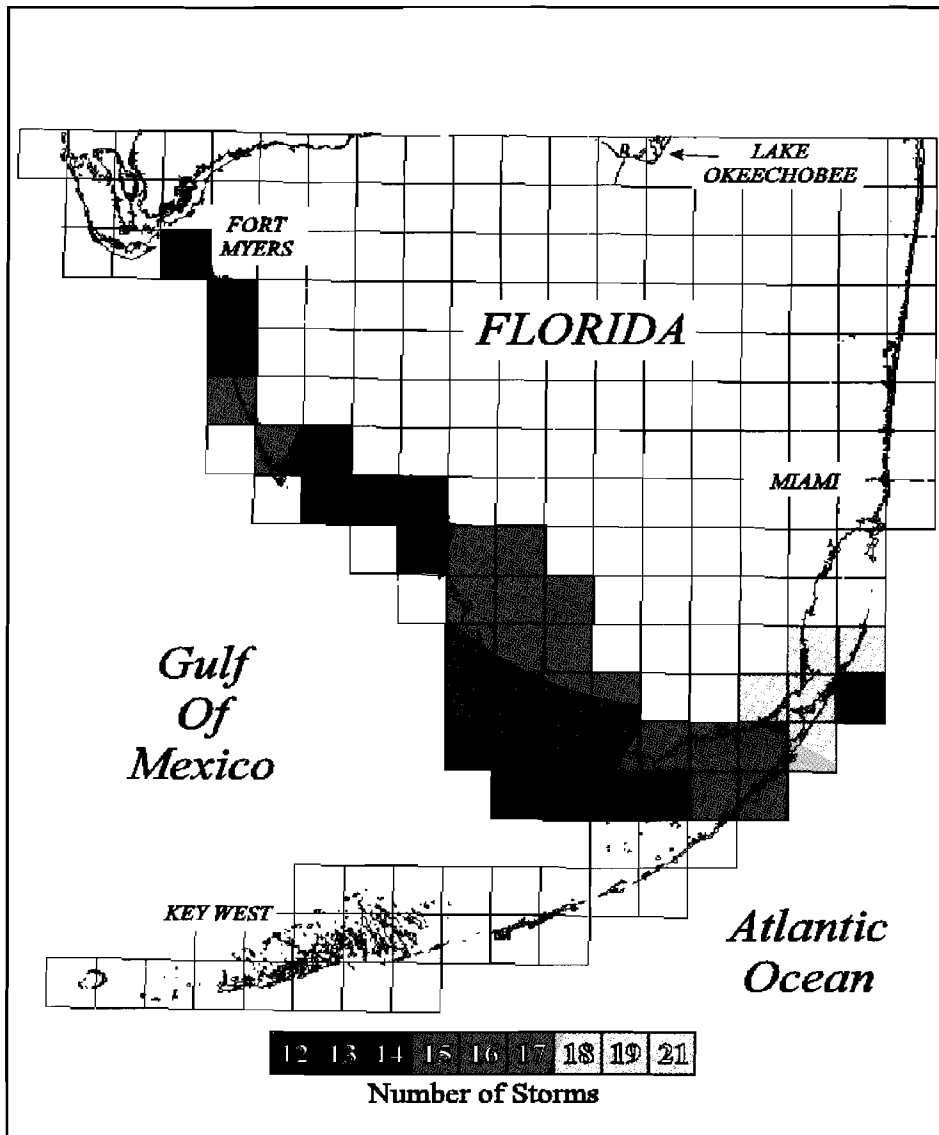
Figure 6-6. Frequency of hurricane strikes of Category 2 storms or greater (> 30 m/s) by quadrangle across south Florida predicted by HURASIM model for mangrove habitat for the period 1886-1989.

ecosystem dynamics in south Florida. The most significant changes in forest structure summarized by decade followed a few major storms with tracks that subtended the larger distribution of mangrove habitat (Fig. 6-7). Global climate change models predict an increase in hurricane intensity over the next century that may further alter the structure and composition of this mangrove landscape (Emanuel 1987). As damage potential increases from low to high, forest structure is increasingly reduced. Model results of climate change scenarios (high damage probability) indicate that future mangrove forests are likely to be diminished in stature and perhaps include a higher

proportion of red mangroves. Present day forest structure from select locations across the south Florida landscape compared similarly to model results from the moderate storm damage function. The integrative modeling approach of combining physical models like HURASIM with biological models like MANGRO offers the ability to assess large scale and long-term processes of climate-related phenomena on natural ecosystems. Decadal and longer time scale changes in hurricane behavior and regularity may be much more significant in shaping mangrove community structure and distribution on the landscape than can be evaluated by field studies alone.
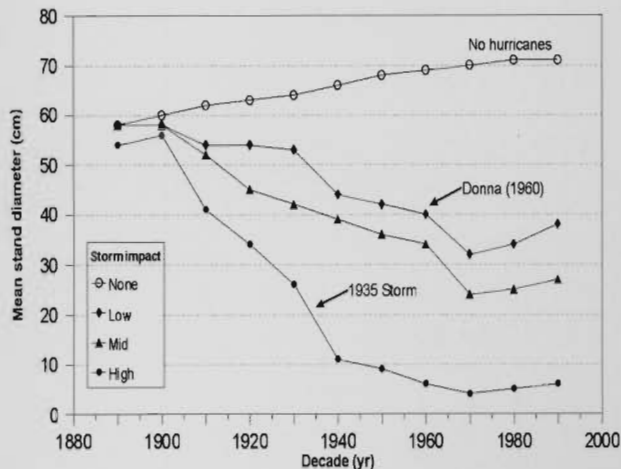
Figure 6-7. Mean stand diameter (cm) for a composite sampling of all 41 stand simulations of mangrove habitat for each decade under no-hurricane, low, moderate, and high impact scenarios for the period of hurricane history 1886-1989.

Projecting Land Cover Change and Shift of Marshes and Forests in Northwest Florida

Wildlife preserves and refuges in coastal areas of our nation are slowly being inundated by increasing sea level. Warming of our global environment threatens to speed the rate of sea-level rise and perhaps further amplify the detrimental effects of tropical storms, droughts, and lightning fires. During this study, research was conducted to examine the impacts of possible climate change scenarios on the functional wetland landbase and habitat of Federal parks and refuges along the Gulf of Mexico. A site application of a GIS-based simulation model, WETLANDS, was developed to predict ecosystem response to changing environmental conditions for wetland complexes of the Big Bend region in northwest Florida. The model contains functional attributes of community sensitivity to hydrologic conditions linked with a GIS data base of site characteristics, including habitat type, elevation, soils and land use.

Regional Study Site, Big Bend, Florida

The site application includes both the aquatic and terrestrial habitats of St. Marks National Wildlife Refuge in the Big Bend region of northwest Florida (Fig. 6-8). The refuge is situated approximately 32 km south of Tallahassee and covers parts of Wakulla, Jefferson, and Taylor counties. The total area of federally owned land incorporates 26,163 ha. Of the total area, 12,758 ha are open water in

■ **Coastal salt marsh**

■ **Barren and urban**

■ **Wetland forest**

□ **Upland forest**

■ **Other**
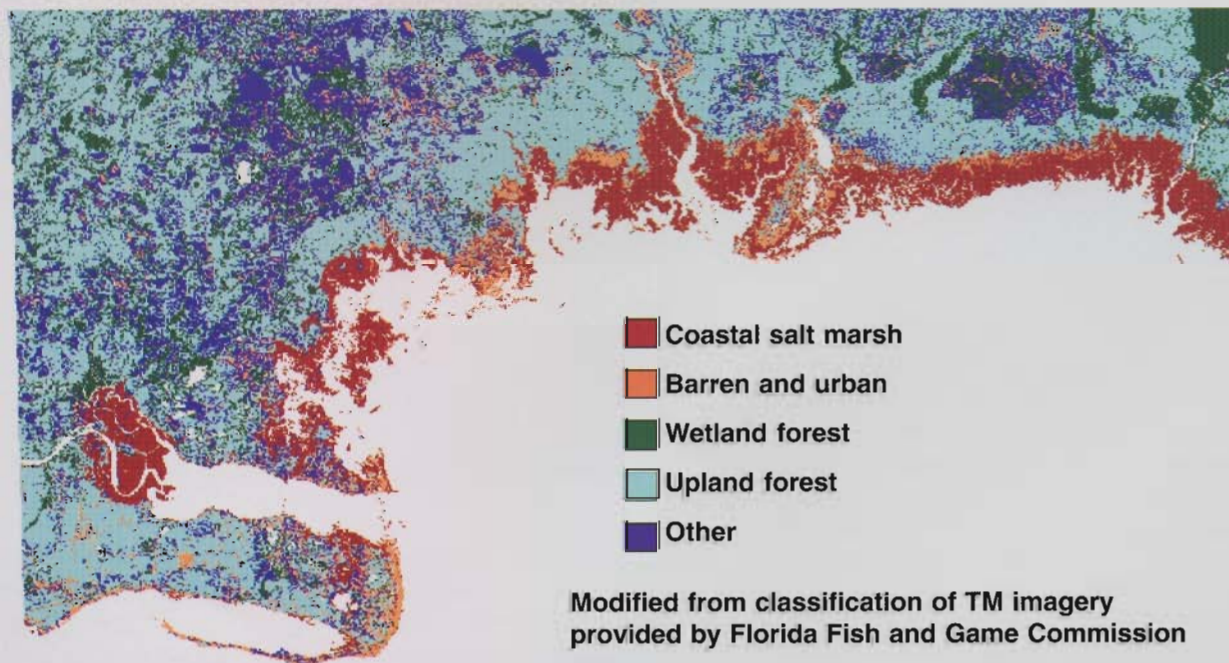
Modified from classification of TM imagery provided by Florida Fish and Game Commission

Figure 6-8. Habitat map of Big Bend coastal region including the area of St. Marks National Wildlife Refuge south of Tallahassee, Florida.

Apalachee Bay and 12,993 ha are forest and marsh. The refuge is bordered by Apalachee Bay on the south, Ochlockonee Bay on the west, and Aucilla River on the east. The reserve was purchased in 1929 and is one of the oldest refuges in the entire system of the U.S. Fish and Wildlife Service. The refuge landscape is characterized by a relatively low elevational gradient that is intersected by several rivers and a number of freshwater springs and intertidal creeks. Upland pine sandhills drain into wet pine flatwoods and hardwood swamps within the freshwater zone and into tidal salt marsh and mudflats at bay's edge. Seagrass beds are abundant throughout Apalachee Bay, a shallow microtidal system open to the Gulf of Mexico. Elevations of these major habitat types range from below sea level for seagrass; 0.0-0.6 m msl for salt and fresh marsh; 0.3-1.2 m msl for lowland pine, palm, and hardwood hammocks; 1.2-1.8 m msl for bottomland hardwood and pine flatwoods; and more than 1.8 m msl for pine sandhill and oak associations in the higher elevations approaching 12.2 m msl. The absence of relief contributes to the largely wetland composite of vegetation types.

Zonation of Coastal Marsh and Forest Species and Systems

Land elevation and water depth are key factors controlling habitat type and distribution in this coastal environment. Plot and transect surveys were conducted to derive a conceptual model of community types and succession under different environmental conditions and disturbance regimes. The ability to predict landward transgression of coastal marsh caused by sea-level rise depends on knowledge of the current vegetation distribution linked to land elevation. Vegetation descriptions and elevation data were collected from the forest-marsh ecotone at St. Marks National Wildlife Refuge near Tallahassee, Florida. First-order benchmarks were used to open and/or close transects across the ecosystem ecotone in several watersheds within the refuge boundary; most surveys closed to within 0.254 cm. Station locations were established every 30 m along a given transect from which land elevation and vegetation cover and stature were recorded. Field data were verified by constructing histograms of vegetation distribution with surface elevation. Eleuterius and Eleuterius (1979) used transit surveys and tide gauge recordings to relate the narrow elevation ranges of smooth cordgrass (*Spartina alterniflora*) and needlegrass rush (*Juncus roemerianus*) in a Mississippi marsh to tidal inundation frequency and duration. Using the same methods, I correlated vegetation to elevation in a needlegrass rush marsh at St. Marks National Wildlife Refuge and used the results to predict elevation from vegetation. The results were applicable to four different drainage basins along the coast.

The significance of this field study was the fact that I was able to plot elevation contours within the needlegrass rush marsh landscape by identifying the vegetation on aerial photography and even satellite imagery. Sand flats occupied by batis and pickleweed (*Salicornia*) are highly visible on remote imagery and occur at the same elevation as mean high water (app. 36–40 cm above mean sea level) from predicted tide tables for the area. Also highly visible is the distinct marsh-forest boundary which occurs near the elevation of the highest predicted tides from the same tide tables (60–70 cm above mean sea level). Additional surveys are required to determine whether those two tide regimes (mean high water and level of highest predicted tides) are significant vegetation delineators in other marshes with different tide ranges. Although Stout (1984) provides excellent descriptions of the community structure and elevation profiles of this type of gulf coast needlegrass rush salt marsh, the results of this study go a step further with a spatial analysis and mapping of the elevation contours using the vegetation as a guide.

Development of Landbase Digital Elevation Model

A digital elevation model of the study area was constructed to track the process and pattern of coastal inundation over space and time for projections of sea-level rise. Map information of hypsography and bathymetry of the study area were digitized from a series of coastal map products obtained from USGS 7.5' quadrangle maps (1:24,000 scale) and National Oceanic and Atmospheric Administration (NOAA) hydrographic charts (1:20,000 scale). A standardized algorithm and application program (ARC-INFO/ TOPOGRID) was used to construct a high resolution, 30-m, digital elevation model (DEM) (Fig. 6-9). Classified thematic mapper imagery at 30-m pixel resolution of aquatic and terrestrial habitat at a community level was obtained from the Florida Department of Transportation to begin model simulation by vegetative type. Model simulations were generated to predict a likelihood index of habitat change and conversion under flooded conditions for different scenarios of sea-level rise. Model results were displayed in a GIS system and format illustrating habitat type and locations subject to change under altered environmental conditions. The WETLANDS model provides an integrated GIS-modeling framework whereby functional processes of ecological change can be linked with data structures of community and landscape composition.

Coastal Wetland Habitat Loss and Migration

Sea-level rise was simulated based on a series of case projections—low, mid, and high—adopted from the Intergovernmental Panel on Climate Change (1990) for 2000 to 2100 A.D. (Fig. 6-10). At these levels, major portions of the coastal zone in this region will be permanently inundated over the next century, bringing about a migration and loss
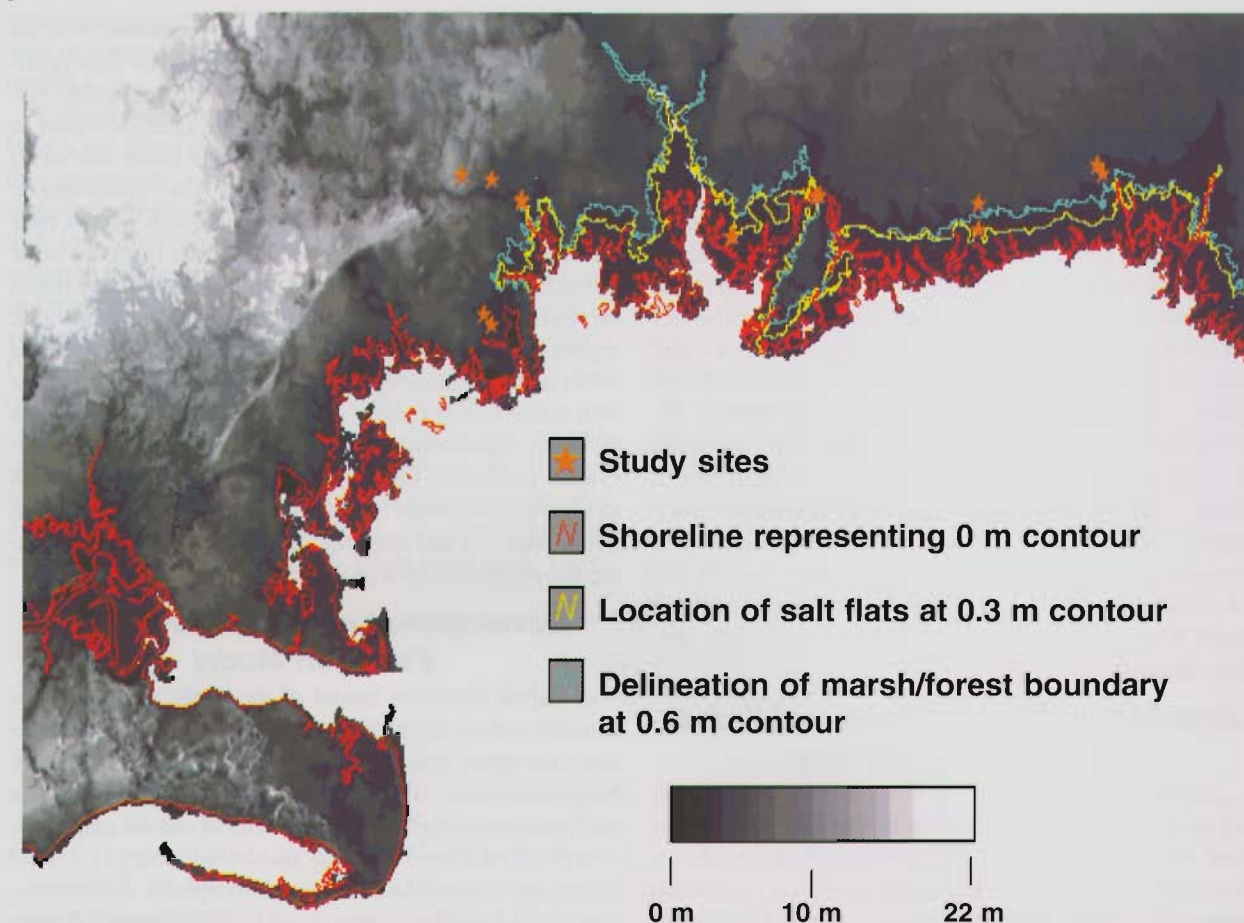
Figure 6-9. Digital elevation model for Big Bend coastal region encompassing St. Marks National Wildlife Refuge south of Tallahassee, Florida.

in the total area and proportion of some habitats. The model incrementally increases the flooding height on an annual basis according to the predicted change in sea-level by year for each sea-level scenario. It determines whether or not habitat conversion and/or loss occur as successive cells from coastal waters exceed the land elevation height of inland terrestrial vegetation and the tolerance of the existing vegetation type for another more tolerant vegetation. Probability functions of species and community tolerance to coastal inundation and elevation have been calibrated from field surveys and are used to predict habitat succession under sea-level rise. The model keeps track of the total number of cells by habitat and net cell loss or gain by year for output.

Because of low relief, model simulations predict significant shoreline changes and inundation of current terrestrial vegetation zones under all three IPCC (1995) sea-level rise projections (Fig. 6-11). Results show that there is a large landbase that will be converted from marsh to open water and forest to marsh. However, due to the slope of the landform, coastal marsh is predicted to increase slightly in land cover as it migrates upslope and replaces existing forest habitat. A significant portion of coastal pinelands standing at or below the 1-m contour will be directly affected by a projected sea level increase of 0.95 m (high) over the next century will be lost (Fig. 6-11). There will be an effective migration of emergent marsh into forested zones though an overall net loss of terrestrial habitat to an open water environment. The use of elevation survey data and surrogate contouring based on ecotone boundaries and tide projections added to the detail and accuracy of interpolating the landform between shoreline and the 1.5-m contour and for predicting habitat loss/gain under increasing sea-level conditions. This modeling approach offers a technological tool for research and policy purposes that allows for effective land and water management, risk assessment, and cumulative impact analysis of wetland systems and landscapes.
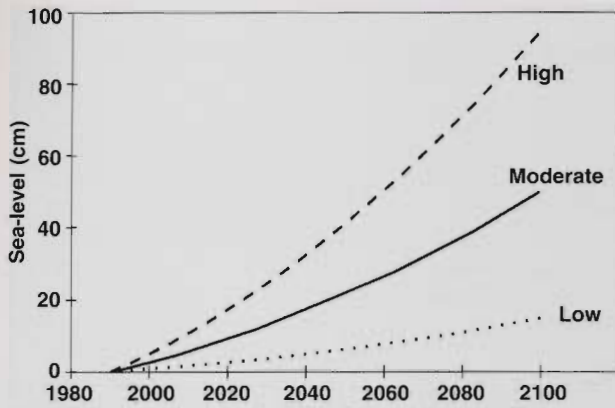
Figure 6-10. Sea-level rise projections and equations for case scenarios of low, moderate, and high cases based on Intergovernmental Panel on Climate Change 1995.
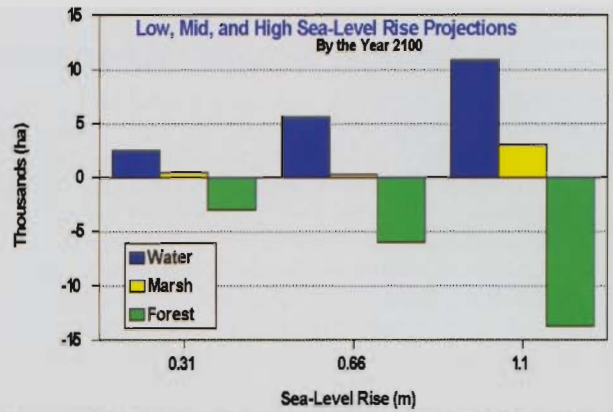

Figure 6-12. Predicted changes of net loss and/or gain of coarse habitat types, open water, emergent marsh, and forest for low, mid, and high sea-level rise (m) projections by the year 2100 as determined from the IPCC 1990.
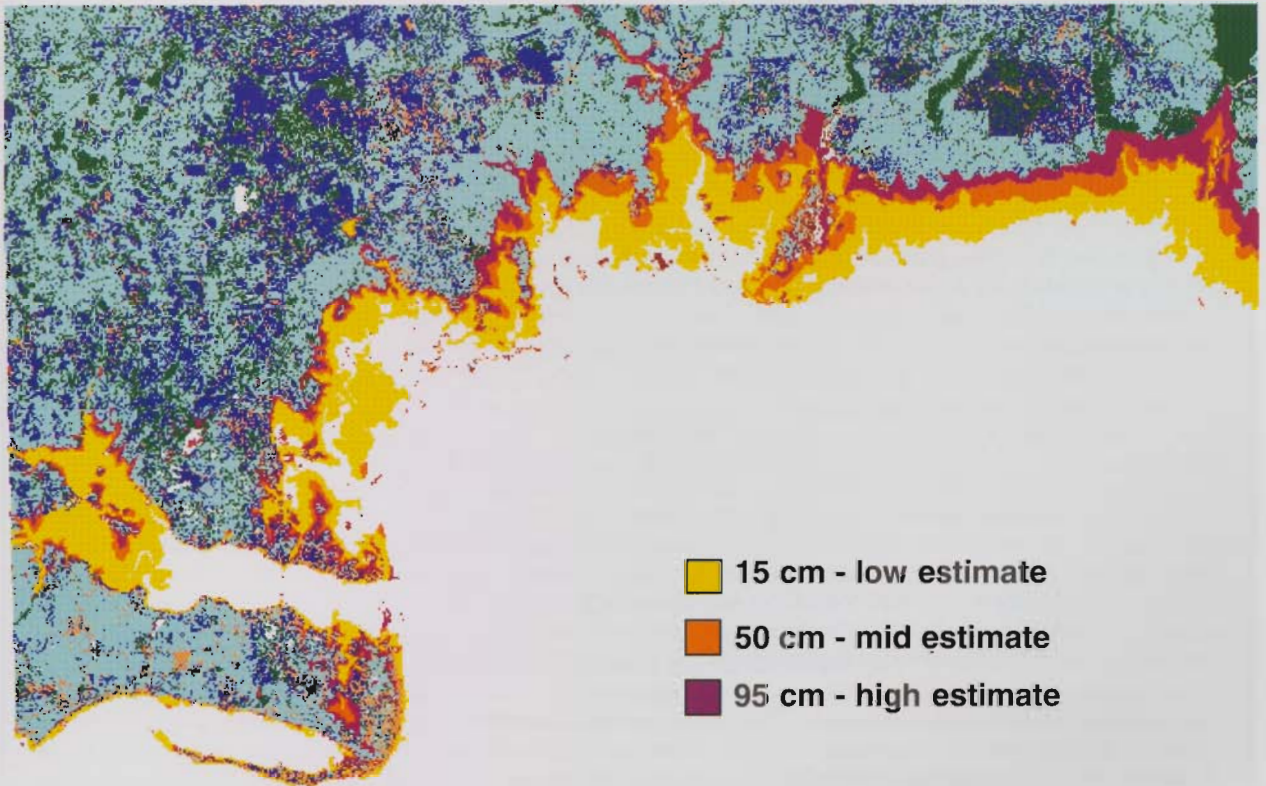

15 cm - low estimate

50 cm - mid estimate

95 cm - high estimate

Figure 6-11. Predicted shoreline change and coastal inundation at 15-, 50-, and 95-cm estimates of sea-level rise by the year 2100 based on IPCC (1995) projections.

Ecological Models: what are they and what do they predict?

Ecological models vary in design and detail but all have a common purpose: to predict change in biological response in relation to a change in environment. Simulation models include sets of dynamic functions and relationships that describe the organization or function of a biotic constituent in relation to a set of biotic and environmental conditions. In either case, a model represents a simplification of a real world phenomenon or process, whether of a single cell, single plant, community, or entire biosphere. The response variable and state conditions will vary depending on the domain and the specific processes and problem involved. A typical model may operate within a single domain of biotic organization such as the cell, organ, organism, species, population, community, ecosystem, or biome. For example, ecophysiological models of leaf layer dynamics may share the same domain (i.e., leaf), but vary in detail and complexity depending on what processes are included (i.e., photosynthesis, respiration, transpiration, stomatal conductance, etc.) and the manner in which they are modeled. Individual-based models are perhaps the most common model type that uses the individual organism, plant or animal, as its common unit of study. Ecosystem models are broadly defined model types that predict the state of some collective association of plant and animal populations for a given environmental setting. Ecological models, therefore, may include a suite of model types applicable across a range of spatial and temporal scales and biological domains.

Most ecological models, however, have been designed to predict dynamic behavior at a single point in space through time. With the advent of workstation technology in recent years, models have become increasingly spatially explicit and computationally robust. Global scale modeling of the carbon cycle has advanced to address issues of the role of terrestrial systems in the larger climatic cycle. Geographic information systems (GIS) program applications provide a software approach to managing and querying large data structures for regional applications in a rule-based manner similar to simulation models. Certain individual-based and ecosystem models have been upgraded to operate within a spatially distributed context to address landscape-scale questions of climate change effects on system function and organization.

The Sea Level Affecting Marshes Model (SLAMM) is one example of a map-based simulation model for predicting sea-level rise for given geographic locations. The U.S. Environmental Protection Agency has used this raster-based model to estimate probable losses of coastal wetlands to tidal inundation under given climate change scenarios. The agency has developed multiple versions of the model to investigate sea-level rise implications for coastal wetlands: SLAMM2 (Park et al. 1989), and SLAMM3 (Park et al. 1993). The model simulates wetland conversion and shoreline erosion under varying rates of future sea-level rise (Lee et al. 1992). Land cover type and elevation serve as the primary data layers. Relative sea-level change is modeled as a function of the historic eustatic trend (e.g., 1.2 mm/year), and regional subsidence factors, augmented with a projected sea-level rise scenario. Sedimentation and accretion rates may vary locally as a function of proximity and connectivity to streams and coastal influences. Model results are saved as habitat class maps that are subsequently tabularized to give grid cell counts of habitat change by time period with respect to sea-level height.

Landscape models are in a relatively sophisticated class of ecosystem models that involve spatially distributed operations and connectivity within a landscape that may include multiple ecosystem types and models. Coastal wetland systems consist of a matrix of wetland (and sometimes upland) landform types that are linked by physical and biological processes. Understanding the contribution and process of controlling factors important at different space and time scales demands a landscape approach that combines ecosystem models with a spatial model. The landscape approach provides a more comprehensive framework for integrating the complex interrelationships of changing environmental and biotic factors across spatially and temporally dynamic landscapes. In wetland systems, landscape models simulate projected changes in the physical environment (i.e., hydrology, soils) interdependently with the associated biotic response to forecast resultant changes in habitat distribution and quality. Landscape level applications often use GIS capabilities to construct spatial data structures of initial conditions and to capture spatial and temporal variability of model predictions.

One approach of modeling spatial dynamics is to arrange various ecosystem models and connect them with fluxes of water and nutrients in a manner analogous to the general circulation models (GCM's) currently used in long term climate modeling. This approach has been attempted in only a few cases for ecosystem modeling in the past (Botkin et al. 1972). In general, these past applications were relatively successful, and their rarity is probably due to the size and complexity of the resultant models, as well as the difficulty of assembling the necessary data bases. These limitations are rapidly disappearing with the increasing availability of remote sensing data and computing capability. The Coastal Ecological Landscape Spatial Simulation (CELSS) model is a process-based spatial simulation model of this construction for two marsh-estuarine complexes in south Louisiana, the Atchafalaya/Terrebonne Basin (2,500 km^2) and Barataria Bay (5,000 km^2; Costanza et al. 1990; White et al. 1991). The study areas are represented as an integrated matrix composed of 1-km^2 cells. Each cell contained a dynamic ecosystem simulation model that was habitat-type dependent. The model tracks the projected change in ecosystem type, water level and flow, sedimentation, subsidence, salinity, primary production, and nutrient pools. Model validation was accomplished by matching model predictions for ecosystem type with current and historical maps of habitat distribution. This modeling approach provides a comprehensive framework for synthesizing the direct and indirect, spatial, and temporal responses of coinciding natural and human-induced factors affecting coastal ecosystems. Model applications included evaluations of surface water management and climate change effects of rising sea level.

Reconstructing Hurricane History and Impact

Hurricanes are episodic climatic events of formidable force and destruction to both developed and undeveloped areas. The regularity and severity of tropical storms are major determinants controlling ecosystem structure and development for coastal forests worldwide. Long-term monitoring of hurricane impact and ecosystem recovery is needed to understand how some coastal systems adapt and respond to large-scale disturbances. Tree-rings have traditionally been used to reconstruct past climate and disturbance phenomena, including drought, fire, floods, insect outbreaks, earthquakes, and volcanic eruptions. A few studies have addressed the effects of hurricane impact on subsequent forest growth and succession. Pillow (1931) associated compression wood development in longleaf pine with hurricane injury. Doyle and Gorham (1996) and Gorham (1992) found missing rings and abrupt growth changes in years immediately following major hurricanes among pines along the gulf coast of Alabama and Mississippi, while a study by Merrens and Peart (1992) noted increased radial growth of hardwoods in New Hampshire following a 1938 hurricane. Akachuku (1993) reported differences in crown morphology and bole shape as a function of 50 years of regrowth following hurricane damage among red pines (*Pinus resinosa*) at Harvard Forest in Petersham, Massachusetts. Using a computer model of forest growth and succession, Doyle (1981) showed that hurricane frequency plays a major role in maintaining the species diversity and structural characteristics of insular forests of the Caribbean.

Field surveys have been conducted throughout the Gulf of Mexico region to establish baseline data on forest response to hurricane impact and history. Aerial videography, permanent plots, and tree-ring analyses have been used to assess the degree and expression of hurricane damage and recovery for more than 20 coastal parks and preserves along the gulf coast areas of Louisiana, Mississippi, Alabama, and Florida. Spatial analyses of these data show a pattern of non-random windthrow orientation and stem class distributions that are related to the size, path, and intensity of past hurricanes, and more recently to Hurricane Andrew (1992). A spatial simulation model of hurricane abiotics, HURASIM, was applied to reconstruct chronologies of hurricane windforce and vectors for each site derived from historic tracking data of North Atlantic tropical storms including Hurricane Andrew. The model generated a matrix of storm characteristics (i.e., quadrant, windspeed, and direction) within discrete spatial units and time slots over the period of Hurricane Andrew's passing and for all previous storms specific to each study site. The HURASIM model output was correlated with ground and mapped data to construct data tables of damage probabilities by site and species and to determine critical windspeeds and vectors for each storm's path. Tree-ring analyses of past growth demonstrated significant departures from expected growth trends coincident with hurricane events. Sites and events demonstrating growth departures were correlated with storm proximity, intensity, and assymetry with respect to windspeed. Impacts could be detected as far as 96.5 km per hour from the eye when windspeeds still exceeded 177 km per hour. This study provides a baseline of the spatial extent to which hurricanes can affect coastal environments depending on storm strength and orientation and on forest conditions. Empirical relationships drawn from this work have been incorporated into simulation models of forest growth and succession for mangrove, pine flatwood, and bottomland hardwood systems of the gulf coastal region.

Chapter 7:
Identifying Wetland Zonation and Inundation Extent by Using Satellite Remote Sensing and Ground-Based Measurements

by
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Abstract: We developed a number of satellite remote sensing tools that could dynamically monitor coastal resource change and response to sea-level rise caused by global climate change and other natural (e.g., fire, storm impact, herbivory) and human (e.g., fire, flood control structures, oil spills, mitigation, and restoration) impacts. Together, these tools could immediately help provide improved coastal regulation and management and eventually produce improved long-term simulations given a variety of "what if" scenarios. Within the package of tools, new methods were developed to dynamically detect flooding under grass canopies, generate coastal maps with microtopography within about 8 to 14 cm, detect and predict the time-since-burn of a black needlerush (*Juncus roemerianus*) marsh up to 900 days after the burn, and combine sensors of different spatial and spectral ranges and resolutions to provide a higher spatial resolution and a more refined coastal classification and detection system.

Introduction

Coastal resources already threatened by natural and human-induced stress are faced with further degradation unless action is taken to provide for increases in sea level and continued development. As part of an effort to provide timely and accurate information on a regional-to-international scale, we developed a number of satellite remote sensing tools that could dynamically monitor coastal hydrology and wetland changes. Equipped with these tools, researchers and managers can begin to link coastal hydrology to vegetation characteristics and, consequently, develop a better understanding of the expected responses of the coastal ecosystem to sea-level rise. Furthermore, these tools provide methods for monitoring, and eventually predicting, coastal response to continued development and natural (e.g., fire, herbivory, storm impact) and managed (e.g., fire, flood control structures, coastal mitigation, and restoration) forces. In turn, these methods could provide information that resource managers and regulatory agencies need to develop improved and consistent wetland response models and provide a basis for allocating financial resources and directing responses to influences causing wetland change or loss.

Background

The formation and health of wetland ecosystems is directly linked to surface hydrology (Imhoff and Gesch 1990). In coastal wetlands, hydrology is dominated by surface topography, terrestrial surface drainage, soil hydraulic character, and local tidal dynamics. The topographic contour and water level, however, determine the frequency, duration, and depth of flooding. As a consequence, critical controls of wetland type, productivity, and health, such as the level of soil salinity, the saturation of the soil, and the balance between particle import and export, are ultimately tied to the topography (Chabreck 1970; Redfield 1972; Stumpf 1983; Stevenson et al. 1985; Hine et al. 1988; Reed 1989; Imhoff and Gesch 1990; DeLaune et al. 1994; Leonard et al. 1995). Forecasting how changes in these controls (e.g., involving new wetland creation, wetland restoration, sea-level rise) will affect present and future wetland species zonation requires identifying the relationships between hydrology and wetland type and health.

Currently, the ability to associate hydrology with wetland type and health is limited because of the lack of both high detail in topographic surface maps (McKee and Patrick 1988) and timeliness in the production of new coastal wetland maps. Available U.S. Geological Survey (USGS) topographic maps for the Gulf of Mexico coast, for example, use a 150-cm contour interval, while the average shore-normal elevation gradient can be as low as 12 cm per kilometer for tens of kilometers (Fruh et al. 1973). Even within this shallow gradient, wetlands are diverse systems that exhibit extreme variations in areal extent,

temporal duration, and spatial complexity (e.g., Chabreck 1970). In addition, wetland vulnerability and intensity of use can further complicate the spatial and temporal patterns. For example, storms, herbivory, and fire can not only confuse the classification of wetland type and indicators of health, but they can also affect the response of a wetland to sea-level rise. Monitoring tools are needed that can discriminate wetland types and health and also identify where wetland change has occurred, what the nature of the change was (from-to), and what the sequence of change was (e.g., recovery). Maps produced by the National Wetlands Inventory provide some of this information (Peters 1994), but the enormous investment in photography acquisitions and interpretation results in a turnaround of nearly 10 years for new map production (Wilen and Frayer 1990). To be effective, the information derived from the remote sensing data must not only be highly detailed, but also timely and cost effective (Teuber 1990). Satellite and aircraft remote sensing can provide timely and cost effective data, but techniques must be developed that can transform the data into information about wetland responses to changes in the hydrologic regime as a function of global climate change and sea-level rise scenarios.

Today, many satellites carry a variety of remote sensing instruments. Of these, optical sensors have the longest history of being used for mapping wetland types and monitoring wetland changes (e.g., Weismiller et al. 1977; Klemas et al. 1980; Hardisky et al. 1986; Jensen et al. 1987; Ramsey et al. 1992, 1993). These sensors include the Landsat Thematic Mapper (TM) and, more recently, SPOT high resolution visible sensors onboard satellite platforms. Traditionally, optical sensors provided nearly all the images of wetland areas; however, with the launch of Seasat in 1978, radar has slowly gained importance in wetland mapping (Lyon and McCarthy 1981; Ramsey 1998).

Satellite optical imagery offers synoptic coverage but is constrained by the restricted ability of visible and near infrared light to penetrate vegetative canopies (Ormsby et al. 1985). Furthermore, optical systems are limited to favorable weather and daylight, hampering the ability to respond effectively to rapidly changing wetland conditions. Radar imaging systems can overcome many of these limitations by providing better canopy penetration and the capability for day and night acquisitions nearly independent of weather conditions (Ormsby et al. 1985; Dobson et al. 1992; Ramsey et al. 1994; Ramsey 1998).

Integration of remotely sensed optical and radar information could provide much of the information necessary for linking hydrology and wetland type and health. In developing tools to link wetland type and health to hydrology, our research combined aircraft and satellite optical and radar data. Together these sensors provided the first step in building an integrated remote sensing system for dynamic monitoring of wetland hydrology and change and,

ultimately, for predicting coastal vegetation responses to changes in sea-level and storm occurrence frequency and intensity. Our objectives were to establish methods that use optical and radar sensors to detect flooding, improve the coastal marsh topographic information currently available, provide timely, high definition (as many wetland types as possible), high spatial detail (to about 10-m resolution) wetland maps, dynamically detect and monitor the impact and recovery of wetlands affected by hurricanes, herbivory, saltwater intrusion, and management practices (e.g., fire), and finally, to link the hydrologic regime to the current distribution of coastal vegetation. The study area is the St. Marks National Wildlife Refuge (NWR) in the Big Bend area of Florida (Fig. 7-1). The primary focus of the study at the beginning was a black needlerush (*Juncus roemerianus*) coastal marsh; however, increasingly work has extended into the transitional vegetation (e.g., palmetto, fresh marsh) and more inland pine and bottomland forests.

Remote Sensing of Wetland Type and Hydrology

Detecting Coastal Flooding

Satellite radar was used to map tidal flooding (Ramsey 1995). Six synthetic aperture radar (SAR) images of the St. Marks NWR were acquired from ERS-1 satellite orbits between May and November 1993. The radar images were collected during flood and nonflood events (Fig. 7-2).

To perform the multidate analysis of the SAR images, it was necessary to first convert the relative radar returns to comparable units and the relative image coordinates to a common georeferenced base map. Near-continuous recordings of ground-based hydrology measurements, taken during the time of the SAR image collections, were then used to link marsh flooding to lowered radar returns. Flood-extent contours extracted from the radar images (PCI Geomatics 1998) and calibrated with point-water depth measurements showed marsh elevation could be estimated to about 8–14 cm, compared to the 150-cm topographic contours previously available. This close estimate demonstrates that ERS-1 SAR can be used to discern flooded from nonflooded black needlerush marsh. Even though restricted to a particular marsh type and to a single SAR sensor, this ability provides a tool for discerning the occurrence and monitoring the extent (within about 25–50 m) of flooding regionally, day and night, and during almost any type of weather. Additionally, when used with ground-based point measures of water level, this tool can be used to generate microtopography.

Generating Coastal Microtopography

A topographic surface map of the low-lying coastal marsh was created by using three flood extent vectors digitized from ERS-1 SAR images and two elevation contours from USGS topographic quadrangles (Ramsey 1995; Ramsey et al. 1998a). Point measurement of water depth at the times of the SAR collections allowed conversion of
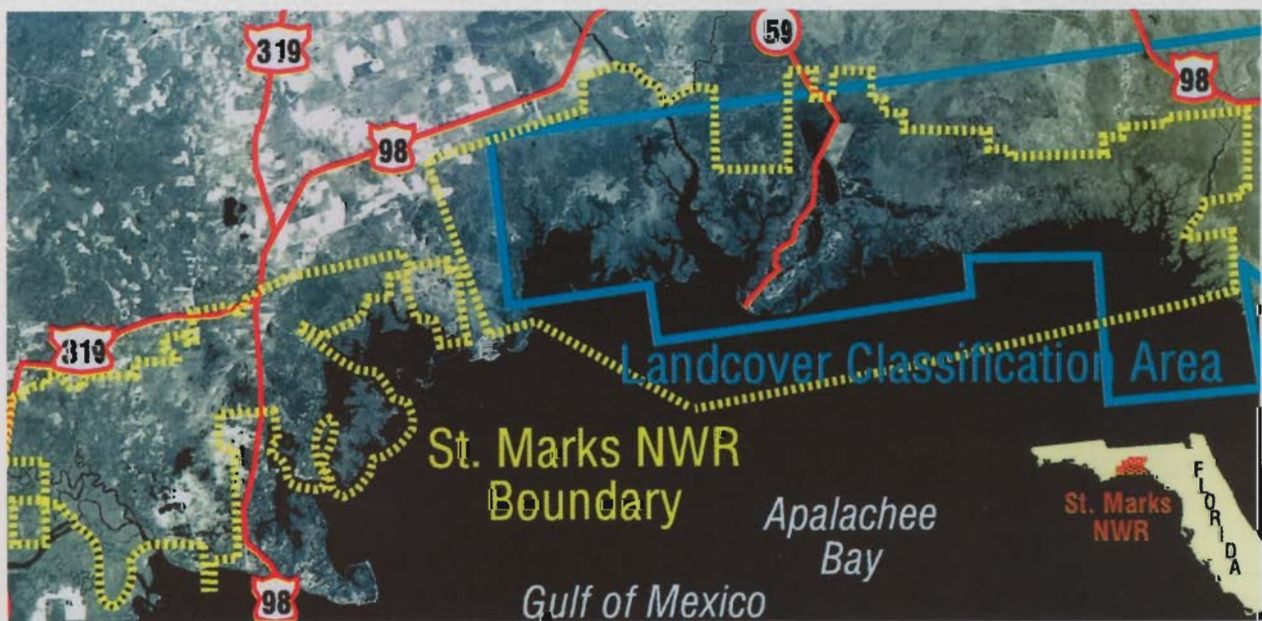

Figure 7-1. Landsat Thematic Mapper band 5 (mid-infrared) image of the study site at the St. Marks National Wildlife Refuge (NWR) in the Big Bend area of Florida. This image was collected on August 25, 1993 and was acquired from USGS EROS Data Center. The blue outline encompasses the actual study area.
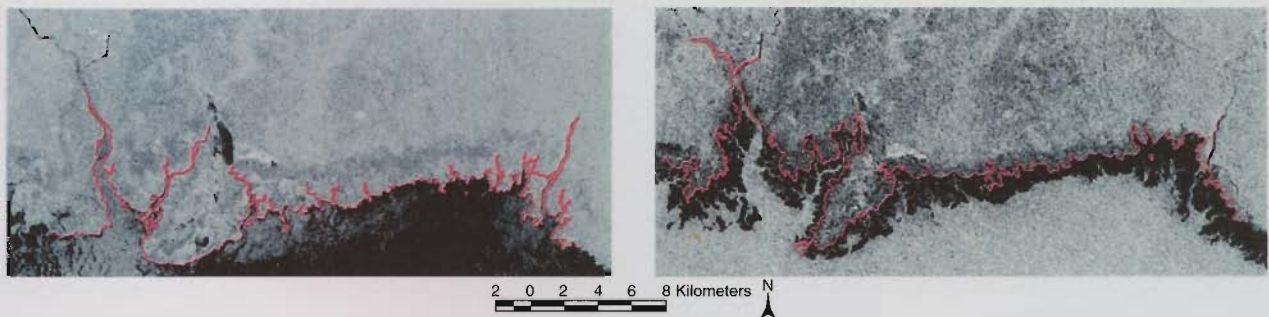
Figure 7-2. ERS-1 SAR images collected on October 18 (left; nonflooded) and September 13 (right; flooded) of 1993 of a black needlerush marsh within the St. Marks NWR. Flooding lowered the radar return in the coastal marsh areas resulting in a darker image. (Ramsey 1995, with permission of Taylor & Francis).

the flood extent vectors to topographic contours related to mean sea level (within about 8–14 cm accuracy). Generation of the topographic surface map was accomplished with a surface gridding algorithm (Smith and Wessel 1990; Wessel and Smith 1991; Fig. 7-3).

Verification of the resulting topographic map was performed by comparing the map to field-measured elevations taken at 10-m intervals along five shore-normal transects (Fig. 7-3). Field measurements were transformed into elevations by linking to USGS primary benchmarks.
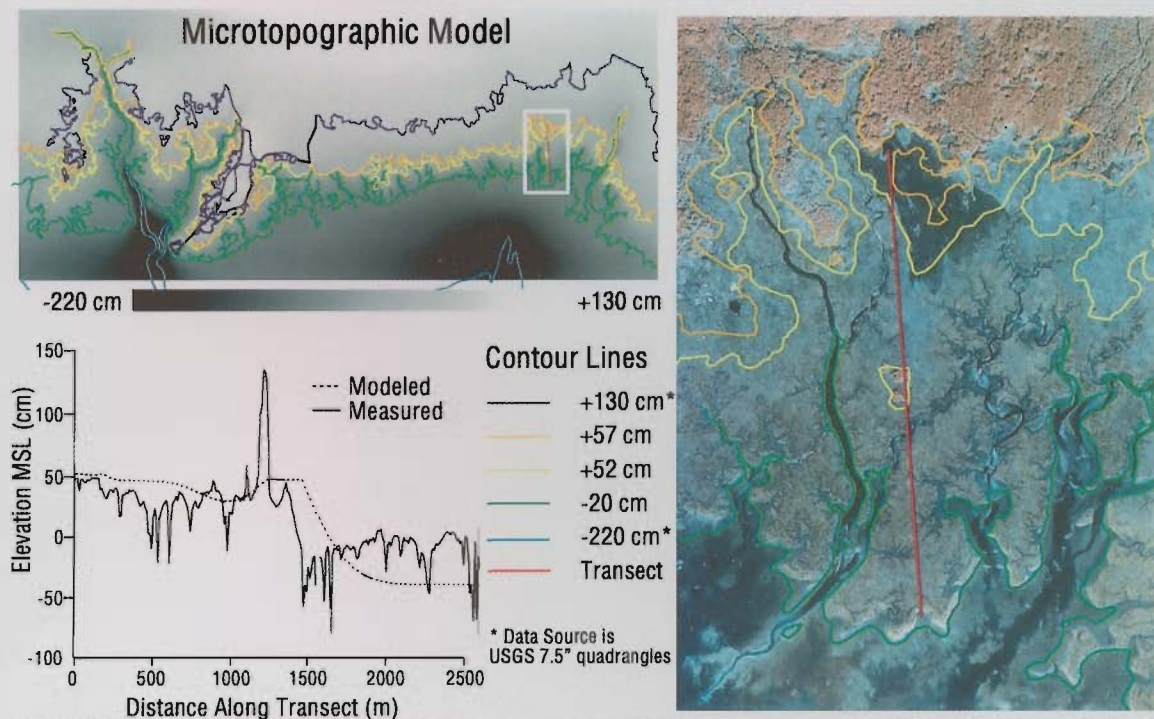

Figure 7-3. The modeled topographic surface map with one transect location. Relief recordings were collected at 10-m intervals and transects were linked to established USGS benchmarks to evaluate the actual mean sea level. Three of the five topographic contours were developed with ERS-1 radar data and on-screen image processing to detail beyond available traditional topographic contours data; two topographic contours (+130 cm and -220 cm) were taken from USGS standard 1:24,000 quadrangles. The resultant topographic surface has < ± 15 cm absolute mean error for the entire area (figure modified after Ramsey et al. 1998a, with permission of Coastal Education & Research Foundation, Inc.). Before this study, the available topographic resolution for this area was about ± 150 cm.

Errors in marsh topography resulting from the surface gridding algorithm were mainly associated with the lack of contours in areas such as narrow-to-broad plateaus and topographic highs and lows and the misplacement of flood extent vectors in sparsely vegetated high marsh, at convoluted marsh-forest boundaries, and at topographic depressions. Overall, the standard deviation of differences between measured and predicted elevations at 747 points was 19 cm. Excluding abrupt boundaries and topographic highs and lows outside the range of available contours, the standard deviation of the differences averaged about 14 cm (568 observations), with most observations around 8 cm. These results suggested a 5- to 9-factor improvement over the 150-cm topographic resolution previously available for this area. With this topographic mapping tool, more realistic simulations of flood extent, duration, and depth can be generated at unprecedented spatial and topographic resolutions. What is now required is a landcover classification that can take advantage of this improved spatial and topographic detail.

Classifying Coastal Resources

Georegistered color infrared (CIR) photography, Landsat TM, and ERS-1 SAR images were combined to create a map of the marsh and upland vegetation of the refuge (Ramsey et al. 1998b). Classifications using only CIR or only TM produced mixed results, with confusion apparent between marsh and forest classes. Furthermore, spatial definition in the TM classification was inadequate, especially in defining features such as hummocks, transition zones, small channels, and heterogeneous and mixed interior forest areas. To alleviate these problems, CIR (for better spatial detail), TM (for higher spectral clarity; six reflective bands), and SAR (for greater textural information) were combined into one data base.

The CIR, originally scanned and mosaicked to a 3-m spatial resolution, was resampled to a 10-m spatial resolution. The TM and SAR images were resampled from 25-m to 10-m spatial resolution. The TM, CIR photographic, and SAR image data were classified by using a clustering algorithm (PCI Geomatics 1998), a computational procedure that combines groups of related variables. Instead of classifying each image separately (Schriever and Congalton 1993; Wotler et al. 1995), the six TM reflective bands, the green CIR band, and a single SAR C band (VV, vertical send and return) were merged into a single classification analysis (Fig. 7-4 a-c). To further improve separation between classes, a progressive classification scheme was used (Jensen et al. 1987; Ramsey and Laine 1997). The 14 final classes included water, marsh, and forest classes, as well as burned marsh and burned forest (Fig. 7-5).

A class-stratified, random-sampling technique (Congalton 1988) was used to generate classification error estimates for the study area. The same CIR photography used in the classification was used as reference data. Fifty samples were used for each class (Congalton 1991).

Even though the overall accuracy was 73%, class definition and spatial detail were greatly improved compared to classifications using solely TM or photography. Multiple marsh and forest types were identified with only minor to moderate overlap in some classes, and small-scale features (down to around 10 m) were detected. Even with the use of progressive classification and multiple image types, however, some confusion still existed between classes. In these cases, final class determination was based on retaining the landscape pattern while minimizing the classification error. This procedure was especially necessary in transition classes (e.g., low-to-medium marsh, high-to-fresh marsh, fresh marsh to fringe forest). Even though higher classification accuracy could have been obtained by aggregating these transitional classes, the classification more correctly represented the actual landcover pattern in this extremely convoluted, nearly monotypic landscape. This new classification tool improves the mapping capabilities of the widely used TM images spatially and in the amount of detail, thus providing the ability to discern subtle differences in the vegetation canopy even within the same species.

Monitoring Damage and Recovery

As an example of monitoring impacted wetlands, the recovery of burned black needlerush marsh areas using radar sensors was examined (Ramsey et al. 1998c). The extent of burned marsh areas identified on a December 1992 CIR photography mosaic were delineated with onscreen digitizing (PCI Geomatics 1998). These polygons were then overlaid on July 1993 ERS-1 (C band VV polarization, defined previously), April 1992 USGS Star-1 (X band HH polarization, horizontal send and return), and July 1993 P3 Orion (L band VV, VH [vertical send and horizontal return], and HH polarizations) radar images (Fig. 7-6 a-b). Mean and standard deviation of the data values within each polygon were extracted from each image. These univariate statistics were entered into a common data base along with the approximate times of each burn. Burn times were from a burn log recorded at the refuge and from direct observations. Plots of the radar means for each burn site versus the time-since-burn and associated regression statistics were generated (SAS 1989).

Inspection of the plots and the regression statistics showed that significant relationships ($p < 0.05$) existed between burn recovery and the ERS-1 C band VV polarization and P3 Orion L band VH polarization (Fig. 7-7 a-b). No significant relationships existed between single L band VV and HH returns and the time-since-burn. Even though the USGS radar returns were not correlated to the time-since-burn, the data suggested burns could be identified
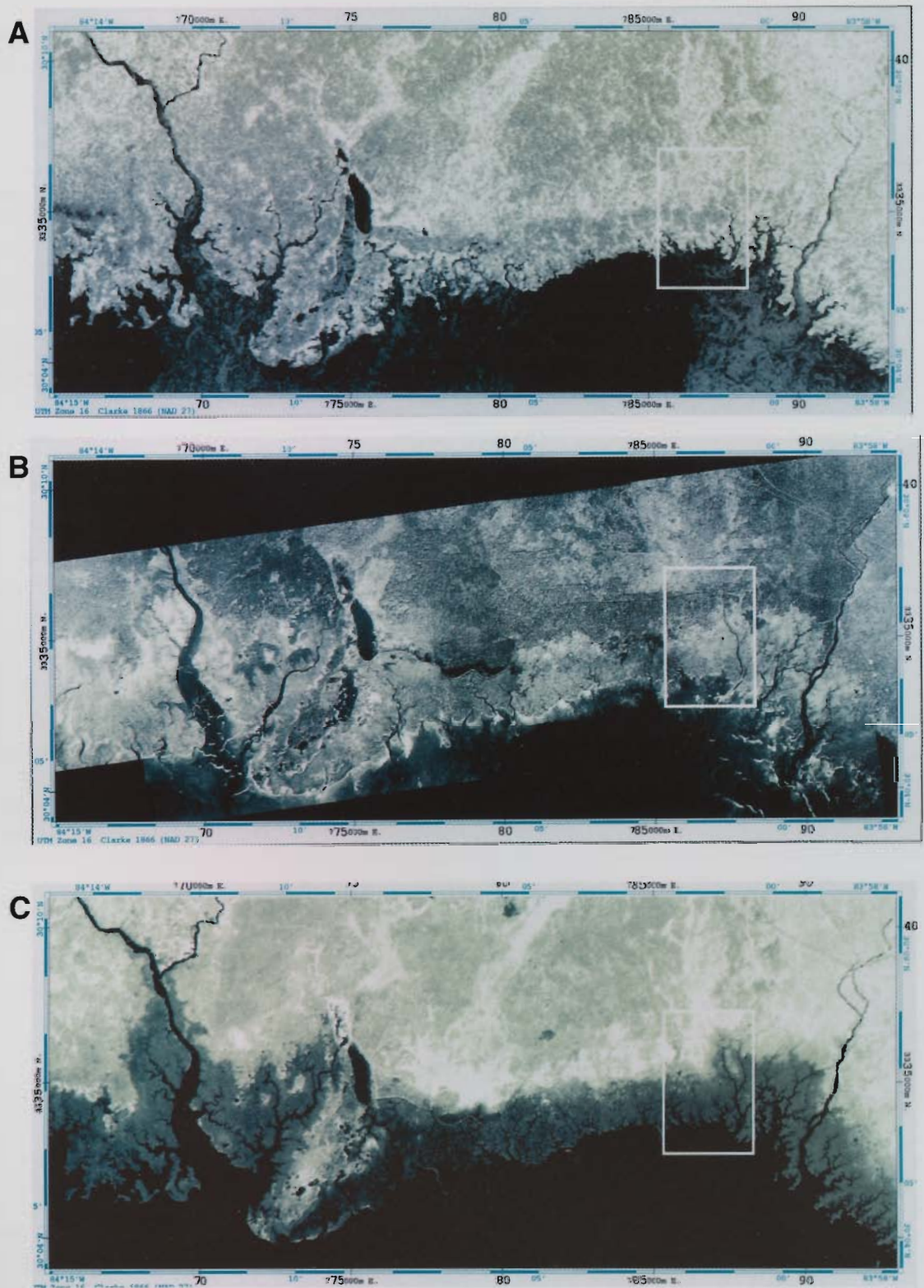
Figure 7-4. Comparison of different data sources. Spatial detail as well as vegetation classification were highly improved by combining the three data sources: (A) green band (0.5-0.6 μm) CIR photography; (B) ERS-1 SAR C band VV polarization; and (C) Landsat Thematic Mapper (TM) band 4 (0.8-0.9 μm). The CIR photography was resampled from original 3-m resolution to a 10-m resolution and ERS-1 SAR and TM from approximately 25-m to a 10-m resolution.
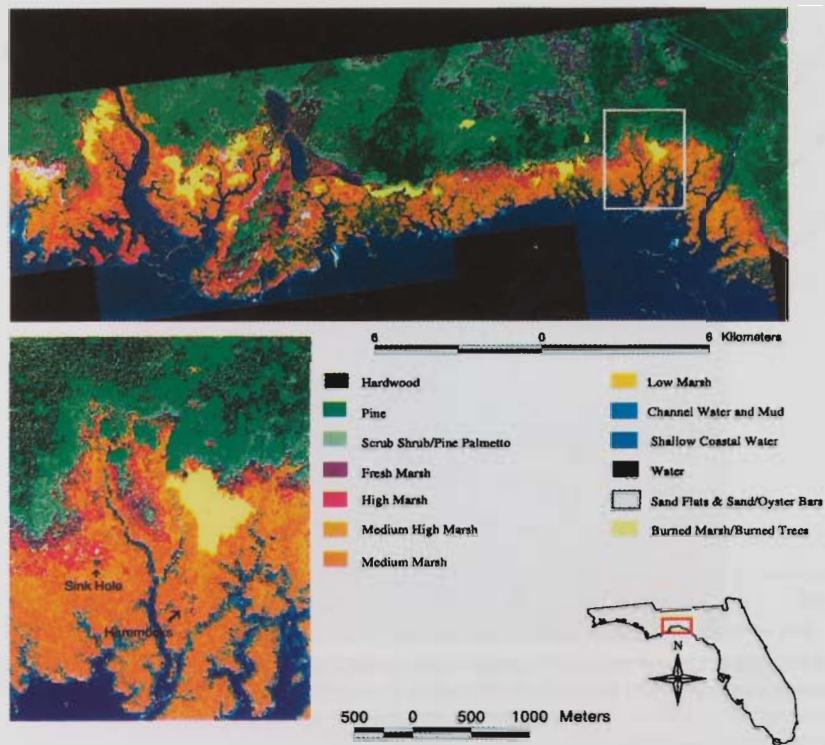
Figure 7-5. Classified map generated from a combination of the three data sources (see Fig. 7-4): high resolution CIR photography, Landsat Thematic Mapper imagery, and ERS-1 SAR imagery shown at a final 10-m spatial resolution. For visual clarity sand flats and oyster bars/sand bars are combined (modified after Ramsey et al. 1998b, with permission of Kluwer Academic Publishers).
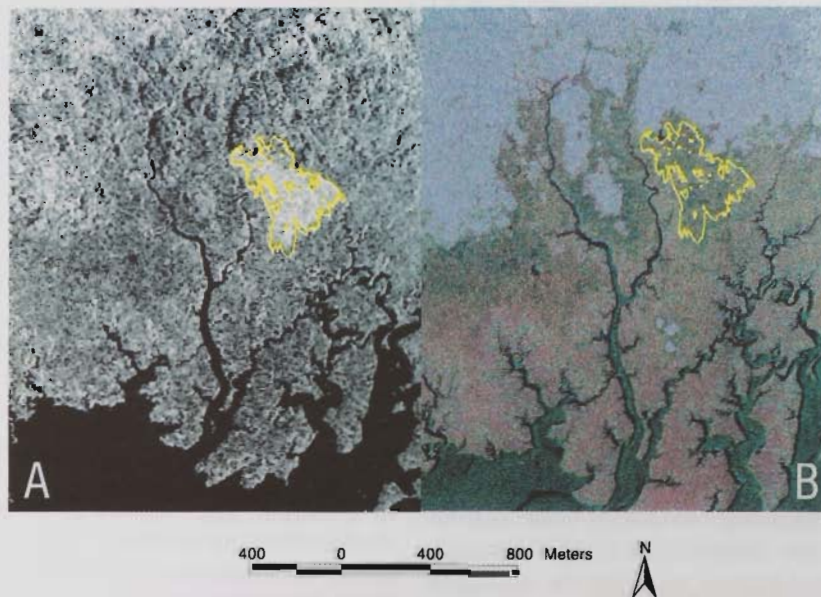

Figure 7-6. Monitoring the recovery of a burned marsh. The burned polygons extracted from color infrared (CIR) photography were overlaid on the radar imageries. (A) The April 1992 USGS Star-1 SAR X band HH polarization and (B) the July 1993 P3-Orion L band multiple polarizations (e.g., HH [red], VV [green], and VH [blue]). The USGS Star-1 and P3-Orion SAR images were collected from aircraft. The outlined area shows a marsh burn that occurred in March 1991.
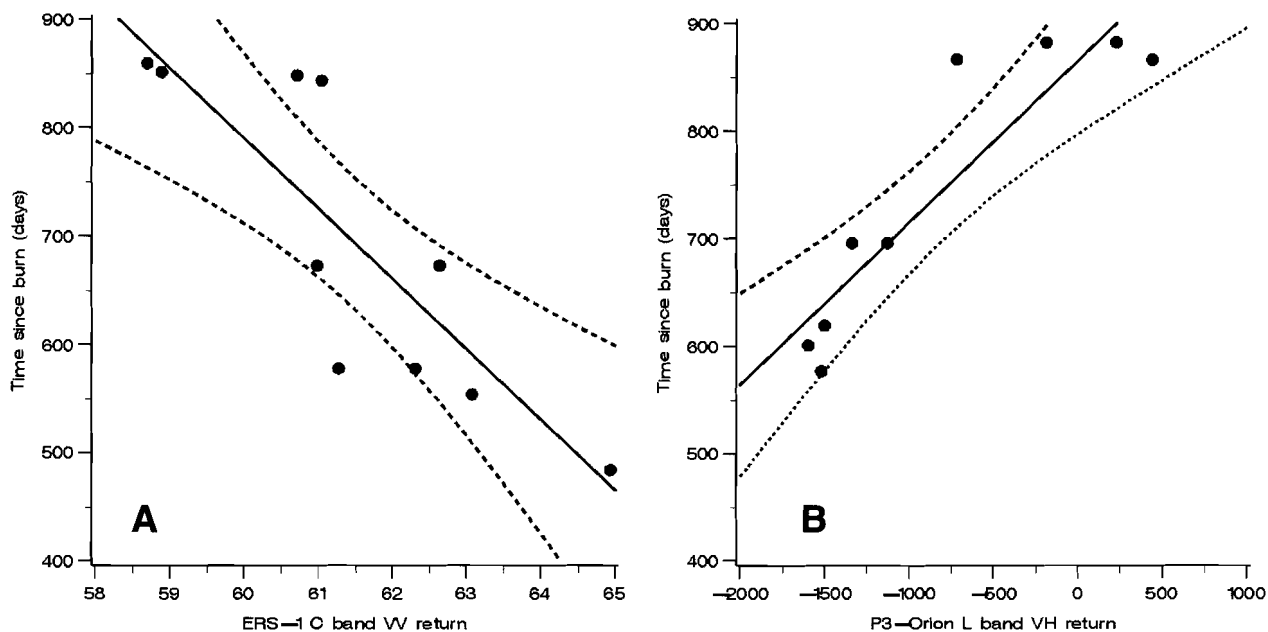
Figure 7-7. Scatter plots of number of days since burn versus signal return from different burned-marsh study sites. Solid lines indicate the predicted linear regression equation, and dashed lines indicate a 95 percent confidence interval of the predicted equation. (A) ERS-1 C band VV polarization and (B) signature difference between the burned and control sites of the P3 Orion L band VH polarization. Both SAR images were collected in July 1993.

with this radar at incident angles (scan angle of sensor) between 70° and 77°.

Overall, the combined data suggested that available ERS-1 satellite and P3 Orion aircraft radars could estimate time-since-burn of between 400 and 900 days for the black needlerush marsh. From the time of burn up to about 400 days, USGS Star-1 radar could detect a burnt marsh at incident angles less than 77°. Expanded to a regional level, these tools would not only aid in correctly detecting change and monitoring recovery, but could help in understanding how wetlands respond to burning and other acute stresses such as oil spills, herbivory, and storm impacts. This knowledge in turn could aid in understanding how these impacts may affect the wetland's ability to respond to rising sea levels and storm impacts.

Linking Hydrology to Coastal Resources

In the previous sections, we demonstrated our ability to detect and monitor coastal hydrology and vegetation type and status. A final objective of our study is to develop dynamic models to explain changes in the coastal landscape. Reaching this objective requires us to link the vegetation characteristics to the hydrologic regime. Establishing this link allows us not only to better understand what affects vegetation health but also to forecast future distributions of coastal resources given different scenarios of sea-level rise, storm occurrence frequency and intensity, and human development. To this end, we have developed and

preliminarily tested a flushing model to explain the changes in coastal landscape by linking the hydrologic regime (e.g., inundation extent—duration and depth, soil moisture, flushing, salinity) to the current and predicted distribution of coastal resources (e.g., vegetation type, dead and live biomass, structure [density, orientation, height, leaf property, and woody material]).

The flushing model is based on predicted and measured water level and salinity and modeled microtopographic data. The model continuously flushes the coastal area, generating duration and depth of flood events over time (Fig. 7-8). Initial results indicated tidal flushing and the depth of inundation can explain up to 69% of the variation in the coastal resources (Ramsey, unpublished data). This model is being validated with site specific measurements. These are simplistic predictions that do not account for factors inhibiting or exacerbating coastal resource loss (e.g., erosion, shoreline protection structures, vegetation loss), but with refinement will at least give resource managers and coastal planners a reasonable long- and short-term look at possible consequences of sea-level rise, unusual flooding due to excessive rain, saltwater intrusion, storm impacts, and human developments.

Summary

Remote sensing tools were developed based on aircraft and satellite optical and radar data to map flooding, generate microtopography, refine landcover classification, and

Platform Sites	Observed 0-5 ppt	Modeled 0-5 ppt	Observed >10 ppt	Modeled >10 ppt	Observed %Flooded	Modeled %Flooded	Pooled %Flooded
Saline Low Marsh	65.61	42.58	11.03	18.55	48.2	40.5	7.5
Saline High Marsh	78.68	47.04	0.95	17.33	44.8	25.7	35.4
Saline High Marsh	72.86	49.40	0.00	17.03	42.0	22.5	12.6
Fresh Marsh	56.09	43.48	4.38	18.46	49.1	32.9	49.5
Saline Marsh	56.21	43.16	1.24	18.42	53.2	34.6	27.0
Fresh Marsh	64.74	49.40	14.69	17.03	41.5	22.5	43.4
Upland Forest	Not flooded during time of measurements.						

Replicate Sites   Transition Sites   Transition Sites

Figure 7-8. Comparison of actual water level and salinity data with the data obtained as an output of the flushing model. Five hydrology sites of eastern St. Marks NWR, Florida, are shown on the photographic subset. The data from three channel sites are placed at the freshwater input and where the river drainage channel bifurcates (saline input and freshwater export - shown downstream of the actual location for clarity). The observed percentages were tabulated from the data collected on site between Jan. 18 and Dec. 16 of 1997 whereas the modeled percentages are the output of the flushing model over the same time period with modeled microtopographic data and actual water level data (from one channel site) as inputs. The summary is preliminary and includes unequal observations due to equipment failures. An average of 7,000 observations were used in comparing modeled and observed salinity and flooding. Some of the differences in observed and modeled salinity may be due to the long periods of pooled water at the sites and the exclusion of freshwater inputs in the model (Ramsey, unpublished data).

detect and monitor change in a coastal wetland. These tools, and tools in development, will be used to link vegetation type and health to surface hydrology and, ultimately, to simulate the vegetation response to sea-level rise and increasing occurrence of storms that may result from global climate change. Additionally, tools are actively being developed to measure and monitor soil moisture and vegetation biomass as necessary additions to complete the link between hydrology and vegetation type and health. In combination, the tools are the beginning of an integrated remote sensing system for dynamic monitoring of hydrology and landcover change day and night, during any weather conditions, and at a higher spatial resolution and landcover detail with less manpower than is now possible with conventional techniques and tools.

Acknowledgments

Literature Cited

Akachuku, A.E. 1993. Recovery and morphology of *Pinus resinosa* Ait. Trees 50 years after they were displaced by a hurricane. Forest Ecology and Management 56:113-129.

Allen, J.A. 1994. Intraspecific variation in the response of baldcypress (*Taxodium distichum*) seedlings to salinity. Ph.D. dissertation, School of Forestry, Wildlife, and Fisheries, Louisiana State University, Baton Rouge, La. 183 pp.

Allen, J.A., J.L. Chambers, and D. McKinney. 1994. Intraspecific variation in the response of *Taxodium distichum* seedlings to salinity. Forest Ecology and Management 70:203-214.

Allen, J.A., J.L. Chambers, and S.R. Pezeshki. 1997. Effects of salinity on baldcypress seedlings: physiological responses and their relation to salinity tolerance. Wetlands 17:310-320.

Anderson, M.C. 1964. Studies of the woodland light climate. I. Photographic computation of light conditions. Journal of Ecology 52:27-41.

Baumann, R.H., J.W. Day, Jr., and C.A. Miller. 1984. Mississippi deltaic wetland survival: sedimentation versus coastal submergence. Science 224:1093-1095.

Beer, S., and R.G. Wetzel. 1981. Photosynthetic carbon metabolism in the submerged aquatic angiosperm *Scirpus subterminalis*. Plant Science Letters 21:199-207.

Bilby, R. 1977. Effects of a spate on the macrophyte vegetation of a stream pool. Hydrobiologia 56:109-112.

Bill, C.J. 1995. Hurricane effects on a *Fagus/Magnolia* forest in southeast Texas, U.S.A., in the context of long-term forest monitoring. M.A. thesis. Rice University, Houston, Tex.

Bonan, G.B., and L. Sirois. 1992. Air temperature, tree growth, and the northern and southern range limits to *Picea mariana*. Journal of Vegetation Science 3:495-506.

Boose, E.R., D.R. Foster, and M. Fluet. 1994. Hurricane impacts to tropical and temperate forest landscapes. Ecological Monographs 64:369-400.

Botkin, D.B., J.F. Janak, and J.R. Wallis. 1972. Some ecological consequences of a computer model of forest growth. Journal of Ecology 60:849-872.

Boumans, R., and J.W. Day, Jr. 1993. High precision measurements of sediment elevation in shallow coastal areas using a sedimentation-erosion table. Estuaries 16:375-380.

Box, G.E.P., and G.M. Jenkins. 1976. Time series analysis: forecasting and control. Holden-Day, San Francisco, Calif. 575 pp.

Braun, E.L. 1950. Deciduous forests of eastern North America. Blakiston, Philadelphia, Penn. 596 pp.

Bray, W.L. 1901. Texas forests and the problem of forest management for the longleaf pine lands. The Forester 7:130-138.

Bretschneigder, C.L., and E.E. Tamaye. 1976. Hurricane wind and wave forecasting techniques. Pages 202–237 *in* Proceedings of the 15th Coastal Engineering Conference, Honolulu, Hawaii, July 11-17 (ASCE).

Bridges, E.L., and S.L. Orzell. 1989. Longleaf pine communities of the West Gulf Coastal Plain. Natural Areas Journal 9:246-263.

Brock, M.A., and J.A.K. Lane. 1983. The aquatic macrophyte flora of saline wetlands in Western Australia in relation to salinity and permanence. Hydrobiologia 105:63-76.

Burns, R.M., and B.H. Honkala, editors. 1990. Silvics of North America. Volume 1: Conifers. U.S. Department of Agriculture, U.S. Forest Service, Washington, D.C.

Cahoon, D.R., J.C. Lynch, and A. Powell. 1996a. Marsh vertical accretion in a southern California estuary, U.S.A. Estuarine, Coastal and Shelf Science 43:19-32.

Cahoon, D.R., J.C. Lynch, and R.M. Knaus. 1996b. Improved cryogenic coring device for sampling wetland soils. Journal of Sedimentary Research 66(5):1025-1027.

Cahoon, D.R., and D.J. Reed. 1995. Relationships among marsh surface topography, hydroperiod, and soil accretion in a deteriorating Louisiana salt marsh. Journal of Coastal Research 11:357-369.

Cahoon, D.R., D.J. Reed, and J.W. Day, Jr. 1995a. Estimating shallow subsidence in microtidal salt marshes of the southeastern United States: Kaye and Barghoorn revisited. Marine Geology 128:1-9.

Cahoon, D.R., D.J. Reed, J.W. Day, Jr., G.D. Steyer, R.M. Boumans, J.C. Lynch, D. McNally, and N. Latif. 1995b. The influence of Hurricane Andrew on sediment distribution in Louisiana coastal marshes. Journal of Coastal Research, Special Issue 21:280-294.

Cahoon, D.R., and R.E. Turner. 1989. Accretion and canal impacts in a rapidly subsiding wetland II. feldspar marker horizon technique. Estuaries 12:260-268.

Campbell, I.D., and J.H. McAndrews. 1993. Forest disequilibrium caused by rapid Little Ice Age cooling. Nature 366:336-338.

Chabreck, R. 1970. Marsh zones and vegetative types in the Louisiana coastal marshes. Ph.D. dissertation, Louisiana State University, Baton Rouge. 112 pp.

Chazdon, R.L., and C.B. Field. 1987a. Determinants of photosynthetic capacity in six rainforest Piper species. Oecologia 73:222-230.

Chazdon, R.L., and C.B. Field. 1987b. Photographic estimation of photosynthetically active radiation: evaluation of a computerized technique. Oecologia 73:525-532.

Christensen, N.L. 1988. Vegetation of the southeastern Coastal Plain. Pages 317-363 in M.G. Barbour and W.D. Billings, editors. North American terrestrial vegetation. Cambridge University Press, Cambridge, U.K.

Clarke, S.M., and H. Kirkman. 1989. Seagrass dynamics. Pages 304-345 in A.W.D. Larkum, A.J. McComb, and S.A. Shepherd, editors. Biology of seagrasses. Elsevier, New York, N.Y.

Clinton, B.D., L.R. Boring, and W.T. Swank. 1993. Canopy gap characteristics and drought influences in oak forests of the Coweeta Basin. Ecology 74:1551-1558.

Congalton, R. 1991. A review of assessing the accuracy of classifications of remotely sensed data. Remote Sensing of Environment 37:35-47.

Congalton, R.G. 1988. A comparison of sampling schemes used in generating error matrices for assessing the accuracy of maps generated from remotely sensed data. Photogrammetric Engineering and Remote Sensing 54(5):593-600.

Conner, W.H. 1994. The effect of salinity and waterlogging on growth and survival of baldcypress and Chinese tallow seedlings. Journal of Coastal Research 10(4):1045-1049.

Conner, W.H. 1988. Natural and artificial regeneration of baldcypress in the Barataria and Lake Verret basins of Louisiana. Ph.D. dissertation, Louisiana State University, Baton Rouge, La. 147 pp.

Conner, W.H. 1995. Response of forested wetland species to flooding and increased salinity. Final Report: Cooperative Agreement No. 14-16-0009-15659. Clemson University, Clemson, S.C.

Conner, W.H., and K. Flynn. 1989. Growth and survival of baldcypress (Taxodium distichum (L.) Rich.) planted across a flooding gradient in a Louisiana bottomland forest. Wetlands 9:207-217.

Conner, W.H., K.W. McLeod, and J.K. McCarron. 1997. Flooding and salinity effects on growth and survival of four common forested wetland species. Wetlands Ecology and Management 5(2):99-109.

Conner, W.H, K.W. McLeod, and J.K. McCarron. 1998. Survival and growth of four bottomland oak species in response to increased flooding and salinity. Forest Science 44(4):618-624.

Cook, E.R. 1985. A time series analysis approach to tree-ring standardization. Ph.D. thesis, University of Arizona, Tucson, Ariz. 171 pp.

Cook, E.R., and J. Cole. 1991. On predicting the response of forests in eastern North America to future climate change. Climatic Change 19:271-283.

Cook, E.R., and L.A. Kairiukstis. 1990. Methods of dendrochronology: applications in the environmental sciences. Kluwer Academic Publishers, Dordrecht, The Netherlands. 394 pp.

Cook, E.R., D. Meko, D. Stahle, and M. Cleaveland. 1997. Reconstruction of past drought across the conterminous United States from a network of climatically sensitive tree-ring data. National Oceanic and Atmospheric Administration. http://julius.ngdc.noaa.gov/paleo/pdsiyear.html. Accessed January 1997.

Cooley, W.W., and P.R. Lohnes. 1971. Multivariate data analysis. John Wiley and Sons, New York, N.Y. 364 pp.

Costanza, R., F.H. Sklar, and M.L. White. 1990. Modeling coastal landscape dynamics. Bioscience 40:91-107.

Craighead, F.C. 1964. Land, mangroves, and hurricanes. Fairchild Tropical Garden Bulletin 19:1-28.

Craighead, F.C. 1971. The trees of south Florida, vol. 1. University of Miami Press, Coral Gables, Fla. 212 p.

Craighead, F.C., and V.C. Gilbert. 1962. The effects of Hurricane Donna on the vegetation of southern Florida. Quarterly Journal of the Florida Academy of Sciences 25:1-28.

Cure, J.D., and B. Acock. 1986. Crop responses to carbon dioxide doubling: a literature survey. Agricultural and Forest Meteorology 38:127-145.

Curtis, P.D., B.G. Drake, P.W. Leadley, W. Arp, and D. Whigham. 1989. Growth and senescence of plant communities exposed to elevated CO_2 concentrations in an estuarine marsh. Oecologia 78:20-26.

Dacey, J.W., and B.L. Howes. 1984. Water uptake by roots controls water movement and sediment oxidation in short Spartina marsh. Science 224:487-489.

Dahlman, R.C. 1993. CO_2 and plants: revisited. Vegetatio 104/105:339-355.

Davis, G.J., and D.F. Carey, Jr. 1981. Trends in submersed macrophyte communities of the Currituck Sound: 1977-1979. Journal of Plant Management 19:3-8.

Day, Jr., J.W., D. Reed, J. Suhayda, G.P. Kemp, D. Cahoon, R. Boumans, and N. Latif. 1994. Physical processes of marsh deterioration. Pages 5.1-5.40 in H.H. Roberts, editor. Critical physical processes of wetland loss. U.S. Geological Survey, Open File Report.

DeLaune, R., J. Nyman, and W. Patrick, Jr. 1994. Peat collapse, ponding and wetland loss in a rapidly submerging coastal marsh. Journal of Coastal Research 10:1021-1030.

DeLaune, R.D., W.H. Patrick, Jr., and S.R. Pezeshki. 1987. Forseeable flooding and the death of coastal wetland forests. Environmental Conservation 14:129-133.

Delcourt, H.R., and P.A. Delcourt. 1977. Presettlement magnolia-beech climax of the gulf coastal plain: quantitative evidence from the Apalachicola River bluffs, north central Florida. Ecology 58:1085-1093.

Dennison, W.C. 1987. Effects of light on seagrass photosynthesis, growth and depth distribution. Aquatic Botany 27:15-26.

Dobson, M., L. Pierce, K. Sarabandi, F. Ulaby, and T. Sharik.1992. Preliminary analysis of ERS-1 SAR for forest ecosystem studies. IEEE Transactions on Geoscience and Remote Sensing 30:203-211.

Doyle, T.W. 1981. The role of disturbance in the gap dynamics of a montane rain forest: an application of a tropical forest succession simulation model. Pages 56-73 in D.C. West, H.H. Shugart and D.B. Botkin, editors. Forest succession: concepts and application. Springer, New York, N.Y.

Doyle, T.W., and G.F. Girod. 1997. The frequency and intensity of Atlantic hurricanes and their influence on the structure of south Florida mangrove communities. Pages 109-120 in H.F. Diaz, and R.S. Pulwarty, editors. Hurricanes: climate and socioeconomic impacts. Springer-Verlag, Heidelberg, Germany.

Doyle, T.W., and L.E. Gorham. 1996. Use of tree-ring analysis to detect historic hurricane impact on coastal forests. Pages 405-412 in J.S. Dean, D.M. Meko, and T.W. Swetnam, editors. Tree-rings, environment and humanity. Radiocarbon Press, Tucson, Ariz.

Doyle, T.W., B.D. Keeland, L.E. Gorham, and D.J. Johnson. 1995. Structural impact of Hurricane Andrew on the forested wetlands of the Atchafalaya Basin in South Louisiana. Journal of Coastal Research 21:354-364.

Doyle, T.W., T.J. Smith III, and M.B. Robblee. 1995. Wind damage effects of Hurricane Andrew on mangrove communities along the southwest coast of Florida, USA. Journal of Coastal Research 18:144-159.

Doyle, T.W., C.J. Wells, K.W. Krauss, and M. Roberts. 1994. The use of videography to analyze the spatial impact of Hurricane Andrew on south Florida mangroves. Pages 222-227 in Proceedings of GIS/LIS 94 Annual Conference held October 27-30, 1994, Phoenix, Ariz. American Congress on Surveying and Mapping, Bethesda, Md.

Duke, T.W., and W.L. Kruczynski, editors. 1992. Status and trends of emergent and submerged vegetated habitats of the Gulf of Mexico. Gulf of Mexico Program, U.S. Environmental Protection Agency, Stennis Space Center, Miss. 161 pp.

Durako, M.J. 1993. Photosynthetic utilization of CO_2 and HCO_3^- in Thalassia testudinum (Hydrocharitaceae). Marine Biology 115:373-380.

Dyer, K.R. 1995. Response of estuaries to climate change. Pages 85-110 in D. Eisma, editor. Climate change: impact on coastal habitation. Lewis Publishers, Boca Raton, Fla. 260 pp.

Eleuterius, L.N., and C.K. Eleuterius. 1979. Tide levels and salt marsh zonation. Bulletin of Marine Science 29(3):394-400.

Emanuel, K.A. 1987. The dependence of hurricane intensity on climate. Nature 326:483-485.

Englund, E., and A. Sparks. 1988. GEO-EAS (Geostatistical Environmental Assessment Software) user's guide. U.S. Environmental Protection Agency, Environmental Monitoring Systems Laboratory, Office of Research and Development, Las Vegas, Nev. 185 pp.

Epstein, E., J.D. Norlyn, D.W. Rush, R.W. Kingsbury, D.B. Kelley, G.A. Cunningham, and A.F. Wrona. 1980. Saline culture of crops: a genetic approach. Science 210:399-404.

Fonseca, M.S. 1989. Sediment stabilization by Halophila decipiens in comparison to other seagrasses. Estuarine Coastal and Shelf Science 29:501-507.

Fonseca, M.S., J.S. Fisher, J.C. Zieman, and G.W. Thayer. 1982. Influence of the seagrass, Zostera marina L., on current flow. Estuarine Coastal and Shelf Science 15:351-364.

Fritts, H.C. 1976. Tree rings and climate. Academic Press, London, U.K. 567 pp.

Fritts, H.C., and T.W. Swetnam. 1989. Dendroecology: a tool for evaluating variations in past and present forest environments. Advances in Ecological Research 19:111-175.

Fruh, E., W. Risher, K. Haynes, J. Hazleton, and J. Malina. 1973. Establishment of operational guidelines for Texas coastal zone management: interim report on resource capability. National Science Foundation, Washington, D.C. 249 pp.

Fulton, M.R. 1991. Adult recruitment as a function of juvenile growth rate in size-structured plant populations. Oikos 62:102-105.

Gear, A.J., and B. Huntley. 1991. Rapid changes in the range limits of Scots pine 4000 years ago. Science 251:544-547.

Giorgi, F., C.S. Brodeur, and G.T. Bates. 1994. Regional climate change scenarios over the United States produced with a nested regional climate model. Journal of Climate 7:375-400.

Glitzenstein, J.S., and P.A. Harcombe. 1988. Effects of the December 1983 tornado on forest vegetation of the Big Thicket, Southeast Texas, U.S.A. Forest Ecology and Management 25:269-290.

Glitzenstein, J.S., P.A. Harcombe, and D.R. Streng. 1986. Disturbance, succession, and maintenance of species diversity in an east Texas forest. Ecological Monographs 56:243-258.

Glitzenstein, J.S., W.J. Platt, and D.R. Streng. 1995. Effects of fire regime and habitat on tree dynamics in north

Florida longleaf pine savannas. Ecological Monographs 65:441-476.

Goldsborough, W.J., and W.M. Kemp. 1988. Light responses of a submersed macrophyte: implications for survival in turbid tidal waters. Ecology 69:1775-1786.

Gorham, L.E. 1992. A dendroecological investigation of hurricane impact and recovery along the central gulf coast. M.S. Thesis, Northeast Louisiana University, Monroe, La. 67 pp.

Gornitz, V. 1995. Sea-level rise: a review of recent past and near-future trends. Earth Surface Processes and Landforms 20:7-20.

Gornitz, V. 1991. Global coastal hazards from future sea level rise. Palaeogeography, Palaeoclimatology, Palaeoecology (Global Planetary Change Section) 89:379-398.

Goyer, R.A. 1996. Effects of insect defoliation on baldcypress in forested wetlands in Louisiana. Louisiana State University Agricultural Center. Final Report WETCOMP 19-92-120. 89 pp.

Goyer, R.A., and J.L. Chambers. 1997. Evaluation of insect defoliation in baldcypress and its relationship to flooding. National Biological Service Biological Science Report 8. 36 pp.

Goyer, R.A., G.J. Lenhard, and J.D. Smith. 1990. Insect herbivores of a baldcypress/tupelo ecosystem. Forest Ecology and Management 33/34:517-521.

Goyer, R.A., T.D. Paine, D.P. Ashley, G.J. Lenhard, J.R. Meeker, and C.C. Hanson. 1995. Geographic and host-associated differentiation in the fruittree leafroller (Lepidoptera: Tortricidae). Annals of the Entomological Society of America 88:391-396.

Graumlich, L.J. 1989. The utility of long-term records of tree growth for improving stand simulation models. Pages 39-49 in Natural areas facing climate change. SPB Academic Publishing, The Hague, The Netherlands.

Greenway, H., and R.A. Munns. 1980. Mechanisms of salt tolerance in non-halophytes. Annual Review of Plant Physiology 31:149-190.

Greller, A.M. 1989. Correlation of warmth and temperateness with the distributional limits of zonal forests in eastern North America. Bulletin of the Torrey Botanical Club 116:145-163.

Guntenspergen, G.R., and B.A. Vairin. 1996. Willful winds: Hurricane Andrew and Louisiana's coast. Louisiana Sea Grant College Program, Baton Rouge, La., and U.S. Department of the Interior, Lafayette, La. 16 pp.

Hackney, C.T., and A.A. de la Cruz. 1980. In situ decomposition of roots and rhizomes of two tidal marsh plants. Ecology 61:226-231.

Hall, R.B.W. 1993. Sapling growth and recruitment as affected by flooding and canopy gap formation in a river floodplain forest in southeast Texas. Ph.D. thesis. Rice University, Houston, Tex. 260 pp.

Hall, R.B.W., and P.A. Harcombe. 1998. Chronic understory disturbance and crown disturbance interact to determine spatial and temporal patterns of sapling occurrence and recruitment. Ecology 79:847-855.

Haller, W.T., D.L. Sutton, and W.C. Barlowe. 1974. Effects of salinity on growth of several aquatic macrophtyes. Ecology 55:891-894.

Handley, L.R. 1995. Seagrass distribution in the northern Gulf of Mexico. Pages 273-275 in E.T. LaRoe, G.S. Farris, C.E. Puckett, P.D. Doran, and M.J. Mac, editors. Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems. U.S. Department of the Interior, National Biological Service, Washington, D.C.

Harcombe, P.A. 1987. Tree life tables. BioScience 37:557-568.

Harcombe, P.A., J.S. Glitzenstein, R.G. Knox, S.L. Orzell, and E.L. Bridges. 1993. Forest communities of the western Gulf Coastal Plain. Pages 83-104 in Proceedings of the Tall Timbers Fire Ecology Conference 18.

Harcombe, P.A., and P.L. Marks. 1983. Tree death in a Fagus-Magnolia forest, southeast Texas (U.S.A.): forms, causes and consequences. Oecologia 57:49-54.

Hardisky, M., M. Gross, and V. Klemas. 1986. Remote sensing of coastal wetlands. BioScience 36: 453-460.

Harris, D.L. 1963. Characteristics of the hurricane storm surge. U.S. Department of Commerce, Technical Paper No. 48, Washington, D.C. 138 pp.

Harris, J.O., P.J. Zwank, and J.A. Dugoni. 1987. Habitat selection and behavior of nesting bald eagles in Louisiana. Journal of Raptor Research 21:27-31.

Hastie, T., and R. Tibshirani. 1986. General additive models. Statistical Science 1:297-318.

Hill, M.O. 1974. Correspondence analysis: a neglected multivariate method. Applied Statistics 3:340-354.

Hine, C., D. Belknap, J. Hutton, E. Osking, and M. Evans. 1988. Recent geological history and modern sedimentary processes along an incipient, low-energy, epicontinental-sea coastline: northwest Florida. Journal of Sedimentary Petrology 58:567-579.

Holmes, R.L. 1982. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bulletin 44:69-75.

Hook, D.D. 1984. Waterlogging tolerance of lowland tree species of the South. Southern Journal of Applied Forestry 8:136-149.

Houghton, J.T., L.G. Meira Filho, B.A. Callander, N. Harris, A. Kattenberg, and K. Maskell. 1995. Climate change 1995: the science of climate change. Cambridge University Press, Cambridge, U.K. 572 pp.

Howard-Williams, C., and M.R.M. Liptrot. 1980. Submerged macrophyte communities in a brackish South African estuarine-lake system. Aquatic Botany 9:101-116.

Howes, B.L., J.W.H. Dacey, and D.D. Goehringer. 1986. Factors controlling the growth form of *Spartina alterniflora*: feedbacks between above-ground production, sediment oxidation, nitrogen and salinity. Journal of Ecology 74:881-898.

Imhoff, M., and D. Gesch. 1990. The derivation of a subcanopy digital terrain model of a flooded forest using synthetic aperture radar. Photogrammetric Engineering and Remote Sensing 56:1155-1162.

Intergovernmental Panel on Climate Change. 1995a. Climate change 1995: the science of climate change. Cambridge Press, New York, N.Y. 572 pp.

Intergovernmental Panel on Climate Change. 1995b. IPCC second assessment, synthesis report. United Nations Framework Convention on Climate Change. United Nations, New York, N.Y. 56 pp.

Iverson, R.L.J., and H.F. Bittaker. 1986. Seagrass distribution and abundance in eastern Gulf of Mexico coastal waters. Estuarine Coastal and Shelf Science 22:577-602.

Javanshir, K. and K. Ewel. 1993. Salt resistance in bald cypress. Pages 285-291 *in* H. Leith and A. Al Masoom, editors. Towards the rational use of high salinity tolerant plants. Vol. 2: Agriculture and forestry under marginal soil water conditions. Kluwer Academic Publishers, Boston, Mass.

Jensen, J., E. Ramsey III, H. Mackey, E. Christensen, and R. Sharitz. 1987. Inland wetland change detection using aircraft MSS data. Photogrammetric Engineering and Remote Sensing 53:521-528.

Jensen, P.R., and R.A. Gibson. 1986. Primary production in three subtropical seagrass communities: a comparison of four autotrophic components. Florida Scientist 49:129-141.

Johnstone, I.M., and P.W. Robinson. 1987. Light level variation in Lake Tutira, New Zealand after transient sediment inflow and its effect on the submersed macrophytes. New Zealand Journal of Marine and Freshwater Research 21:47-54.

Jones, R.H., and K.W. McLeod. 1989. Shade tolerance in seedlings of Chinese tallow tree, American sycamore, and cherrybark oak. Bulletin of the Torrey Botanical Club 116:371-377.

Jones, R.H., and K.W. McLeod. 1990. Growth and photosynthetic responses to a range of light environments in Chinese tallow tree and Carolina ash seedlings. Forest Science 36:851-862.

Jones, R.H., and R.R. Sharitz. 1990. Effects of root competition and flooding on growth of Chinese tallow seedlings. Canadian Journal of Forest Research 20:573-578.

Jones, R.H., R.R. Sharitz, P.M. Dixon, D.S. Segal, and R.L. Schneider. 1995. Woody plant regeneration in four floodplain forests. Ecological Monographs 64:345-367.

Jones, R.H., R.R. Sharitz, S.M. James, and P.M. Dixon. 1994. Tree population dynamics in seven South

Carolina mixed-species forests. Bulletin of the Torrey Botanical Club 121:360-368.

Jubinsky, G. 1995. Chinese tallow (*Sapium sebiferum*). Technical Report TSS-93-03, Florida Department of Environmental Protection, Tallahassee, Fla. 12 pp.

Kaiser, L.K. 1995. The future of longleaf pine in a mixed pine-oak forest. M.A. thesis, Rice University, Houston, Tex.

Kaye, C., and E. Barghoorn. 1964. Late Quaternary sea-level change and crustal rise at Boston, Massachusetts, with notes on the autocompaction of peat. Geological Society of America Bulletin 75:63-80.

Kearney, M., and L. Ward. 1986. Accretion rates in brackish marshes of a Chesapeake Bay estuarine tributary. Geo-Marine Letters 6:41-49.

Keller, C.E., J.A. Spendelow, and R.D. Greer. 1984. Atlas of wading bird and seabird nesting colonies in coastal Louisiana, Mississippi, and Alabama: 1983. U.S. Fish and Wildlife Service, FWS/OBS-84/13.

Kemp, W.M., W.R. Boynton, R.R. Twilley, J.C. Stevenson, and L.G. Ward. 1984. Influences of submersed vascular plants on ecological processes in upper Chesapeake Bay. Pages 367-394 *in* V.S. Kennedy, editor. The estuary as a filter. Academic Press, Orlando, Fla.

Kenworthy, W.J. 1994. Conservation and restoration of the seagrasses of the Gulf of Mexico through a better understanding of their minimum light requirements and factors controlling water transparency. Pages 17-31 *in* H.A. Neckles, editor. Indicator development: seagrass monitoring and research in the Gulf of Mexico. U.S. Environmental Protection Agency, Office of Research and Development, Environmental Research Laboratory, Gulf Breeze, Fla. EPA/620/R-94/029.

Keys, Jr., J.E., C.A. Carpenter, S. Hooks, F. Koenig, W.H. McNab, W. Russell, and M.L. Smith, compilers. 1995. Ecological units of the eastern United States - first approximation. U.S. Department of Agriculture, U.S. Forest Service, Southern Region, Washington, D.C.

Kjerfve, B., K.E. Magill, J.W. Porter, and J.D. Woodley. 1986. Hindcasting of hurricane characteristics and observed storm damage on a fringing reef, Jamaica, West Indies. Journal of Marine Research 44:119-148.

Klemas, V., D. Bartlett, and M. Murillo. 1980. Remote sensing of coastal environment and resources. Proceedings of the 14th International Symposium on Remote Sensing of Environment. ERIM, Ann Arbor, Mich.

Knox, R.G., and R.K. Peet. 1989. Bootstrapped ordination: a method for estimating sampling effects in indirect gradient analysis. Vegetatio 80:153-165.

Knutson, T.R., R.E. Tuleya, and Y. Kurihara. 1998. Simulated increase of hurricane intensities in a CO_2-warmed environment. Science 279:1018-1020.

Kobe, R.K., S.W. Pacala, J.A. Silander, and C.D. Canham. 1995. Juvenile tree survivorship as a component of shade tolerance. Ecological Applications 5(2):517-532.

Krauss, K.W. 1997. Intraspecific variation in baldcypress (*Taxodium distichum* (L.) Rich.): responses to salinity and potential for restoration of wetlands impacted by saltwater intrusion. M.S. thesis, School of Forestry, Wildlife and Fisheries, Louisiana State University, Baton Rouge, La. 132 pp.

Krauss, K.W., J.L. Chambers, and J.A. Allen. 1996. Intraspecific variation in the physiological response of baldcypress (*Taxodium distichum* (L.) Rich.) to a rapid influx of saltwater. Pages 183–189 *in* K.M. Flynn, editor. Proceedings of the Southern Forested Wetland Ecology and Management Conference, Clemson University, S.C., March 25-27, 1996.

Krauss, K.W., J.L. Chambers, and J.A. Allen. 1998. Salinity effects and differential germination of several half-sib families of baldcypress from different seed sources. New Forests 15:53-68.

Krauss, K.W., J.L. Chambers, J.A. Allen, B.P. Luse, and A.S. DeBosier. 1999a. Root and shoot responses of *Taxodium distichum* seedlings subjected to saline flooding. Environmental and Experimental Botany 41:15-23.

Krauss, K.W., J.L. Chambers, J.A. Allen, D.M. Soileau, Jr., and A.S. DeBosier. 1999b. Growth and nutrition of baldcypress families planted under varying salinity regimes in Louisiana, USA. Journal of Coastal Research. In press.

Küchler, A.W. 1964. Potential natural vegetation of the conterminous United States. Special Publication 36, American Geographical Society, New York, N.Y.

Larsen, H.S. 1980. Baldcypress-tupelo. Page 68 *in* F.H. Eyre, Jr., editor. Forest cover types of the United States and Canada. Society of American Foresters, Washington, D.C.

Lee, J.K., R.A. Park, and P.W. Mausel. 1992. Application of geoprocessing and simulation modeling to estimate impacts of sea level rise on the northeast coast of Florida. Photogrammetric Engineering and Remote Sensing 58(11):1579-1586.

Leonard, L., A. Hine, M. Luther, R. Stumpf, and E. Wright. 1995. Sediment transport processes in a west-central Florida open marine marsh tidal creek; the role of tides and extra-tropical storms. Estuarine, Coastal and Shelf Science 41:225-248.

Little, E.L., Jr. 1971. Atlas of United States trees. Vol. 1: conifers and important hardwoods. U.S. Department of Agriculture, U.S. Forest Service, Washington, D.C. 400 pp.

Liu, C., P.A. Harcombe, J.S. Glitzenstein, and R.G. Knox. 1997. Tornado and fire effects on tree species composition in a southeast Texas savanna. Forest Ecology and Management 91:279-289.

Lyon, J., and J. McCarthy. 1981. Seasat imagery for detection of coastal wetlands. Pages 1475-1485 *in* Proceedings of the Fifteenth International Symposium on Remote Sensing of Environment. ERIM, Ann Arbor, Mich.

MacDonald, G.M., T.W.D. Edwards, K.A. Moser, R. Pienitz and J.P. Smol. 1993. Rapid response of treeline vegetation and lakes to past climatic warming. Nature 361:243-246.

Madsen, T.V., K. Sand-Jensen, and S. Beer. 1993. Comparison of photosynthetic performance and carboxylation capacity in a range of aquatic macrophytes of different growth forms. Aquatic Botany 44:373-384.

Marks, P.L., and P.A. Harcombe. 1981. Forest vegetation of the Big Thicket, southeast Texas. Ecological Monographs 51:287-305.

Marmer, H. 1954. Tides and sea level in the Gulf of Mexico. Pages 101-118 *in* Gulf of Mexico, its origin, waters, and marine life. U.S. Fish and Wildlife Service, Fisheries Bulletin 55.

Maul, G.A., and D.M. Martin. 1993. Sea level rise at Key West, Florida, 1846-1992: America's longest instrument record? Geophysical Research Letters 20:1955-1958.

Mayle, F.E., and L.C. Cwynar. 1995. Impact of the Younger Dryas cooling event upon lowland vegetation of Maritime Canada. Ecological Monographs 65:129-154.

Mazella, L., and R.S. Alberte. 1986. Light adaptation and the role of autotrophic epiphytes in primary production of the temperate seagrass, *Zostera marina* L. Journal of Experimental Marine Biology and Ecology 100:165-180.

McCarron, J.K., K.W. McLeod, and W.H. Conner. 1998. Flood salinity stress of wetland woody species, buttonbush (*Cephalanthus occidentalis*) and swamp tupelo (*Nyssa sylvatica* var. *biflora*). Wetlands 18:165-175.

McKee, K., and W. Patrick, Jr. 1988. The relationship of smooth cordgrass (*Spartina alterniflora*) to tidal datum: a review. Estuaries 11:143-151.

McKnight, J.S., D.D. Hook, O.G. Langdon, and R.L. Johnson. 1981. Flood tolerance and related characteristics of trees of the bottomland forests of the southern United States. Pages 29-69 *in* J.R. Clark and J. Benforado, editors. Wetlands of bottomland forests. Elsevier Scientific Publishing Co., Amsterdam.

McLeod, K.W., J.K. McCarron, and W.H. Conner. 1996. Effects of inundation and salinity on photosynthesis and water relations of four southeasern coastal plain forest species. Wetlands Ecology and Management 4(1):31-42.

McLeod, K. W., J. K. McCarron, and W. H. Conner. Photosynthesis and water relations of four oak species: impact of flooding and salinity. Trees. In press.

McWilliams, W.H., and J.F. Rosson, Jr. 1990. Composition and vulnerability of bottomland hardwood forests of the Coastal Plain Province in the south central United States. Forest Ecology and Management 33/34:485-501.

Melillo, J.M., I.C. Prentice, G.D. Farquhar, E.D. Schultze, and O.E. Sala. 1996. Terrestrial biotic responses to environmental change and feedbacks to climate. Pages 449-481 in J.T. Houghton, L.G. Meira Filho, B.A. Callander, N. Harris, A. Kattenberg, and K. Maskell, editors. Climate change 1995: the science of climate change. Cambridge University Press, Cambridge, U.K.

Menges, E.S., and D.M. Waller. 1983. Plant strategies in relation to elevation and light in floodplain herbs. American Naturalist 122:454-473.

Merrens, E.J., and D.R. Peart. 1992. Effects of hurricane damage on individual growth and stand structure in a hardwood forest in New Hampshire, USA. Journal of Ecology 80:787-795.

Michener, W.K., E.R. Blood, K.L. Bildstein, M.M. Brinson, and L.R. Gardner. 1997. Climate change, hurricanes, and tropical storms, and rising sea level in coastal wetlands. Ecological Applications 7:770-801.

Mitsch, W.J., and J.G. Gosselink. 1986. Wetlands. Van Nostrand Reinhold, New York, N.Y. 539 pp.

Mitsch, W.J., and J.G. Gosselink. 1993. Wetlands, 2nd ed. Van Nostrand Reinhold, New York, N.Y. 722 pp.

Mohler, C.L. 1979. An analysis of floodplain vegetation of the lower Neches drainage, Southeast Texas, with some considerations on the use of regression and correlation in plant synecology. M.S. thesis, Cornell University, Ithaca, N.Y. 658 pp.

Mohler, C.L. 1990. Co-occurrence of oak subgenera: implications for niche differentiation. Bulletin of the Torrey Botanical Club 117:247-255.

Moncreiff, C.A., M.J. Sullivan, and A.E. Daehnick. 1992. Primary production dynamics in seagrass beds of Mississippi Sound: the contributions of seagrass, epiphytic algae, sand microflora, and phytoplankton. Marine Ecology Progress Series 87:161-171.

Mooney, H.A., B.G. Drake, R.J. Luxmoore, W.C. Oechel, and L.F. Pitelka. 1991. Predicting ecosystem responses to elevated CO_2 concentrations. Bioscience 41:96-104.

Morgan, M.D., and C.L. Kitting. 1984. Productivity and utilization of the seagrass Halodule wrightii and its attached epiphytes. Limnology and Oceanography 29:1066-1076.

Morris, J.T., and G.J. Whiting. 1985. Gas advection in sediments of a South Carolina salt marsh. Marine Ecology Progress Series 27:187-194.

Morse, L.E., L.S. Kutner, and J.T. Kartesz. 1995. Potential impacts of climate change on North American flora. Pages 392-395 in E.T. LaRoe, G.S. Farris, C.E. Puckett, P.D. Doran, and M.J. Mac, editors. Our living resources: a report to the nation on the distribution, abundance and health of U.S. plants, animals and ecosystems. U.S. Department of the Interior, National Biological Service, Washington, D.C.

Murray, L., and R.L. Wetzel. 1987. Oxygen production and consumption associated with the major autotrophic components in two temperate seagrass communities. Marine Ecology Progress Series 38:231-239.

National Academy of Sciences. 1983. Firewood crops: shrub and tree species for energy production. Vol. 2. National Academy Press, Washington, D.C. 92 pp.

National Climatic Data Center. 1994. NCDC Summary of the day: West 2 CD. EarthInfo, Inc., Boulder, Colo.

Neckles, H.A., editor. 1994. Indicator development: seagrass monitoring and research in the Gulf of Mexico. U.S. Environmental Protection Agency, Office of Research and Development, Environmental Research Laboratory, Gulf Breeze, Fla. EPA/620/R-94/029.

Neilson, R.P., G.A. King, and G. Koerper. 1991. Toward a rule-based biome model. In J.L. Betancourt and F.L. Tharp, editors. Proceedings of the seventh annual Pacific Climate (PACLIM) Workshop, April 1990, Asilomar, California. California Department of Water Resources. Interagency Ecological Studies Program for the Sacramento-San Joaquin Estuary.

Neilson, R.P., and L.H. Wullstein. 1983. Biogeography of two southwest American oaks in relation to atmospheric dynamics. Journal of Biogeography 10:275-297.

Neumann, C.J. 1987. The National Hurricane Center Risk Analysis Program (HURISK). National Oceanic and Atmospheric Administration Technical Memorandum NWS NHC 38, Washington D.C. 56 pp.

Neumann, C.J., B.R. Jarvinen, C.J. McAdie, and J.D. Elms. 1993. Tropical cyclones of the North Atlantic Ocean, 1871-1992. National Oceanic and Atmospheric Administration Climatic Center, National Weather Service, Asheville, N.C. 193 pp.

Nielsen, S.L., and K. Sand-Jensen. 1989. Regulation of photosynthetic rates of submerged rooted macrophytes. Oecologia 81:364-368.

Nuttle, W.K., H.F. Hemond, and K.D. Stolzenbach. 1990. Mechanisms of water storage in salt marsh sediments: the importance of dilation. Hydrological Processes 4:1-13.

Nyman, J.A., R.D. DeLaune, H.H. Roberts, and W.H. Patrick, Jr. 1993. Relationship between vegetation and soil formation in a rapidly submerging coastal marsh. Marine Ecology Progress Series 96:269-279.

Office of Technology Assessment. 1993. Preparing for our uncertain climate - Volume II. OTA, 0-568. Washington, D.C., U.S. Government Printing Office.

Onuf, C.P. 1995. Seagrass meadows of the Laguna Madre of Texas. Pages 275-277 in E.T. LaRoe, G.S. Farris, C.E. Puckett, P.D. Doran, and M.J. Mac, editors. Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems. U.S. Department of the Interior, National Biological Service, Washington, D.C.

Onuf, C.P., and M.L. Quammen. 1983. Fishes in a California coastal lagoon: effects of major storms on distribution and abundance. Marine Ecology Progress Series 12:1-14.

Ormsby, J., B. Blanchard, and A. Blanchard. 1985. Detection of lowland flooding using active microwave systems. Photogrammetric Engineering and Remote Sensing 51:317-328.

Orth, R. J., and J. van Montfrans. 1990. Utilization of marsh and seagrass habitats by early stages of Callinectes sapidus: a latitudinal perspective. Bulletin of Marine Science 46:126-144.

Park, R.A., J.K. Lee, and D.J. Canning. 1993. Potential effects of sea-level rise on Puget Sound wetlands. Geocarto 8:99-110.

Park, R.A., M.S. Trehan, P.W. Mausel, and R.C. Howe. 1989. Coastal wetlands in the twenty-first century: profound alterations due to rising sea level. Pages 71-81 in D.W. Fisk, editor. Wetlands: concerns and successes. American Water Resources Association, Bethesda, Md.

Patriquin, D.G. 1975. "Migration" of blowouts in seagrass beds at Barbados and Cariacou, West Indies, and its ecological and geological implications. Aquatic Botany 1:163-189.

PCI Geomatics. 1998. Version 6.3. PCI Geomatics, Richmond Hill, Ontario, Canada.

Penland, S., and K. Ramsey. 1990. Relative sea-level rise in Louisiana and the Gulf of Mexico: 1908-1988. Journal of Coastal Research 6:323-342.

Penland, S., K. Ramsey, R. McBride, T. Moslow, and K. Westphal. 1989. Relative sea level rise and subsidence in Louisiana and the Gulf of Mexico. Coastal Geology Technical Report 3, Louisiana Geological Survey, Baton Rouge. 65 pp.

Peters, D.D. 1994. Use of aerial photography for mapping wetlands in the United States: National Wetlands Inventory. Pages III 165-III 173 in Proceedings of the First International Airborne Remote Sensing Conference and Exhibition: Applications, Technology, and Science. Volume III. 11-15 September, 1994. Strasbourg, France. Environmental Research Institute of Michigan (ERIM), Ann Arbor, Mich.

Pezeshki, S.R. 1990. A comparative study of the response of Taxodium distichum and Nyssa aquatica seedlings to soil anaerobiosis and salinity. Forest Ecology and Management 33/34:531-541.

Pezeshki, S.R., R.D. DeLaune, and W.H. Patrick, Jr. 1990. Flooding and saltwater intrusion: Potential effects on survival and productivity of wetland forests along the U.S. gulf coast. Forest Ecology and Management 33/34:287-301.

Pillow, M.Y. 1931. Compression wood records hurricane. Journal of Forestry 4:575-578.

Poljakoff-Mayber, A. 1988. Ecological physiology studies on the responses of higher plants to salinity and drought. Reviews of Arid Zone Research 6:163-183.

Prentice, I.C., M.T. Sykes, and W. Cramer. 1991. The possible dynamic response of northern forests to global warming. Global Ecology and Biogeography Letters 1:129-135.

Putz, F.E., and R.R. Sharitz. 1991. Hurricane damage to old-growth forest in Congaree Swamp National Monument, South Carolina, USA. Canadian Journal of Forest Research 13:1011-1020.

Quarterman, E., and K. Keever. 1962. Southern mixed hardwood forest: climax in the southeast coastal plain, USA. Ecological Monographs 32:167-185.

Quayle, R.G. and T.R. Karl. 1997. Observed climate trends: global warming and the southeastern United States. Pages 7-12 in Regional vulnerabilities to climate variability and climate change in the Southeastern United States. White paper for Workshop on Climate Variability and Water Resources Management in the Southeastern United States. Vanderbilt University, June 25-27, 1997.

Ramsey, E., III. 1995. Monitoring flooding in coastal wetlands by using SAR imagery and ground-based measurements. International Journal of Remote Sensing 16:2495-2502.

Ramsey, E., III. 1998. Radar remote sensing of wetlands. Pages 213-245 in R. Lunetta and C. Elvidge. Remote sensing change detection: environmental monitoring methods and applications. Ann Arbor Press, Inc., Mich.

Ramsey, E., III, and S. Laine. 1997. Comparison of Landsat Thematic Mapper and high resolution photography to identify change in complex coastal wetlands. Journal of Coastal Research 13(2):281-292.

Ramsey, E., III, S. Laine, D. Werle, B. Tittley, and D. Lapp. 1994. Monitoring Hurricane Andrew damage and recovery of the coastal Louisiana marsh using satellite remote sensing data. Pages 1841-1852 in Proceedings of the Coastal Zone Canada '94 held in Halifax, Nova Scotia on 20-23 September 1994.

Ramsey, E., III, G. Nelson, S. Laine, R. Kirkman, and W. Topham. 1998a. Generation of coastal marsh topography with radar and ground-based measurements. Journal of Coastal Research 14:1158-1164.

Ramsey, E., III, G. Nelson, and S. Sapkota. 1998b. Classifying coastal resources by integrating optical and radar imagery and color infrared photography. Mangroves and Salt Marshes 2(2):109-119.

Ramsey, E., III, G. Nelson, S. Sapkota, S. Laine, J. Verdi, and S. Krasznay. 1998c. Polarization L band radar to monitor marsh burn recovery. IEEE Transactions on Geoscience and Remote Sensing. In press.

Ramsey, E., III, R. Spell, and R. Day. 1992. Light attenuation and canopy reflectance as discriminators of gulf

coast wetland types. Pages 1176-1189 *in* Proceedings of the International Symposium on Spectral Sensing Research, held in Maui, Hawaii on 15-20 November 1992.

Ramsey, E., III, R. Spell, and R. Day. 1993. Measuring and monitoring wetland responses to acute stress by using remote sensing techniques. Pages 43-54 *in* Proceedings of the 25th International Symposium on Remote Sensing and Global Environmental Change, held in Graz, Austria on 4-8 April 1993.

Rattray, M.R., C. Howard-Williams, and J.M.A. Brown. 1991. The photosynthetic and growth rate responses of two freshwater angiosperms in lakes of different trophic status: responses to light and dissolved inorganic carbon. Freshwater Biology 25:399-407.

Redfield, A. 1972. Development of a New England salt marsh. Ecological Monographs 42:201-237.

Reed, D.J. 1995. The response of coastal marshes to sea-level rise: survival or submergence? Earth Surface Processes and Landforms 20:39-48.

Reed, D.J. 1989. Patterns of sediment deposition in subsiding coastal salt marshes, Terrebonne Bay, Louisiana: the role of winter storms. Estuaries 12:222-227.

Reed, D.J., and D.R. Cahoon. 1992. The relationship between marsh surface topography, hydroperiod, and growth of *Spartina alterniflora* in a deteriorating Louisiana salt marsh. Journal of Coastal Research 8:77-87.

Reed, D.J., and D.R. Cahoon. 1993. Marsh submergence vs. marsh accretion: interpreting accretion deficit data in coastal Louisiana. Pages 243-257 *in* O. Magoon, W. Wilson, H. Converse, and L. Tobin, editors. Proceedings 8th Symposium on Coastal and Ocean Management, Coastal Zone '93 (New Orleans, La.). ASCE, New York, N.Y.

Reed, D.J., J.W. Day, Jr., N. De Luca, and D. NcNally. 1995. An evaluation of the impact of hydroperiod on marsh surface elevation change in marshes subjected to varying rates of relative sea-level rise. Unpublished Final Report, Cooperative Agreement 14-48-0009-92-955, submitted to National Biological Service, Lafayette, La. 65 pp.+ appendices.

Richman, M.B. 1986. Rotation of principal components. Journal of Climatology 6:293-335.

Rizzo, W.M., and H.A. Neckles. 1993. Global climate change: implications for submerged aquatic vegetation. Pages 211-223 *in* R. Gale, W.J. Catallo, R.C. Mohanty, and J.B. Johnston, editors. Environmental concerns, public policies and remediation technologies. American Society of Environmental Sciences. Baton Rouge, La.

Roemmich, D. 1992. Ocean warming and sea level rise along the southwest U. S. coast. Science 257:373-375.

Roth, L.C. 1992. Hurricanes and mangrove regeneration: effects of Hurricane Joan, October 1988, on the vegetation of Isla del Venado, Bluefields, Nicaragua. Biotropica 24:375-384.

Rybicki, N.B., and V. Carter. 1986. Effect of sediment depth and sediment type on the survival of *Vallisneria americana* grown from tubers. Aquatic Botany 24:233-240.

Salinas, L.M., R.D. DeLaune, and W.H. Patrick, Jr. 1986. Changes occurring along a rapidly subsiding coastal area: Louisiana, USA. Journal of Coastal Research 2:269-284.

Sand-Jensen, K., N.P. Revsbech, and B.B. Jørgensen. 1985. Microprofiles of oxygen in epiphyte communities on submerged macrophytes. Marine Biology 89:55-62.

SAS Institute Inc. 1989. SAS/STAT User's Guide, Version 6. 4th Edition. Volume 2. SAS Institute, Inc., Cary, N.C. 846 pp.

Schmeda, A., and S.P. Ellner. 1984. Coexistence of plant species with similar niches. Vegetatio 58:29-55.

Schriever, J.R., and R.G. Congalton. 1993. Mapping forest cover-types in New Hampshire using multi-temporal Landsat Thematic Mapper data. Pages 333-342 *in* Proceedings of the 1993 ACSM/ASPRS Annual Convention and Exposition held on February 15-18 in New Orleans, La. Vol. II.

Short, F.T., and C.A. Short. 1984. The seagrass filter: purification of estuarine and coastal water. Pages 395-413 in V.S. Kennedy, editor. The estuary as a filter. Academic Press, Orlando, Fla.

Shugart, H.H. 1984. A theory of forest dynamics: the ecological implications of forest succession models. Springer-Verlag, New York, N.Y. 278 pp.

Smith, W., and P. Wessel. 1990. Gridding with continuous curvature splines in tension. Geophysics 55:293-305.

Smith, T.J., III, M.B. Robblee, H.R. Wanless, and T.W. Doyle. 1994. Mangroves, hurricanes, and lightning strikes. Bioscience 44:256-262.

Solomon, A.M. 1986. Transient response of forests to CO_2 induced climate change: simulating modeling experiments in eastern North America. Oecologia 68:567-579.

Solomon, A.M., and H.H. Shugart. 1993. Vegetation dynamics in global climate change. Chapman and Hall, London, England, UK. 338 pp.

Steever, E.Z., R.S. Warren, and W.A. Niering. 1976. Tidal energy subsidy and standing crop production of *Spartina alterniflora*. Estuarine and Coastal Marine Science 4:473-478.

Stevenson, J., M. Kearney, and E. Pendleton. 1985. Sedimentation and erosion in a Chesapeake bay brackish marsh system. Marine Geology 67:213-235.

Stevenson, J., L. Ward, and M. Kearney. 1986. Vertical accretion in marshes with varying rates of sea-level rise. Pages 241-259 *in* D. Wolfe, editor. Estuarine variability. Academic Press, Orlando, Fla.

Stevenson, J.C., and N.M. Confer. 1978. Summary of available information on Chesapeake Bay submerged vegetation. U.S. Fish and Wildlife Service, Office of Biological Services, Washington, D.C. FWS/OBS-78/66. 335 pp.

Stoddart, D.R. 1963. Effects of Hurricane Hattie on the British Honduras Reefs and Cays, October 30-31, 1961. Atoll Research Bulletin 95:1-142.

Stout, J.P. 1990. Estuarine habitats. Pages 63-88 in NOAA Estuarine Programs Office, editors. Mobile Bay: issues, resources, status, and management. Mississippi-Alabama Sea Grant Consortium MASGP-89-023.

Streng, D.R. 1986. Patterns of seedfall and seedling establishment in an east Texas river floodplain forest: the contribution of seedling dynamics to species coexistence. Ph.D. dissertation, Rice University, Houston, Tex.

Streng, D.R., J.S. Glitzenstein, and P.A. Harcombe. 1989. Woody seedling dynamics in an east Texas floodplain forest. Ecological Monographs 59:177-204.

Stumpf, R. 1983. The process of sedimentation on the surface of a salt marsh. Estuarine, Coastal, and Shelf Science 17:495-508.

Ter Braak, C.J.F. 1987. CANOCO - a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis, and redundancy analysis (Version 2.1). Agriculture Mathematics Group, Wageningen, The Netherlands.

Ter Braak, C.J.F., and I.C. Prentice. 1988. A theory of gradient analysis. Pages 272-317 in M. Begon, A.H. Fitter, E.D. Ford, and A. Macfayden, editors. Advances in ecological research. Volume 18. Academic Press, San Diego, Calif.

Teskey, R.O., and T.M. Hinckley. 1977. Impact of water level changes on woody riparian and wetland communities. 6 volumes. U.S. Department of the Interior, U.S. Fish and Wildlife Service, Kearneysville, W.V.

Teuber, K. 1990. Use of AVHRR imagery for large-scale forest inventories. Forest Ecology and Management 33/34:621-631.

Tharp, B.C. 1926. Structure of Texas vegetation east of the 98th meridian. University of Texas Bulletin, Austin, Tex.

Tharp, B.C. 1939. The vegetation of Texas. Texas Academy Publications in Natural History, Nontechnical series. The Anson Jones Press, Houston, Tex. 74 pp.

Titus, J.G. 1988. Greenhouse effect, sea level rise and coastal wetlands. U.S. Environmental Protection Agency EPA-230-05-86-013. 152 pp.

Titus, J.G., and V.K. Narayanan. 1995. The probability of sea level rise. U. S. Environmental Protection Agency, Office of Policy, Planning, and Evaluation (2122), EPA 230-R-95-008, Washington, D.C. 186 pp.

Titus, J.G., R.A. Park, S.P. Leatherman, J.R. Weggel, M.S. Greene, P.W. Mausel, S. Brown, and C. Gaunt. 1991. Greenhouse effect and sea level rise: the cost of holding back the sea. Coastal Management 19:171-204.

Titus, J.E., and W.H. Stone. 1982. Photosynthetic response of two submersed macrophytes to dissolved inorganic carbon and pH. Limnology and Oceanography 27:151-160.

Twilley, R.R., and J.W. Barko. 1990. The growth of submerged macrophytes under experimental salinity and light conditions. Estuaries 13:311-321.

Urban, D.L., and H.H. Shugart. 1990. Appendix D: forest response to climatic change: a simulation study for southeastern forests. In J.B. Smith and D.A. Tirpak, editors. The potential effects of global climate change on the United States. U.S. Environmental Protection Agency. Hemisphere Publishing Corporation. New York, N.Y. 689 pp.

Vadstrup, M., and T.V. Madsen. 1995. Growth limitation of submerged aquatic macrophytes to inorganic carbon. Freshwater Biology 34:411-419.

Verhoeven, J.T.A., and W. van Vierssen. 1978. Distribution and structure of communities dominated by Ruppia, Zostera and Potamogeton species in the inland waters of "De Bol," Texel, The Netherlands. Estuarine Coastal and Marine Science 6:417-428.

Wanless, H. R., R.W. Parkinson, and L.P. Tedesco. 1994. Sea level control on stability of Everglades wetlands. Pages 199–222 in S.M. Davis and J.C. Odgen, editors. Everglades, the ecosystem and its restoration. St. Lucie Press, Delray Beach, Fla.

Ward, L.G., W.M. Kemp, and W.R. Boynton. 1984. The influence of waves and seagrass communities on suspended particulates in an estuarine embayment. Marine Geology 59:85-103.

Ware, S., C. Frost, and P.D. Doerr. 1993. Southern mixed hardwood forest: the former longleaf pine forest. In W.H. Martin, S.G. Boyce, and A.C. Echternacht. Biodiversity of the southeastern United States. John Wiley and Sons, New York, N.Y.

Waring, R.H., and W.H. Schlesinger. 1987. Forest ecosystems: concepts and management. Academic Press, New York, N.Y.

Watson, R.T., M.C. Zinyowera, and R.H. Moss, editors. 1996. Climate change 1995—impacts, adaptations and mitigation of climate change: scientific-technical analyses. Cambridge University Press, New York, N.Y. 880 pp.

Webb, T., III. 1986. Is vegetation in equilibrium with climate? How to interpret late-Quaternary pollen data. Vegetatio 67:75-91.

Weismiller, R., S. Kristof, D. Scholz, P. Anuta, and S. Momin. 1977. Change detection in coastal zone

environments. Photogrammetric Engineering and Remote Sensing 43:1533-1539.

Wessel, P., and W. Smith, 1991. Free software helps map and display data. EOS Transactions 72:441-448.

Wetzel, R.G. 1975. Limnology. W.B. Saunders Co., Philadelphia, Penn. 743 p.

Wetzel, R.G., and J.B. Grace. 1983. Aquatic plant communities. Pages 223-280 in E.R. Lemon, editor. CO_2 and plants: the response of plants to rising levels of atmospheric carbon dioxide. Westview Press, Boulder, Colo.

Wharton, C.H., W.M. Kitchens, E.C. Pendleton, and T.W. Sipe. 1982. The ecology of bottomland hardwood swamps of the Southeast: a community profile. U.S. Fish and Wildlife Service, FWS/OBS-81/37. 133 pp.

White, M.L., T. Maxwell, R. Costanza, and T.W. Doyle. 1991. Ecosystem modeling of Barataria Basin, Louisiana utilizing desktop parallel technology. Pages 225-234 in D. Dhamotharan and H.C. McWreath, editors. Water Management of River Systems and Symposium: Resource Development of the Lower Mississippi River, November 18-20, 1991, Bethesda, Md. American Water Resources Association, Washington D.C.

Wicker, A.M., and K.M. Endres. 1995. Relationship between waterfowl and American coot abundance with submersed macrophytic vegetation in Currituck Sound, North Carolina. Estuaries 18:428-431.

Wicker, K.M., D. Davis, M. DeRouen, and D. Roberts. 1981. Assessment of extent and impact of saltwater intrusion into the wetlands of Tangipohoa Parish, Louisiana. Coastal Environments, Inc., Baton Rouge, La.

Wilen, B. and W. Frayer. 1990. Status and trends of U.S. wetlands and deepwater habitats. Forest Ecology and Management 33/34:181-192.

Williams, S.L. 1990. Experimental studies of Caribbean seagrass bed development. Ecological Monographs 60:449-469.

Wolter, P.T., D.J. Mladenoff, G.E. Host, and T.R. Crow. 1995. Improved forest classification in the northern lake states using multi-temporal Landsat imagery. Photogrammetric Engineering and Remote Sensing 61(9):1129-1143.

Wunderle, J.M., D.J. Lodge, and R.B. Waide. 1992. Short-term effects of Hurricane Gilbert on terrestrial bird populations on Jamaica. The Auk 109:148-166.

Yanosky, T.M., C.R. Hupp, and C.T. Hackney. 1995. Chloride concentrations in growth rings of Taxodium distichum in a saltwater-intruded estuary. Ecological Applications 5:785-792.

Young, R.S. 1995. Coastal wetland dynamics in response to sea-level rise: transgression and erosion. Ph.D. dissertation, Duke University, Durham, N.C. 141 pp.

Zackrisson, O., M.C. Nilsson, I. Steijlen, and G. Hornberg. 1995. Regeneration pulses and climate-vegetation interactions in non-pyrogenic boreal Scots pine stands. Journal of Ecology 83:469-484.

Zedler, J.B., J. Covin, C. Nordby, P. Williams, and J. Boland. 1986. Catastrophic events reveal the dynamic nature of salt-marsh vegetation in southern California. Estuaries 9:75-80.

Zieman, J.C. 1982. The ecology of the seagrasses of south Florida: a community profile. U.S. Fish and Wildlife Service, Office of Biological Services, FWS/OBS-82/25. 158 pp.

Zieman, J.C., and R.T. Zieman. 1989. The ecology of the seagrass meadows of the west coast of Florida: a community profile. U.S. Fish and Wildlife Service Biological Report 85(7.25). 155 pp.

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As part of the USGCRP research framework on coastal lands and ecosystems, the Biological Resources Division of the U.S. Geological Survey (National Wetlands Research Center) entered into partnership with Rice University, Louisiana State University, Duke University, Clemson University, University of Southwestern Louisiana, University of Georgia, and the Virginia Institute of Marine Studies (University of Virginia) to (1) document the current state and vulnerability of coastal ecosystems including an assessment of past changes in land cover, (2) develop an understanding of the processes which underlie these changes, and (3) predict the extent of future alterations to these habitats and the consequences for the sustainability of the resource and land base. This document summarizes the initial findings of our collaborative efforts. Overall, the studies exemplify an integrated approach addressing questions at the species, community, and landscape levels of organization and focusing on factors related to hydroperiod, sea-level rise, disturbance events, and coastal marsh submergence.

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