

U.S. DEPARTMENT OF THE INTERIOR

U.S. GEOLOGICAL SURVEY

Sea-level Rise and Coastal Forests on the Gulf of Mexico



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INTRODUCTION AND OVERVIEW

Kimberlyn Williams, Zuleika S. Pinzon, Richard P. Stumpf, and Ellen A. Raabe

In this report, we review literature pertaining to the response of coastal forests on the Gulf of Mexico to sea-level rise. The report is divided into chapters that discuss effects of sea-level rise on non-mangrove forests, effects of sea-level rise on mangrove forests, and responses of Gulf coast trees to increased flooding and salinity. An assessment of the extent of coastal forest likely to be affected by sea-level rise in the near future is beyond the scope of this report.

Chapter 1 discusses sea-level effects on non-mangrove forests of the Gulf of Mexico including descriptions of how coastlines and, therefore, coastal forests have changed through the Holocene, a discussion of how coastal geomorphology and hydrology may affect interactions of coastal forest with sea-level rise, and an evaluation of the role that hurricanes might play in coastal forest retreat.

Literature on geological changes throughout the Holocene is not fully reviewed; sufficient information is given to place current rates of coastal forest retreat into historical perspective. Similarly, effects of hurricanes on coastal forests are not fully reviewed. Information that is pertinent to the role of hurricanes in coastal forest retreat and to the effects of hurricanes on the forest's interaction with sea level is presented. For more extensive reviews of hurricane effects on coastal forests of the Caribbean and the southeastern United States, the reader is referred to issues of BioScience (1994, Vol 44, no. 4), Biotropica (1991, "Special Issue: Ecosystem, Plant, and Animal Responses to Hurricanes in the Caribbean", Vol. 23, No. 4, Part A) and the Journal of Coastal Research (1991, "Impacts of Hurricane Hugo, Special Issue No. 8; and 1995, "Impacts of Hurricane Andrew on the Coastal Zones of Florida and Louisiana: 22-26 August 1992", Special Issue No. 21).

Selected pertinent information from Virginia, South and North Carolina has been included in this review, because much of our knowledge of coastal forest response to hurricanes, salinity and flooding comes from the Atlantic coast. These areas are floristically similar to the northern Gulf of Mexico. Species distribution of coastal forest trees and shrubs on the Gulf of Mexico are listed in Appendix 1.

Extensive research has been conducted on the responses of individual tree species to increased salinity and flooding. Synthesis of this research, although very important for evaluating effects of sea-level rise and various hydrological modifications on coastal forest, is beyond the scope of this review. These studies are included as an annotated bibliography (Appendix 2). Selected field studies on tree responses to changes in hydrology and salinity (impoundments, drainage, etc.) are referenced in Appendix 3.

A review of mangrove response to sea-level rise is included in Chapter 2. Mangrove forests are discussed in the context of Holocene changes in geomorphology. Predictions of the fate of

mangroves in the face of future sea-level rise, as well as a review of factors that affect interactions between mangroves and sea-level rise are discussed. Selected references from outside the United States are included, because much of our knowledge of how mangroves react to sea-level rise comes from other tropical areas of the world. A discussion of hurricane effects on the mangroves of south Florida highlights gaps in our knowledge of how hurricanes affect responses of mangrove vegetation to sea-level rise there. Mangrove responses to temperature and elevated CO₂ are briefly mentioned. These factors, as well as sea level, are expected to change in the future and may affect mangrove distribution.

Chapter 1

SEA-LEVEL RISE AND NON-MANGROVE FORESTS OF THE GULF OF MEXICO

Kimberlyn Williams

COASTAL FORESTS OF THE GULF OF MEXICO

Coastal forest composition around the Gulf of Mexico varies with substrate type, latitude (or temperature), longitude, and aridity. Forests exist on well drained sands (characteristic of the barrier islands and certain stretches of mainland coast), low-lying silty sediments of river deltas throughout the Gulf Coast, and low-lying limestone platforms in much of Florida. Terrell (1979) divided the coastline of the Gulf of Mexico into ten regions with different geomorphic and hydrologic characteristics (Figure 1, Table 1). These characteristics affect both the species composition of forests adjacent to the coast and their interaction with sea-level rise.

Bottomland hardwood forests and swamp forests exist at the mouths of most rivers around the Gulf (Figure 1). Swamp forests, dominated by baldcypress (*Taxodium distichum*) and often water tupelo (*Nyssa aquatica*), occur in frequently flooded areas of floodplains. Bottomland hardwood forests (dominated by a variety of species, Appendix 1) occur in the drier, less frequently flooded areas. Due to the aridity of Texas, bottomland forests are generally restricted to narrow floodplains; swamp forests occur only to a minor extent in floodplains of northern coastal Texas (Shew et al. 1981). Swamp forests reach their greatest development in the Mississippi Delta and in south Florida, west of the Everglades. Bottomland hardwood forests are generally similar in composition throughout the Gulf, with minor variations (Appendix 1). Most notably, palms (*Sabal palmetto*, in Florida, and *Sabal texana* at the mouth of the Rio Grande) and other tropical tree species become important components of wetland coastal forests at low latitudes. Additionally, bottomland forests east and west of the Mississippi River may differ somewhat in composition: the Mississippi marks the eastern or western limit of distribution of several tree species (Appendix 1). Hydric hammocks, wetland hardwood forests in Florida that are in still-water wetlands, rather than riverine systems (Vince et al. 1989), share many species with the bottomland hardwood forests.

Sandy ridges near the coast (forested barrier islands, the Ingleside strand in Texas, cheniers of the Chenier plain, sandy shorelines of north and central Florida) generally support live oak (*Quercus virginiana*). In eastern Texas, live oak may be accompanied by mesquite (*Prosopis* sp.) and saltcedar (*Tamarix gallica*) (Shew et al. 1981). To the east of the Mississippi River, coastal sandy ridges may also be dominated by sand live oak (*Quercus geminata*), myrtle oak (*Quercus myrtifolia*), sand pine (*Pinus clausa*), and slash pine (*Pinus elliottii*). Cabbage palm (*Sabal palmetto*), saw palmetto (*Serenoa repens*), rosemary (*Ceratiola ericoides*), and wax myrtle (*Myrica cerifera*) may also be important in these areas (Johnson and Barbour 1990). Portions of barrier

islands that are low in elevation, and barrier islands of the south Texas coast (Shew et al. 1981) are generally not forested.

Where a shallow limestone platform supports coastal forest in a nonestuarine environment, the forest may be pine flatwoods or a coastal hardwood hammock. The flatwoods are dominated by slash pine (*Pinus elliottii*), loblolly pine (*Pinus taeda*), longleaf pine (*Pinus palustris*) and/or pond pine (*Pinus serotina*), and often contain an understory of saw palmetto (*Serenoa repens*) (Abrahamson and Hartnett 1990). Live oak (*Quercus virginiana*), southern red cedar (*Juniperus virginiana* var. *silicicola*), and cabbage palm (*Sabal palmetto*) often dominate the coastal fringes of hardwood hammock (Vince et al. 1989). These systems dominate the Big Bend region of Florida (Figure 1). Forest stands on the coastal margin may exist as isolated stands on topographic highs surrounded by salt marsh. These elevated areas may be highs in the underlying limestone platform or old Indian middens.

Upland vegetation changes drastically between the Rio Grande and Florida. In south Texas, forests are confined to river bottoms, while the uplands are dominated by grassland and chaparral (Figure 1). Grasslands and forests occur in upland areas in western Louisiana. The coastal prairies of Texas and Louisiana have been heavily converted to agricultural use (Brown et al. 1976, 1977, 1980; McGowen et al. 1976a, b). East of the Mississippi River, the uplands are forested with various mixtures of pine, oak, and other southern hardwoods (Küchler 1965).

Mangrove forests gradually replace salt marsh from central Florida southward (Davis 1940, Figure 1), and from the southern tip of Texas southward. Isolated stands of mangrove occur sporadically along the Gulf of Mexico (Little 1976).

Coastline characteristics, and consequently coastal forest characteristics, have been shaped by changing sea-levels and variation in sediment supply. Sea level has fluctuated greatly in the past, resulting in sea-level stands much higher and much lower than present (Haq et al. 1987). Low sea-level stands left beaches, platforms, and terraces behind, partially shaping the uplands into which seas are currently rising. Flat, lowlying limestone platforms formed under shallow seas, support coastal forest over much of Florida (Schomer and Drew 1982, Hine and Belknap 1986, and references therein). The Ingleside barrier strand-plain in Texas, a sandy ridge that supports oak forest near the coast, was a Pleistocene barrier island (Shepard and Moore 1960). The cheniers, sandy ridges that support live oak forest in the marshes of western Louisiana's Chenier Plain, are old barrier islands, river mouth accretions, and recessional beach ridges (Gosselink et al. 1979).

Features left by higher seas at inland locations promise to affect coastal forest fates in the future. Sandy flanks of the Brooksville range, lying just 10 km east of the presently marshy shoreline in central Florida, were coastal deposits at a higher sea stand (White 1970). Hine and

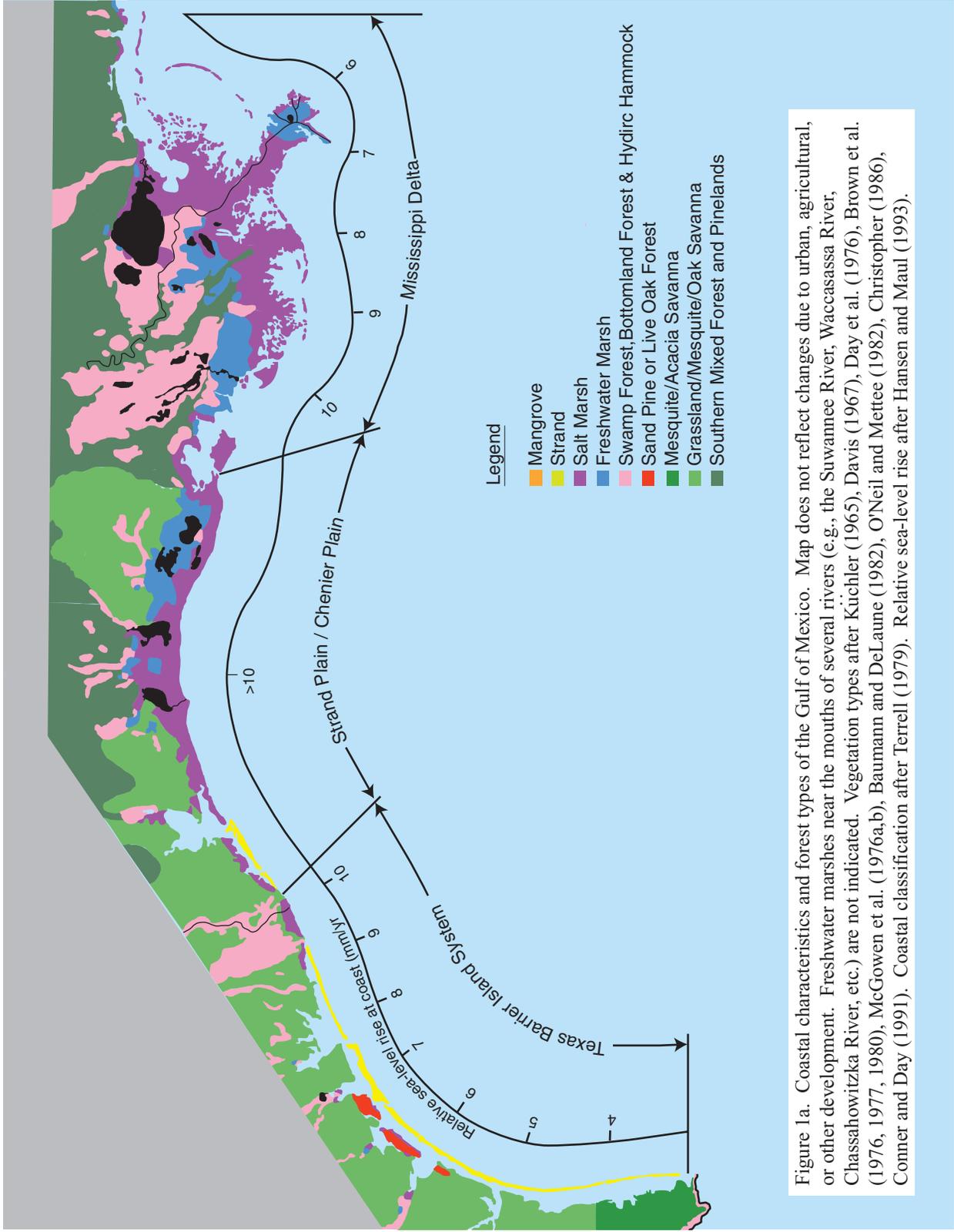


Figure 1a. Coastal characteristics and forest types of the Gulf of Mexico. Map does not reflect changes due to urban, agricultural, or other development. Freshwater marshes near the mouths of several rivers (e.g., the Suwannee River, Waccasassa River, Chassahowitzka River, etc.) are not indicated. Vegetation types after Küchler (1965), Davis (1967), Day et al. (1976), Brown et al. (1976, 1977, 1980), McGowen et al. (1976a,b), Baumann and DeLaune (1982), O'Neil and Mettee (1982), Christopher (1986), Conner and Day (1991). Coastal classification after Terrell (1979). Relative sea-level rise after Hansen and Maul (1993).

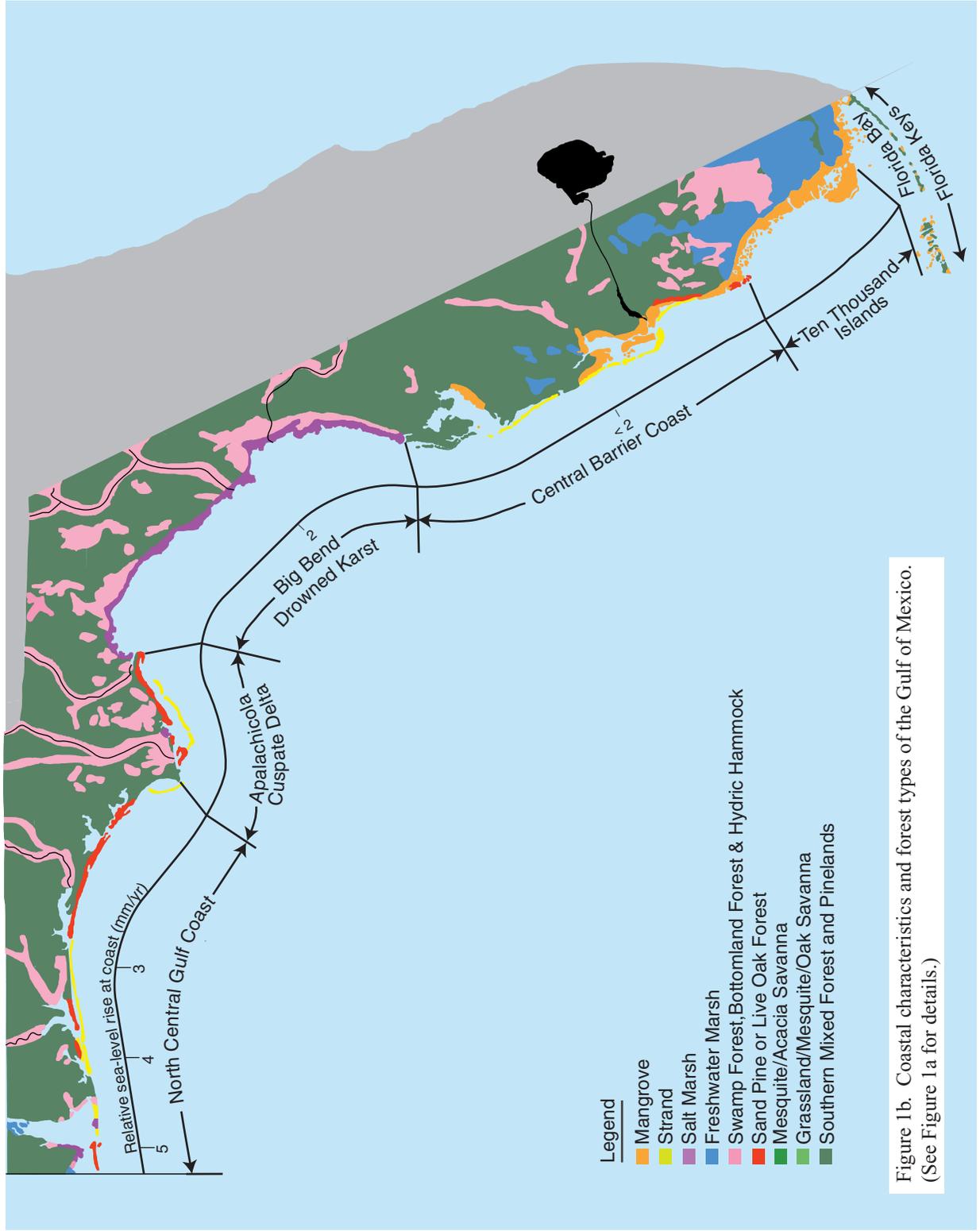


Figure 1b. Coastal characteristics and forest types of the Gulf of Mexico. (See Figure 1a for details.)

Table 1. Classification of Gulf Coast regions from Terrell (1979).
See Figure 1 for locations.

Texas Barrier Island System	Extensive lagoon system formed by drowned river mouths and barrier islands, freshwater inflow regular on upper coast to limited with hypersaline condition on lower coast, marshes common along upper coast, submerged grass beds common along lower coast, barrier islands of sand.
Strandplain-Chenier Plain	Extensive marsh system, freshwater inflow from several small river systems, but lacking direct influence from Mississippi; cheniers present.
Mississippi Delta	Extensive marsh systems, barrier island system, sediments silty, silt terrigenous, water turbid, very extensive shallows area, extensive influence from Mississippi River.
North-central Gulf Coast	White sand beaches, clear water, extensive dune system, and barrier island system. High-energy beaches compared to others of the Gulf Coast.
Apalachicola Cuspate Delta	Smooth sand beaches, mud-bottomed bays, turbid water, barrier islands present, little or no seagrass.
Big Bend Drowned Karst	Rugged shoreline, rocky bottoms, very wide shallows area, clear water, extensive seagrass beds and marshes, high fish production, extensive oyster bars.
Central Barrier Coast	Sandy beaches with a few rocky areas, extensive marshy and swampy areas present, narrow shallows area; <i>Juncus</i> , <i>Spartina</i> , or mangroves characteristic, depending on latitude.
Ten Thousand Islands	Coastline dominated by a multitude of small mangrove islands and tidal channels, extremely complex, direct marine action on the coast.
Florida Bay	Coastline part of Everglades National Park, area of numerous mangrove-covered islands and very extensive swamps covering the entire southern tip of Florida. Marine influence from Gulf of Mexico, but area is fairly protected.
Florida Keys	Low limestone islands with pinnacle rock coasts or very narrow shell beaches bordered with mangroves, extensive shallow areas with soft marl or shell fragment bottoms extending out to coral reefs, very extensive seagrass and algal beds.

Belknap (1986) point out that when sea-level reaches this point, the entire character of the coastline will change from the present, low marsh (and low-elevation forest) coastline, to one characterized by eroding sandy bluffs, resembling that found west of the Apalachicola River Delta today.

COASTAL FOREST CHANGE DURING THE HOLOCENE

Sea-level at the height of the last ice age (ca. 20,000 years BP) is estimated to have been 90 - 130 m lower than at present (Chappell and Shackleton 1986, Fairbanks 1989), exposing a large expanse of coastal plain that is currently submerged. Based on the bathymetry of the shallow coastal shelf of the Gulf of Mexico, this shoreline would have lain 150-250 km gulfward of the modern Florida coast, and 60-80 km gulfward of the modern Texas coast (McGowan 1976a, Figure 2). Due to alteration by currents, the submerged shorelines are more difficult to map than those left by high sea stands (Webb 1990).

Data on the vegetation of this former coastline during the last glacial maximum are limited. Delcourt and Delcourt (1981, 1987) have carried out extensive stratigraphic analyses, based on 162 fossil pollen sites in North America, detailing the dynamics of forests between the height of the last ice age, approximately 20,000 years ago and the present. These records indicate that southeastern evergreen forest has dominated fossil pollen sites in Gulf states east of Texas since approximately 10,000 years B.P. This forest is generally similar to that which exists along much of the Gulf of Mexico today, and includes southern pine species, oak, tupelo (*Nyssa* spp.), baldcypress (*Taxodium distichum*), and sweetgum (*Liquidambar styraciflua*). During the full glacial and late glacial (ca. 20,000 - 14,000 years B.P.), northern species, notably spruce (*Picea* sp.), achieved dominance as far south as 31° N in southern Louisiana and Mississippi (Delcourt and Delcourt 1996), but warm temperate taxa such as *Liquidambar* and *Nyssa* still appear in the full- to late-glacial strata dominated by spruce. Deposits prior to 38,000 year B.P., and presumably Sangamonian or Altonian in age, lack spruce and again reflect dominance by pine/oak forests with hickory, beech, hornbeam (*Ostrya* and/or *Carpinus*), and warm-temperate taxa of *Liquidambar styraciflua*, *Nyssa* sp., and *Leitneria floridana* (Florida corkwood) (Delcourt and Delcourt 1996).

We have little palynological data on forest composition along the Gulf coast during the last glacial, because that coastline is currently submerged, and because erosion of coastal sediments during sea-level rise has largely eliminated stratigraphic records (Hine et al. 1988). Fossil pollen sites used by Delcourt and Delcourt (1987) in Texas, are fairly distant from the current coastline (near Austin), and even more distant from the former coastline. Sites in Florida are much closer to the current coastline, and while evidence exists for the presence of xeric, sand dune scrub vegetation there during the height of the last glacial (Watts 1975), Delcourt and Delcourt (1987) consider evidence tentative, due largely to major gaps in the pollen record. Moreover, because of

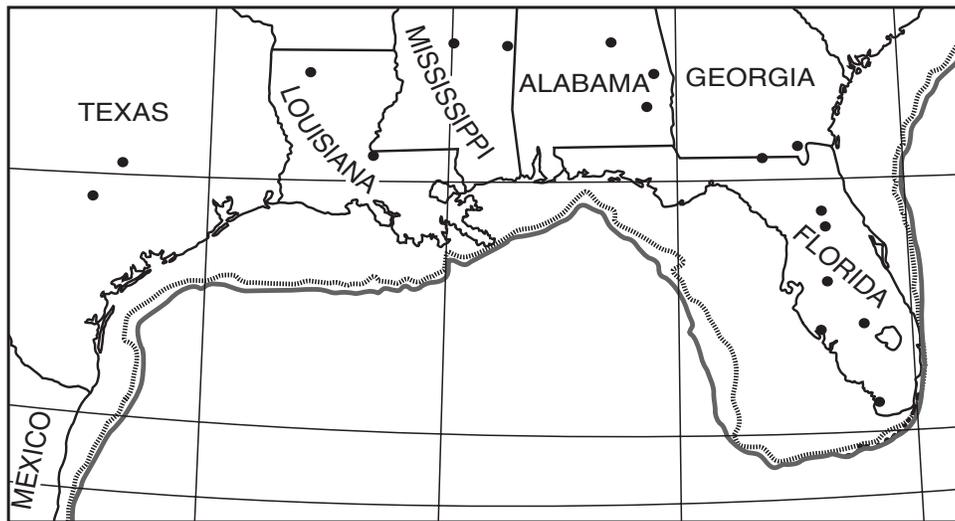


Figure 2. Current coastline of the Gulf of Mexico and isobaths at 100 m and 200 m. Dots indicate fossil pollen sites used by Delcourt and Delcourt (1987) in reconstructing forest change in North America.

changes in the coastline, xeric dune vegetation at currently coastal sites reflect what would have been inland, upland vegetation at the height of the interglacial. Delcourt and Delcourt (1987) state that “to date, no definitive paleoecological evidence is available to document the full-glacial locations of coastal warm-temperate or subtropical swamps in eastern North America”. Such swamps are currently common in many of the floodplains of the Gulf coast and in low-lying areas west of Florida’s Everglades.

Forests that more recently occupied coastal marsh in the southern United States were generally similar in composition to the current coastal forest. As early as the 1700’s, William Bartram recognized coastal forest conversion to salt marsh and, writing of islands off the Georgia coast, stated that “it seems evident, even to demonstration, that those salt marshes adjoining the coast of the main, and the reedy and grassy islands and marshes in the rivers, which are now overflowed at every tide, were formerly high swamps of firm land, affording forests of Cypress, Tupilo, Magnolia grandiflora, Oak, Ash, Sweet Bay, and other timber trees, the same as are now growing on the river swamps, whose surface is two feet or more above the spring tides that flow at this day; and it is plainly to be seen, by every planter along the coast of Carolina, Georgia, and Florida, to the Mississippi, when they bank in these grassy tide marshes for cultivation, that they cannot sink their drains above three or four feet below the surface, before they come to strata of

Cypress stumps and other trees, as close together as they now grow in the swamps.” (Bartram, 1792, pp. 66-67). At St. Marks Wildlife Refuge, in the Florida panhandle, Kurz and Wagner (1957) found preserved live oak roots in mud flats 225 feet gulfward from the barrier beaches that then supported scrubby live oak. Early workers, such as Bartram, attributed these vegetation changes to coastal subsidence, rather than sea-level rise. Only later was the importance of both factors recognized (Gehrels and Leatherman 1989).

Sea level rose rapidly after the end of the last ice age (ca. 0.25 cm/yr) until approximately 4,000 years ago, when rates appeared to slow dramatically to a mean rate of 0.04 cm/yr (Shepard 1960a, Digerfeldt and Hendry 1987, Wanless 1989, Hendry 1993 and references therein, Wanless et al. 1994). Estimates of eustatic sea-level rise over the past century are higher. Davis and Mitrovica (1996) estimated recent eustatic sea-level rise at 0.14 - 0.17 cm/yr, whereas Warrick et al. (1995) allowed greater uncertainty (0.18 cm/yr with a range of 0.10 - 0.25 cm/yr). Due to subsidence, coastlines along the northwestern Gulf of Mexico (primarily Louisiana and east Texas) are experiencing dramatically higher rates of relative sea-level rise (Penland and Ramsey 1990, Turner 1991, Hanson and Maul 1993, Figure 1).

The slowing of sea-level rise at approximately 4,000 years B.P. significantly influenced hydrology, geomorphology and, consequently, the modern distribution of coastal forests on the Gulf of Mexico. Many of the barrier islands around the Gulf began to form near their present position at this time. Most of the higher islands support forest, especially those east of Texas. Even treeless barrier islands influence mainland coastal forests through their effects on waves, tides and estuarine salinity. There are indications that some swamp forests expanded near the current coastline in north Florida, and mangroves expanded in south Florida beginning ca. 4,000 years B.P.

Although some barrier islands on the Gulf of Mexico have core areas formed by Pleistocene highs (e.g., Dauphin Island, Alabama; Otvos 1985), some coastal islands represent relict Pleistocene dunes (Hine and Belknap 1986), and some have formed recently (e.g., as a result of delta abandonment and subsidence in the Mississippi Delta; Penland et al. 1985), most current barrier islands around the Gulf coast began to grow ca. 3,000-4,000 years B.P. (Shepard and Moore 1960, Shew et al. 1981 and references therein, Davis and Kuhn 1985, Evans et al. 1985, Stapor et al. 1991). Over most of the Gulf coast, islands formed as sand deposits accumulated on shallow platforms, around Pleistocene highs, or in deltaic deposits detached from the mainland (e.g., Davis and Kuhn 1985, Otvos 1985). Barrier islands are not static. Some have moved seaward, some coastward, and some have remained stationary in historical times (Shepard 1960b). Louisiana has lost a large fraction of its barrier system over the past century (Penland and Boyd 1982, McBride et al. 1993), and although some barrier islands are prograding, the general trend in barrier systems around the Gulf of Mexico today is considered erosional (Dolan et al. 1988, Hendry 1993).

In south Florida, the slowed rate of sea-level rise allowed reefs and oyster bars to build. In the Ten Thousand Islands region of south Florida, Parkinson (1989) dated the base of the vermetid reefs that underlie the gulfward islands to 3,390 years B.P. Oyster bars that form the base of interior islands were dated to 1,800 years B.P. Parkinson (1989) suggested that the vermetid reef buildup promoted oyster buildup in inshore waters by reducing salinity. Both oyster bars and vermetid reefs became colonized by mangroves, accumulated sand deposits and were colonized locally by other terrestrial vegetation. On the mainland, Parkinson (1989) found red mangrove peat beginning ca. 3,500 years B.P. over Pleistocene sands. Thus, he found evidence for mangrove expansion both inland, as mangrove peat buildup kept pace with sea-level rise, and gulfward, as reef-building kept pace with (or outpaced) sea-level rise and gave rise to mangrove-dominated islands. Notes of continuing colonization of oyster bars by mangrove on the west coast of Florida (Alexander and Crook 1974), suggest that this expansion has continued, at least into the latter half of the 20th century. Marl levees and mangroves near Cape Sable at the southern tip of Florida accreted and prograded seaward after 3,200 yrs B.P., and only on the sediment-starved southeastern tip of Florida (southwestern Biscayne Bay and northeastern Florida Bay) did mangrove-dominated shorelines continue to retreat (Wanless et al. 1994).

Freshwater swamp forests may have also expanded after sea-level rise slowed 4,000 years B.P. Such swamp forests, often dominated by cypress and tupelo, are common near the mouths of rivers, often just landward of tidal freshwater marsh (Odum and Smith 1981). Beginning ca. 4,000 years ago, the slowing of sea-level rise allowed progradation of several river deltas around the Gulf of Mexico that currently support coastal forest (primarily swamp forest).

Swamp and bottomland forest near the Apalachicola River of North Florida occupy a delta that appears to have expanded since 4,000 years B.P. Archaeological evidence suggests that much of the current Apalachicola River delta was open water and uninhabitable prior to 4,000 year B.P. (Donoghue and White 1995). The delta has prograded 16 km coastward since then, due in part to a shift in the position of deltaic deposition and to slowing of sea-level rise (Donoghue and White 1995). Land formed since 4,000 years B.P. currently supports a combination of swamp and mixed hardwood forest and, on the coastal fringe, sand pine scrub (Figure 3, Edmiston and Tuck 1987, Wolfe et al. 1988).

The Mississippi Delta has also prograded since sea-level rise slowed ca. 4,000 years ago by depositing sediment in a series of imbricating deltas. During active deposition, delta lobes have prograded as much as 120 km seaward and the delta surface has aggraded to as much as 5 m above sea level (Penland and Boyd 1982). The oldest of the overlapping deltas that comprise the Mississippi delta began to develop ca. 3,800 years ago (Fisk et al. 1954). Scruton (1960) considered the shoreline at this time to lie near the current surface contact of the recent deltaic sediments and the Pleistocene Prairie Terrace (Figure 4). This contact is close to 5 feet (1.5 m)

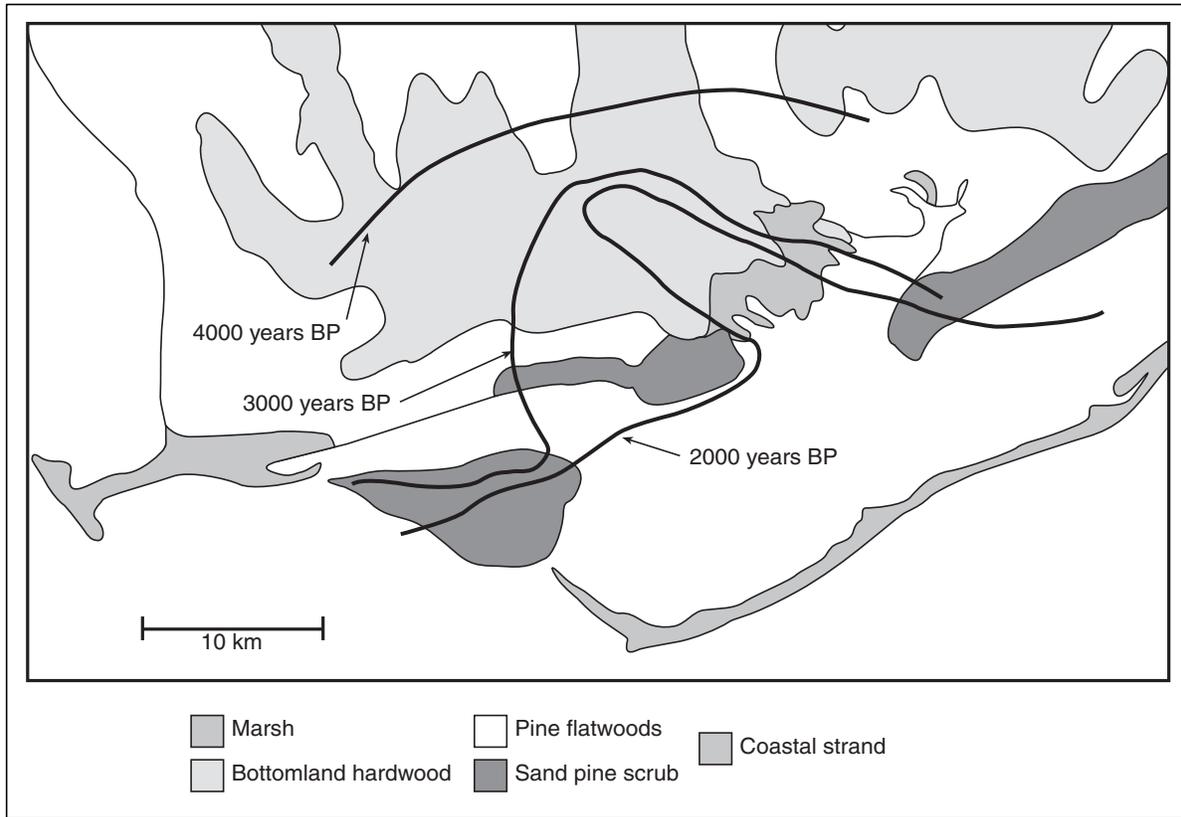


Figure 3. Past coastlines and recent natural vegetation of the Apalachicola delta. Past coastlines were estimated from maximum dates of human occupation at archaeological sites in the area (Donoghue and White 1995). General vegetation map after Davis (1967) and Christopher (1986). Areas cleared in ranch and timber operations (Livingston 1984) are not shown.

above sea level (Craig et al. 1979). Examination of underlying deposits, however, suggest that this shoreline lay at New Orleans (McFarlan 1961, Gould 1970). The land formed since that time supports marsh (saline, brackish and freshwater), swamp forest (primarily cypress and tupelo), and levee forests supporting live oak (Gould 1970). Not only do these recent deposits near the ocean support swamp forest, but cypress-tupelo forest in the northern Gulf states are now concentrated on these recent deposits (McWilliams and Rosson 1990, Figure 4). Such a concentration suggests that the slowing of sea-level rise ca. 4,000 years B.P., with consequent delta building, allowed expansion of cypress-tupelo forests in this region.

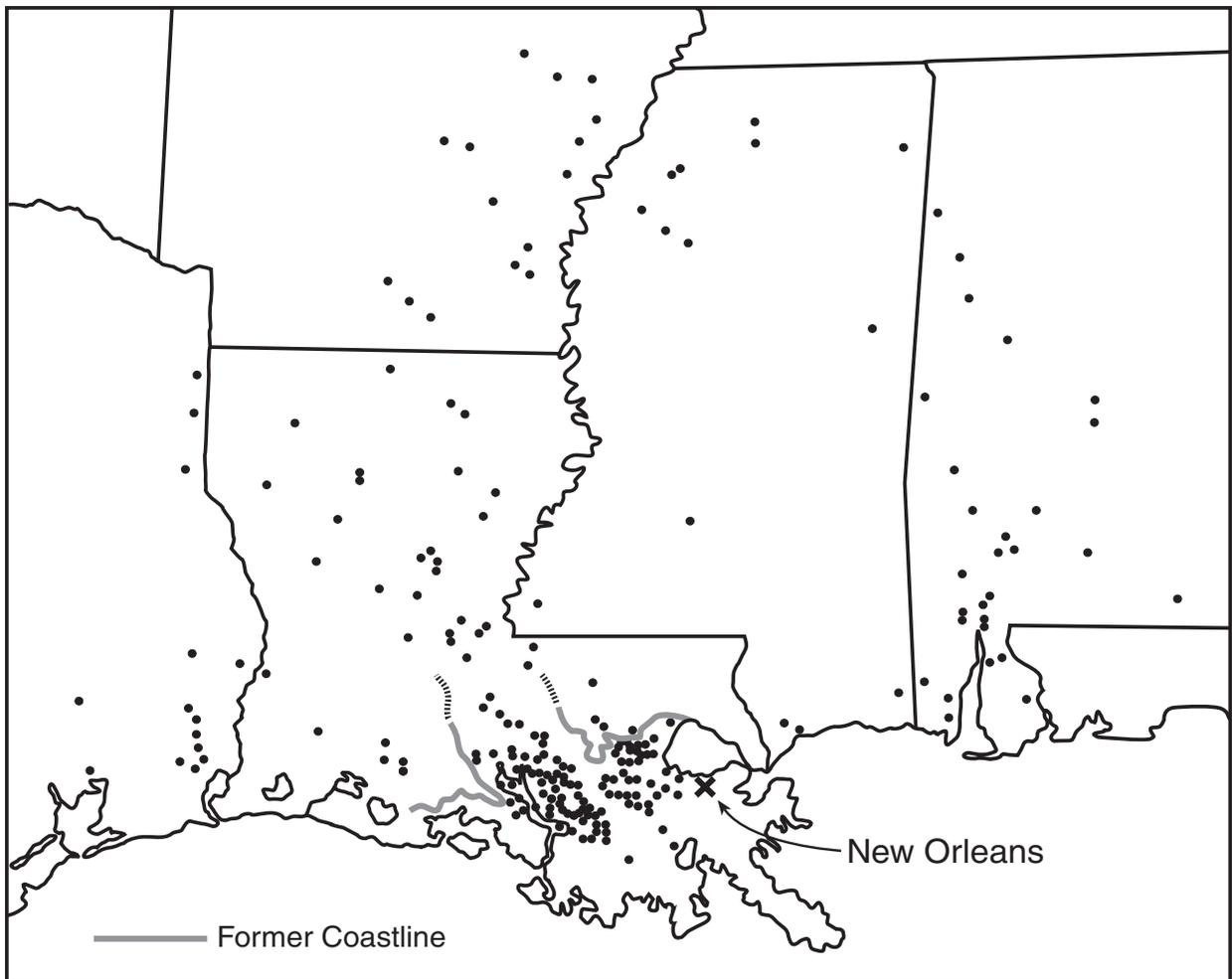


Figure 4. Cypress/tupelo distribution in the northern Gulf states. Dots represent the long-term forest inventory plots of the U.S. Forest Service that are classified as cypress-tupelo (after McWilliams and Rosson 1990; Vissage et al. 1992). Data were from plots laid out on a 4.8 km grid throughout the region. The contact between Pleistocene deposits and recent alluvial and deltaic deposits in the Mississippi Delta is shown (after Scruton 1960; Gould 1970).

Several rivers, whose valleys flooded with sea water as sea level rose, have partially refilled their river valleys with sediment since sea level rise slowed ca. 4,000 years B.P. These valleys typically support bottomland forest, and the bottom reaches may support more cypress-tupelo than other forest types (see section on “Forest change and retreat in estuarine floodplains”). Delta building by the Brazos River, Colorado River, and Rio Grande in Texas have eliminated lagoons that existed behind barrier islands in their vicinity (Shepard and Moore 1960). The Brazos and Colorado Rivers have the largest continuous floodplain habitat along the coast of Texas (Shew

et al. 1981), and although the floodplain of the Rio Grande is not large, due to the aridity in south Texas, that floodplain supports the only large trees in the region (Shew et al. 1981). Such coastal floodplain expansion, while promoted by relatively stable sea level and the development of protective barrier systems (a development which is, itself, often attributed to a slowing in sea-level rise), requires adequate riverine water and sediment supplies. Baffin Bay, 160 km north of the Rio Grande, represents a drowned valley of rivers carrying little sediment; it supports little floodplain forest (Shew et al. 1981). Rivers of peninsular Florida carry little sediment, and support very narrow bands of riverine swamp forest (Wharton et al. 1977). The extensive wetland forests in Florida are attributable instead to flat antecedent geology and topography.

As rapid sea-level rise drowned forests on former coastlines, swamp forest peats were often left below newer marsh and estuarine deposits (e.g., Nelson and Bray 1970, Goodbred et al. 1998), and forest peats were left under beach sand (e.g., Wells 1942). Swamp forest peat deposits have been used as an indicator of sea-level in coastal stratigraphy, based on their position above deltaic deposits and below estuarine deposits (Nelson and Bray 1970). Peat thickness has occasionally been linked to ocean still-stands. Nelson and Bray (1970) attributed a peat deposit in the drowned Sabine River channel to an ocean still-stand occurring ca. 10,200 year B.P. Goodbred et al. (1998) attributed the development of swamp forest peat near the mouth of the Waccasassa River on the west coast of peninsular Florida, to the slowing of sea-level rise at ca. 4,000 years B.P. Under salt marsh in this estuary, they found swamp forest peats resting on Pleistocene deposits, and dated the oldest forest peat deposits to ca. 4,400 years B.P. They calculated that at this time, sea level was approximately 1 m below these sediments, presumably supporting a fresh water lens that flooded the lower river basin and promoted a transition from upland forest to swamp forest with accreting peat deposits. Whether expansion of swamp forest accompanied this period of peat accretion, or whether the period of accretion simply reflected a period of vegetation stability is unclear.

Although the slowing of sea-level rise at ca. 4,000 year B.P. appeared to be associated with the expansion of some coastal wetland forests, most researchers suggest that sea-level rise has not been monotonic since that time. Drops and rapid rises in sea-level may have affected the dynamics of coastal forest expansion and retreat. Around the Apalachicola Bay, evidence of human habitation alternates with strata of estuarine muds, suggesting fluctuations in sea-level with associated movements in the position of the habitable edge (Donoghue and White 1995). Rapid replacement of swamp forest by marsh in Waccasassa Bay on the west coast of Florida at approximately 1,800 years B.P. (Goodbred et al. 1998) coincides with a rise in sea-level between 2,100 years B.P. and 1,800 years B.P. identified by Tanner (1991) and Stapor et al. (1991; see below). These events also coincide with the drowning of tidal marshes in Delaware ca. 2,000 years B.P. (John and Pizzuto 1995). Thus, the dynamics of sea-level rise, allowing accretion of peats and deltaic sediments at low rates of rise and overrunning such processes at high rates of

rise, appear to be important in the fate of coastal wetland forest, both mangrove and freshwater swamp forest.

Whether sea level has risen and fallen repeatedly during the past several thousand years is debated (e.g., Otvos 1995, Donoghue et al. 1998). Scholl et al. (1969) dated peats in southwest Florida and obtained a record suggesting a fairly smooth rise in sea level over the past 7,000 years (at least on the 100-1,000 year scale). Several researchers, however, (e.g., Holmes and Trickey 1974, Fairbridge 1974, Stapor et al. 1991, Tanner 1991, 1992) give evidence for cycles of rising and falling seas that have occurred with a periodicity of ca. 1,000 yrs. Stapor et al. (1991), dating shells in beach ridges of sandy barrier islands near Charlotte Harbor, southwest Florida, found that ridges were deposited during discrete periods. They interpreted patterns they observed as effects of periodic rises in sea level with intervening drops. Rises occurred at ca. 2,000 yrs B.P., 1,100 yrs B.P., and 150 yrs B.P. (the current rise), with intervening periods of lowered sea-level. Tanner (1991, 1992) performed grainsize analysis of beach ridges on St. Vincent Island off the Panhandle of Florida, examined the timing of formation of different subdeltas of the Mississippi delta, and examined Gould and McFarland's (1959) dating of cheniers of southwest Louisiana. He found commonalities in dates from the three lines of evidence that suggested four rises in sea-level since ca. 3000 yrs B.P. with probable intervening drops. Fairbridge (1974) suggested that there have been 5.5 cycles of submergence and emergence since 6,000 yr B.P., and other researchers, dating submerged barrier spits and beach deposits, gave evidence for earlier Holocene sea-level fluctuations (Curry 1960, Locker et al. 1996). Kidson (1982) noted that alternating strata of marine and terrestrial sediments in coastal sites may simply indicate changes in rates of sea-level rise, rather than rises and drops. During periods of slow rise sediment accretion may outpace sea-level rise, and during periods of rapid rates terrestrial sediments are drowned. In either case, coastal forest retreat in low-lying areas may be sporadic and associated with periods of relatively rapid sea-level rise.

SEA-LEVEL RISE AND RECENT COASTAL FOREST CHANGE: SHIFTS IN VEGETATION ZONES

In addition to stratigraphic records of forest peat below salt marsh, frequent observations of dead stands of trees in salt marsh, on beaches, and in open water have yielded evidence of more recent conversions of forest to marsh and/or unvegetated beach and ocean. Sir Charles Lyell interpreted the presence of cypress and pine stumps in salt marshes of Georgia as evidence of "a change in the relative level of land and sea" (Lyell, 1849 p. 249). Penfound and O'Neill (1934) described evidence of vegetation changes on Cat Island, a sandy barrier island off the coast of

Mississippi. On the gulfward, eroding shore they noted that “ghost forests of pine and oak extend more than a hundred feet into the gulf, and black, peaty soil, which could have been formed only in the marshes, is a conspicuous feature of the lower beach”. Oak stumps in salt marsh near shell mounds of the Mississippi delta in Louisiana were interpreted as evidence of subsidence by Brown (1936). Dying trees at the marsh/forest border were noted in 1957 on the Atlantic coast of Florida near the Georgia border (Nassau County) and interpreted as victims of sea-level rise (Kurz and Wagner 1957). Dying cabbage palms on the west coast of peninsular Florida, 5 km NW of Yankeetown, Florida, near Waccasassa Bay, were attributed by Vernon (1951) to a “drowning of coastal margins”.

Likewise, indications of recent expansion of South Florida mangroves into other forest types have been interpreted as indications of sea-level rise or a combination of sea-level rise and human-induced saltwater intrusion. Alexander and Crook (1974) considered the presence of dead pine stems in mangrove swamps on Key Largo, Florida, evidence of recent sea-level rise. They found stumps of cabbage palms (*Sabal palmetto*) throughout mangrove fringe forest and on inland mangrove-dominated tree islands, and noted that cypress stands in the Loxahatchee River estuary, further north on the east coast of Florida, had been invaded by mangrove. Because the pines in mangrove stands on Key Largo appeared to have died after 1900 but before much human alteration of the hydrology in the area took place, they attributed the vegetation change there to recent sea-level rise. The mangrove areas of the mainland had experienced severe reductions in freshwater supplies as a result of water diversions and groundwater pumping, and the authors speculated that the vegetation changes observed there were due to a combination of sea-level rise and saltwater intrusion resulting from human activities. Craighead (1974) attributed the presence of dead pines in Mahogany Hammock and coastal areas of Collier County (southwest Florida) to a combination of rising seas and “recent salt water intrusions while there was no fresh water buffer in the glades”.

EFFECT OF HYDROLOGIC AND GEOMORPHOLOGIC CHARACTERISTICS OF THE COAST ON RATES, PATTERNS, AND MECHANISMS OF FOREST RETREAT

The effects of sea-level rise on coastlines vary as geomorphological and hydrological characteristics vary. Davis (1997) summarized variation in shoreline dynamics along the United States coast of the Gulf of Mexico, noting both physical and anthropogenic influences. In analyzing effects of sea-level rise on coastlines, Bird (1993) recognized several categories of shorelines: steep and cliffed coasts, beach-fringed coasts, deltaic coasts, swampy coasts, estuaries and coastal lagoons, intertidal and nearshore areas, coral reefs and reef islands and artificial (man-made) coasts. Similarly, Gornitz (1991) recognized 18 coastal landforms in assessing risk from

sea-level rise, and French et al. (1995) classified coasts as either clastic (sandy beach and barrier systems) or bio-geomorphic (vegetated dunes and coastal wetlands) for the purpose of describing and predicting effects of sea-level rise. For simplicity, we will recognize only 3-4 types of coasts (Figure 5) in discussing effects of rising seas on coastal forest. These include marshy coasts near high freshwater outflows, marshy coasts without high freshwater supplies, and sandy coasts, typically characterized by beaches and dunes.

Sea-level rise may kill forest species at the coastal forest margin through increases in soil salinity, increases in hydroperiod, or through coastal erosion. The relative importance of these factors varies as coastal hydrology and geomorphic characteristics vary along the Gulf coast. In general, freshwater supply and nature of the substrate (primarily, whether forest abuts marsh or sand dune/beach) determine the pattern of forest change and the relative importance of salinity, flooding and erosion in causing that retreat (Figure 5, 6). Coastal topography (steep vs. gradual slopes) affects the lateral rate of forest retreat (m/yr), condenses vegetation zones and may affect fresh groundwater supply to the forest margin (Hmielski 1994, Brinson et al. 1995). Near large estuaries, coastal forest often abuts tidal freshwater marsh (e.g., Doumlele et al. 1985, Hackney and Yelverton 1990, Figure 1, Figure 5a). It may be inferred that sea-level rise has caused forest retreat primarily through its effect on the the flooding regime in these areas, because the conversion of forest to freshwater marsh is generally associated with increased hydroperiod (e.g., Wells 1942), rather than increased salinity. Farther from large estuaries on marshy coasts, the freshwater supply is less and forest abuts salt marsh (Figure 5b). In these areas forest retreat appears to be linked to increasing salt exposure, rather than increased flooding (Ish-Shalom et al. 1992, Ross et al. 1994, Williams et al. 1999). Both near estuaries and farther from them on marshy coasts, the forest edge often exists in zones influenced by high tides. However, hydroperiod and salinity at the forest/marsh boundary varies. Where the coastal forest edge is on a sandy beach or in a dune environment, forest retreat is usually attributed to erosion of the sandy substrate or burial by sand (Figure 5c,d), although damage by salt spray and flooding during storm surges are also frequently invoked (see section on “Forest change and retreat on sandy shorelines”). Often, barrier beaches and barrier islands supporting forest occur seaward of marshes which front another forest edge. In these areas, erosion may dominate forest decline on the barrier beach, while increased flooding or salinity may force forest retreat behind the barrier beach and intervening marsh (Figure 6).

While the relationships outlined above are useful for a general understanding of forest retreat in different coastal environments, it should be recognized that human intervention has altered the hydrology in many areas along the Gulf coast, modifying the predicted patterns of forest decline. Reductions in freshwater supply, and consequent saltwater intrusion, may be caused naturally by drought (Thomas 1974) or delta abandonment by a river (Madden et al. 1988). During the past century, however, human activity has also reduced freshwater outflows in many coastal

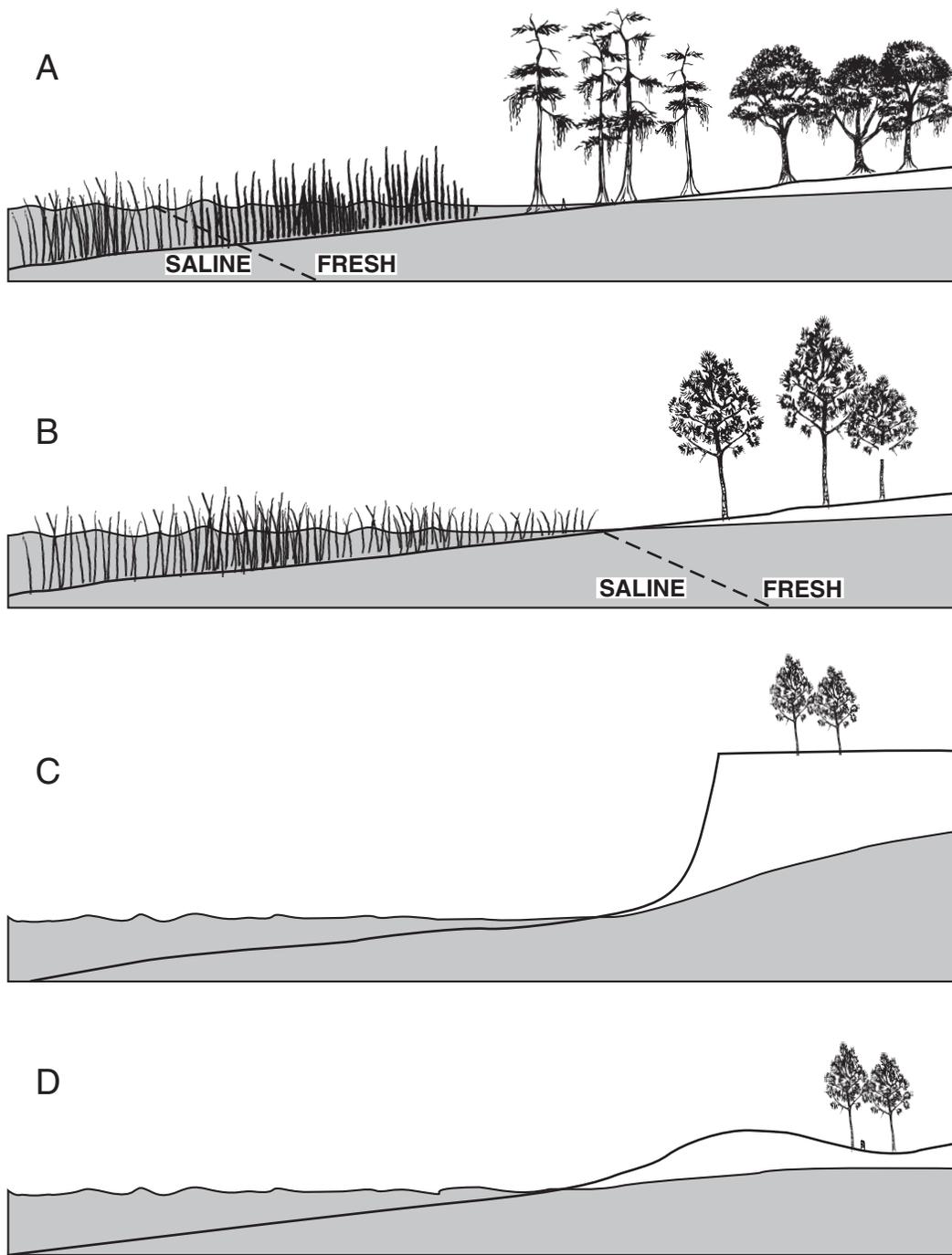


Figure 5. Four coastal forest environments. (A) Forest in region with large freshwater outflow; freshwater marsh and swamp forest form the forest edge. (B) Forest in region with lesser freshwater supply; forest abuts salt marsh. (C) Forest on eroding dune cliffs, and (D) forest behind active dunes.

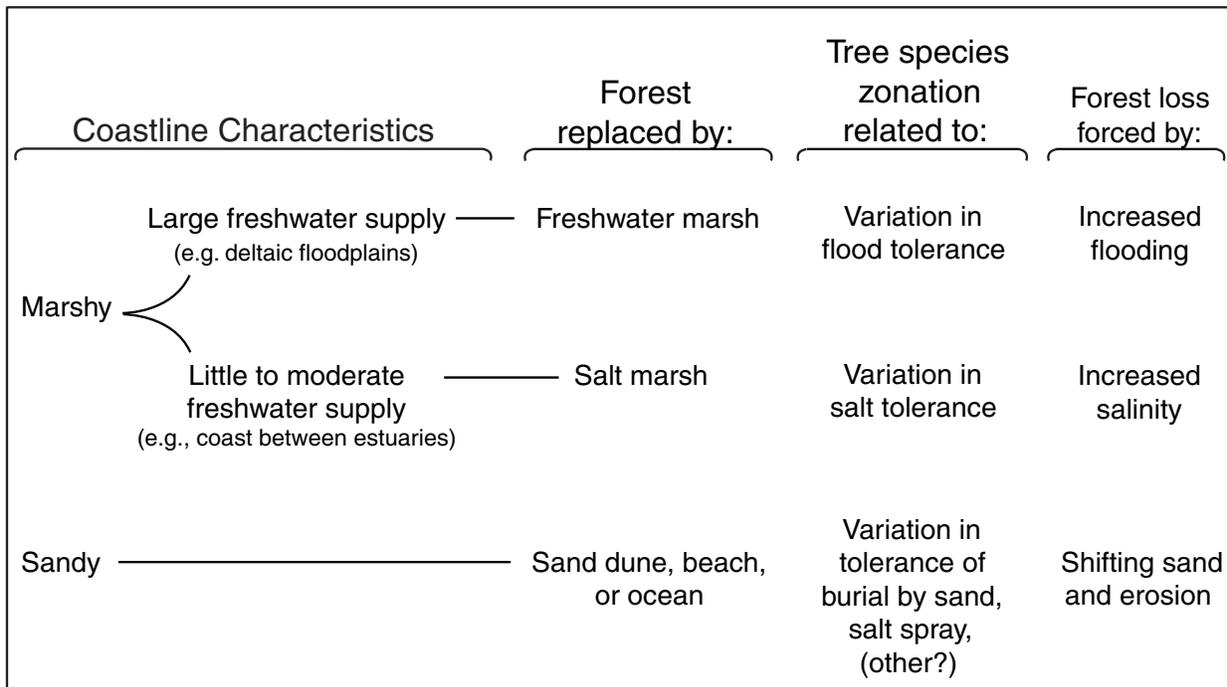


Figure 6. Conceptual scheme of forest response to sea-level rise on different coastlines.

areas. Most notably, canalization in the Mississippi Delta has altered freshwater flows through coastal swamp forest and marsh, fostering saltwater intrusion (Chabreck and Linscombe 1982, Salinas et al. 1986) in areas where sea-level rise might have been expected to eliminate forests first through increased flooding. Similarly, freshwater diversions and drainage schemes have fostered saltwater intrusions in south Florida (Thomas 1974, Fernald and Patton 1984). Because the best-studied low-lying areas on the Gulf of Mexico have also been subjected to extensive modification of their hydrologic regimes, it is often difficult to separate the contributions of sea-level rise and freshwater diversions to observed saltwater intrusion.

Common patterns in forest retreat: Relict stands at the coastal margin.

In retreating forests of both sandy and marshy coastlines, tree regeneration generally ceases before canopy trees are eliminated. This pattern has often been recognized (e.g., Brown 1973, Clark 1986, Conner and Day 1988a, Williams et al. 1999) but deserves emphasis. Because canopy death and widespread vegetation change lag the changes wrought by rising seas (e.g., Conner and Brody 1989), it is difficult to detect the onset of forest decline by monitoring canopy trees. Additionally, it is difficult to evaluate the role of hurricanes and other destructive events in coastal

forest retreat without determining whether affected forest stands were already relict stands or healthy, regeneration stands at the time of the destruction.

Although often not noted, coastal tree stands in published photographs often lack tree regeneration. Stands of slash pine and sand live oak (*Quercus geminata*) photographed on sand dunes of Cat Island, Mississippi by Penfound and O'Neill (1934) consist only of taller, mature trees with no saplings visible. Photographs of cabbage palm surrounded by salt marsh generally show stands of older trees with no signs of recent regeneration (e.g., Vernon 1951).

Several authors have specifically noted the failure of tree regeneration in coastal stands. Brown (1973) noted that where salt marsh is encroaching on coastal forest, mature cabbage palms exist much farther into the marsh than do their seedlings. He also notes that on sandy beaches, mature cabbage palms are frequently found on beaches, but “reproduction on the fore dune and beach face is conspicuously absent no doubt due to the erosional nature of the rising sea and frequent storm tides” (Brown 1973, p. 79). Williams et al. (1999) studying vegetation changes in Waccasassa Bay, Florida, where hydric hardwood hammock abuts *Juncus roemerianus* salt marsh, found that this was true for all tree species in their most tidally influenced plots. They found sequential elimination of *Celtis laevigata*, *Quercus virginiana*, *Juniperus virginiana* var. *silicicola* and *Sabal palmetto*, across a gradient of tidal flooding frequency. For each of these species, they found relict stands at the seaward limit of the species (i.e., plots with living mature trees but no regeneration), and calculated that regeneration failed decades before final loss of the canopy trees. The formation of relict stands has also been noted for swamp forest. In Louisiana, Penfound and Hathaway (1938) studied 7 transects with forest and marsh communities, finding cypress/tupelo forest in the 3 least saline transects. Where cypress swamp bordered a brackish marsh, they noted an absence of seedlings and saplings of cypress, except near the adjacent oak forest where elevation was slightly higher and soil salinity was lower (ca. 3 ppt in the oak forest as compared to ca. 6 ppt in the cypress swamp). There may be situations in which tree regeneration does not fail before loss of canopy trees (e.g., on high coastal bluffs where forest may be lost through catastrophic erosion). However, loss of regeneration before loss of canopy trees has been found in several, diverse coastal environments.

Studies in other regions of the United States have documented the formation of relict stands with sea-level rise. Coastal forests studied by Clark (1986) on Long Island, New York, were marked by nonregenerating stands of eastern red cedar (*Juniperus virginiana*), black oak (*Quercus velutina*), black locust (*Robinia pseudoacacia*), and pitch pine (*Pinus rigida*) at the coastal (low-elevation) limit of each species. Regeneration ceased at different elevations for each of the species. Clark concluded that “mature cohorts occupied lower elevations than did their progeny because, during the period from germination to seed production, suitable soil-moisture conditions shifted upslope in response to sea-level rise”.

The formation of relict stands may be expected to be the general response to sea level rise because tree seedlings are generally more sensitive to salt, flooding, and burial by sand than mature trees. The proximal causes of tree death and regeneration failure that results from sea-level rise may differ depending on the geomorphological and hydrological characteristics of the coast. We consider different types of coastlines (Figure 5a,b,d) separately below.

Forest Change and Retreat in Estuarine Floodplains

Freshwater swamp forests and tidal freshwater marsh exist near their mouths of major rivers and springs along most of the Gulf coast. This is not true in south Texas, where high evaporation rates and low river discharge limit freshwater availability and create hypersaline conditions in the coastal lagoons (Shew et al. 1981). Farther north in Texas (from approximately Matagorda Bay north) there is very limited occurrence of swamp forest near the coast (Shew et al. 1981). However, along the coasts of Louisiana, Mississippi, Alabama, and Florida, swamp forest and often freshwater marsh occur (or occurred) near the mouths of major rivers, in areas of coastal spring discharge in Florida, and in the vicinity of the Everglades of south Florida. The Mississippi Delta has the most extensive system of coastal freshwater marshes and swamp forests along the Gulf coast (Figure 1). Because subsidence and sediment diversion have accelerated the rate of relative sea-level rise in this region (Gagliano et al. 1981, Baumann et al. 1984, Salinas et al. 1986, Conner and Day 1988b), extensive research on forest response to sea-level rise has been conducted in these swamp forests.

As sea level rises in these areas of coastal swamp forest, it is expected that sea-level rise will boost the water table, increase surface flow (Nuttle and Portnoy 1982) and increase hydroperiods in the coastal forest. Shifts in vegetation zones are expected to respond to changes in hydroperiod (DeLaune et al. 1987, Conner and Day 1988b, Pezeshki et al. 1990). Salinas et al. (1986) predicted that with rising sea level “the upland forests will eventually be replaced by bottomland hardwoods and then, as the water level continues to rise, by the more flood-tolerant baldcypress/water-tupelo swamps. The final stage in this progression will be an open body of water”. Current zonation patterns in floodplains are consistent with this prediction. In the floodplains of the Pearl River in Louisiana (White 1983) and the Choctawhatchee River in Florida (Pratt et al. 1989), bottomland forest is more common than swamp forest in the upper reaches of the floodplain, swamp forest becomes more common toward the coast, and the forest is bordered by freshwater tidal marsh. These patterns suggest that rising sea-levels will cause swamp forests to move inland at the expense of less flood-tolerant bottomland forests and that swamp forest will be replaced at the coastal margin by freshwater marsh.

Swamp and Bottomland Forests of the Mississippi Delta

Studies of rates of forest loss in the Mississippi Delta (and elsewhere) generally do not identify losses to sea-level rise, and losses tend to be dominated by urban and agricultural development (e.g., Craig et al. 1979, Conner and Toliver 1990, McWilliams and Rosson 1990). Craig et al. (1979) analyzed studies of land loss (conversion to water) in the Mississippi deltaic plain during the period 1890-1960. They concluded that much less swamp forest than marsh had been lost. Mean annual rate of land loss in swamp forests was 223 ha/yr per year, whereas that for saline, brackish and fresh marshes was 701 ha/yr, 1366 ha/yr, and 499 ha/yr, respectively. Much of the land loss they identified, however, was attributable to direct development such as canal building.

Allen (1992) estimated that observed dead and dying cypress-tupelo stands in the Mississippi Delta accounted for “tens of thousands of acres” of forest loss, citing numerous problems with cypress forest regeneration in the area. Conner et al. (1981, 1986) found poor cypress regeneration in the Lake Verret and Barataria Basins of the lower Mississippi Delta. Browsing by nutria, introduced into Louisiana in the 1930’s, browsing by deer, damage from crayfish, and competition from vines in logged areas have all been identified as factors limiting baldcypress regeneration (Conner and Toliver 1990, Platt and Brantley 1990, Myers et al. 1995). Most studies, however, have focused on increased flooding and/or salinity as primary causes of regeneration failure and stand decline (e.g., Conner et al. 1981, DeLaune et al. 1987, Conner and Day 1988a, Conner and Toliver 1990, Allen 1992)

In the Lake Verret and Barataria Basins of Louisiana, water levels have been rising and drowning cypress-tupelo forest. The rise of water, relative to the land, is much more rapid in this region than in most other areas of the Gulf coast due to land subsidence. The most heavily studied swamp forests in the Mississippi Delta occur in the Lake Verret and Barataria Basins. In these swamp forests, water levels have been rising at rapid rates over the past several decades (0.85 - 1.49 cm/yr; DeLaune et al. 1987, Conner and Day 1988a). As of the late 1980s, the water in Barataria Basin’s swamp forest was still fresh (Madden and DeLaune 1987) although saltwater intrusion and resultant community change had been extensive in the adjacent freshwater marsh (Chabreck and Linscombe 1982, Madden and DeLaune 1987). Seasonal variation in flooding in swamp forests of the Lake Verret and Barataria Basins is minor, but the summer is relatively dry. In swamp forests studied by Conner and Day (1988a, 1988c), flooding occurred during the winter and spring, with either a short dry period during July - early August, or dry periods during most of the growing season. Baumann (1980) found that swamp forest in the Barataria Basin flooded continuously during May and September with flood-free periods occurring during other months (Baumann 1980, 1987). The spring peak, which increases in strength with distance from the coast (Baumann 1987), is generally attributed to conditions in which precipitation exceeds evapotranspiration. The autumn

peak corresponds to the annual peak of water level in the adjacent Gulf of Mexico (Baumann 1987), and may reflect seasonal coupling between ocean levels and water levels in the coastal freshwater swamp forests.

Some studies have linked regeneration failure of trees in the Mississippi delta to increased hydroperiods. Conner and Day (1988c) examined tree growth and community composition across and elevational gradient in the upper Lake Verret Basin. The density of large trees (<10 cm dbh) did not differ across this gradient, and the lowest 0.1 ha plot, continuously flooded during most years, supported 8 species of large trees (<10 cm dbh). Few seedlings were observed in that plot, however. The distribution of seedlings and large trees of several species differed, with seedlings occurring in plots with shorter hydroperiods than larger trees. This pattern was most notable for baldcypress, and suggests future displacement of bottomland species by swamp forest species.

DeLaune et al. (1987) transplanted seedlings of baldcypress (*Taxodium distichum*) and overcup oak (*Quercus lyrata*) across elevational gradients near Lake Verret, Louisiana. Despite the fact that the seedlings were fairly large at the time of transplanting (50-60 cm tall), none survived one year in cypress-tupelo forests that remained flooded all year, few survived in areas flooded approximately 4 months, but 53% of the baldcypress and 60% of the overcup oak survived the first year on ridges (1 m higher in elevation than the lowest sites).

Other studies have demonstrated that changes in flooding frequency have eliminated swamp forest regeneration in parts of the Mississippi Delta, but most of those studies relate to effects of artificial impoundments (see Appendix 3). The studies described above suggest progressive elimination of swamp forest and movement of swamp forest into bottomland forest zones as hydroperiod is increasing due to subsidence and sea-level rise. Conner and Day (1988a) noted that not only were swamp forests being drowned in the Mississippi Delta, but the potential for them to migrate into bottomland forest was limited throughout much of the delta region, where bottomland forests occur on narrow low ridges that will eventually succumb to rising water themselves.

Other studies have linked regeneration failure in swamp forest to increased salinity. Penfound and Hathaway (1938), studying vegetation transects in the Barataria Basin and to the east of Lake Ponchartrain, Louisiana, found that the most saline stand of cypress they studied (6 ppt porewater salinity) lacked regeneration. Cypress seedlings occurred in the nearby oak forest where elevations were higher and soil water less saline. "Ghost forests" of cypress occurred near this transect. The authors ascribed death of these cypress stands to increased salinity, but speculated that the increased salinity was due to human intervention (canalization in the area south of the transect) and/or storm tides (specifically, a hurricane in 1915). Platt and Brantley (1990) mention that plantings of baldcypress seedlings in the Manchac Wildlife Management Area, in the Lake Ponchartrain estuary, suffered from "increased soil salinity during the growing season". This area was clearcut in the early 1900's and was an intermediate-salinity marsh at the time of their study.

(Myers et al. (1995), however, found that the main limitation to baldcypress seedling survival in this area was herbivory). Allen (1992) identified 52 areas of cypress-tupelo dieback from the air, and found high soil salinity (6-8 ppt) in the largest dying stands.

Early vegetational studies found no cypress-tupelo swamps at salinities greater than 4-6 ppt, and a transition from freshwater marsh to brackish marshes in the same salinity range (Penfound and Hathaway 1938, Penfound 1952). Allen et al. (1994) demonstrated intraspecific variation for salt-tolerance in baldcypress, however, and a few healthy, mature individuals of cypress have been noted in more saline stands (Pezeshki et al. 1990, Allen 1992, Allen et al. 1994).

It is difficult to evaluate the role of sea-level rise in the observed saltwater intrusion in the Mississippi Delta. Construction of flood-control levees in the vicinity of New Orleans began in the 1700's (Day et al. 1990). Levee construction along the Mississippi River after the 1927 floods greatly reduced riverine water and sediment input into the Barataria Basin (Madden et al. 1988), and modifications to the hydrology of the wetlands of the Mississippi Delta were advanced by the time the earlier vegetation studies of the 1930's and 1940's were carried out. Even the earlier studies of Penfound and Hathaway (1938) attributed salinity increases to canal building. Reductions in freshwater outflows would tend to change the system from a high-volume estuarine system in which swamp forest meets freshwater marsh, toward a system more similar to inter-estuarine coasts, where upland forest meets saltmarsh (Figure 5). Thus, while some stands of swamp forest in the Mississippi Delta may be succumbing to increases salinity, it is not clear that these increases are the result of relative sea-level rise.

In this vein, it should be noted that decline of coastal cypress swamps in the Cape Fear River estuary in North Carolina has been linked to increased salinity. Yanosky et al. (1995) measured chloride concentrations in growth rings of *Taxodium distichum* to determine the history of salinization in swamp forest stands. As in the Mississippi Delta, however, saltwater intrusion into cypress stands of the Cape Fear estuary appears to have been caused more by human intervention than by sea-level rise. Hackney and Yelverton (1990) noted that channel dredging in the Cape Fear River estuary increased saltwater flow inland, increasing the tidal range at Wilmington, N.C. 26 cm in <50 years and causing saltwater intrusion into cypress stands.

In Louisiana, studies of regeneration failure in inland freshwater areas of the Lake Verret and Barataria Basins suggest rising seas and subsidence have eliminated tree recruitment there through increased flooding. These stands will already be functionally dead or relict stands by the time sea-level rise increases the salinity in that area. However, observations made by Penfound and Hathaway (1938) suggest that there are areas in the Mississippi Delta where regeneration failure in swamp forest is now caused by increased salinity.

Effect of sedimentation on swamp forest response to sea-level rise

As in coastal marshes, sediment accretion in swamp forest can partly to wholly counteract sea-level rise. In the Mississippi Delta, high accretion rates have been found in swamp forest. In the Lake Verret and Barataria Basins, however, these rates have not been sufficient to keep pace with rates of deltaic subsidence and rising water. DeLaune et al. (1987) examining ^{137}Cs activity in cores from wetland forests near Lake Verret, Louisiana found average sedimentation rates of 0.63 cm/yr. They compared these rates to water level increases of 1.49 cm/yr. Similarly, Conner and Day (1988a) found short-term (3-year) sedimentation rates of 0.88 cm/yr and 0.60 cm/yr in cypress-tupelo forests of the Lake Verret and Barataria Basins, respectively. These too were insufficient to keep pace with the relative water level rise in these areas (1.37 and 0.85 cm/yr in the Lake Verret and Barataria Basins, respectively). Conner and Day (1988a) found that sedimentation rate in bottomland forest (0.27 cm/yr) was less than that in swamp forest, and Conner and Day (1991) found that sedimentation rates in swamp forests were negatively correlated with flooding frequency. The lower rates of sedimentation found for bottomland forest and infrequently flooded swamp forest (0.27 cm/yr, Conner and Day 1988a; 0.21 cm/yr, Conner and Day 1991) would be sufficient to keep pace with current sea-level rise if eustatic sea-level rise were the only factor effecting forest change.

In contrast to sedimentation in marshes of the Mississippi Delta, where hurricanes and extratropical storms account for much of the deposited sediment (Baumann et al. 1984, Day et al. 1995), Conner and Day (1991) found that sedimentation in swamp forests near Lake Verret were highest during the winter and spring rainy season, rather than during seasons with hurricanes. They speculated that the major source of sediments for these forests was erosion of agricultural fields surrounding wetland areas, rather than sediment from open water bodies resuspended by storms. Conner et al. (1989) recognized the importance of hurricanes in providing inorganic sediments to coastal wetlands of the Gulf of Mexico. However, with the exception of Conner and Day's study (1991), little research has been carried out on the impact of hurricanes on accretion in coastal freshwater swamp forests.

Whether or not accretion in other estuaries on the Gulf coast are sufficient to stabilize the boundary between swamp forest and freshwater marsh under current or projected rates of sea-level rise should depend on the sedimentary environments in those swamps. The Mississippi carries more sediment than any other river on the Gulf coast (Shepard 1960c). However, sediment supply in the lower Mississippi delta has been reduced by flood-control levees that tend to funnel sediments into deep offshore waters (Gagliano et al. 1981). Sediment supply to the Barataria Basin was reduced when natural shifting of deltaic deposition initiated a new subdelta in the Atchafalaya

estuary (Morgan 1967, Roberts and van Heerden 1982, Conner and Brody 1989) and sediment supply to the Lake Verret Basins was reduced by the construction of flood-control levees (Conner and Brody 1989, Conner and Day 1991). Under natural conditions, accretion would exceed subsidence in the Lake Verret Basin forests, and swamp forest would be replaced by bottomland forest (Conner and Brody 1989). Under the present depositional environment, bottomland forest is being replaced by swamp forest, and former stands of swamp forest are not regenerating (DeLaune et al. 1987, Conner and Day 1988a, c, Conner and Brody 1989).

Swamp forests of south Florida

It is difficult to determine how swamp forests of south Florida interact with sea-level rise. They exist in low-lying, vulnerable areas. However, a hectic stratigraphic record in the south Florida peats makes reconstruction of past regional vegetation changes difficult and massive drainage schemes during this century have changed the interaction between sea-level and the freshwater terrestrial systems.

Holocene sea-level rise is credited with the conversion of xeric vegetation to mesic vegetation in peninsular Florida (Delcourt and Delcourt 1981, 1987). Basal peats in the Everglades (Gleason 1974) and in cypress stands of the Big Cypress watershed north and west of the Everglades (Kropp 1976) date to ca. 5000 yr B.P. or slightly thereafter. In other areas of the southeastern United States, rising seas have raised the water table to create vast swamp forests (Long 1974, Parrish and Rykiel 1979). Beyond evidence that sea-level rise has helped create the present marsh/cypress system, however, there is little evidence to indicate how vegetation zones in south Florida responded to sea-level rise in the past. Peat cores from the Everglades have revealed changes from hydric (water lily) to marsh to woody vegetation, sometimes showing that such sequences occurred repeatedly (Gleason et al. 1974, Spackman et al. 1974, Kremer and Spackman 1981, Willard et al. 1999). Evidence of peat fires are common in these cores (Gleason et al. 1974), and the stratigraphic records may primarily reflect successional patterns that occur after a lowering of surface elevation, or over long-term cycles of drought and flooding. In all of the stratigraphic studies reviewed by Gleason et al. (1974) there is no evidence that extensive swamp forests previously occurred in areas that are now dominated by saw-grass.

The interactions between swamp forest and sea-level rise in south Florida may differ from that on river deltas due to the combined influences of a shallow limestone platform and frequent fire in south Florida. In deltaic forests with significant freshwater supplies (above), there are indications that rising seas boost freshwater tables, eliminating swamp forest through increased hydroperiod. In south Florida, depth to the limestone bedrock influences cypress distribution, and cypress stands may flood more deeply than adjacent stands of prairie/marsh (Duever et al. 1976,

Drew and Schomer 1984). Cypress and other forests tend to develop over limestone depressions or limestone highs with solution holes where deep peat accumulates (Spackman et al. 1974, Wade et al. 1980, Drew and Schomer 1984). Dwarf cypress forest occupies shallow soils with little or no peat accumulation (Craighead 1971, Coultas and Duever 1984). This dwarf cypress forest has low productivity, and often an herbaceous understory (Wade et al. 1980). The lack of swamp forest peats below today's Everglades marshes, therefore, may reflect bedrock restriction of tree growth in the region as sea level rose and freshwater flooding increased. Whereas in deltaic areas around the Gulf coast, marshes overlie drowned swamp forests which appear to have developed as rising seas moved into upland forests, the marshes and prairies of the Everglades may have replaced a very poorly developed cypress forest, or directly replaced xeric herbaceous or scrub vegetation as sea-level rose. Because of frequent destruction of the south Florida peats by fires, however, the full Holocene history of south Florida vegetation is speculative. Sea-level rise and bedrock structure influence peat accumulation, as well as hydroperiod, making effects of sea-level rise on freshwater swamp forest difficult to predict. Duever et al. (1984), however, suggested that the cypress-dominated Corkscrew Swamp of southwest Florida had expanded over the past 5000 years as sea level rose and the ancient limestone channel beneath it filled with peat.

The hydrology of south Florida has been vastly modified by groundwater pumping and water diversion projects that have reduced hydroperiod in natural communities, caused subsidence of peat soils, and caused salt water intrusion. Historically, the marsh and swamp forest islands of the Everglades were supplied by outflow from Lake Okeechobee during the rainy season, with water traveling to the estuaries of Florida Bay and the Ten Thousand Islands region (Thomas 1974, Fernald and Patton 1984). The more extensive swamp forests of the Big Cypress watershed were supplied primarily from rainfall falling west of the Everglades (Drew and Schomer 1984). During very wet periods, water from the Everglades spilled over into other coastal basins (Fernald and Patton 1984). Due to massive diversions of freshwater in south Florida, initiated in the late 1800's and early 1900's, the hydraulic heads in these systems have been reduced and saltwater intrusion has been noted (Klein et al. 1974, Thomas 1974, Fernald and Patton 1984). In inland reaches of the Everglades, lowering of water table as much as 1.5 feet below sea level in 1962, 1965 and 1971 were associated with severe fires in the Everglades that destroyed hardwood hammocks (Craighead 1974). Drainage and resulting fires caused subsidence and loss of the peaty soil (Davis 1946). In the Big Cypress watershed, drainage projects of the 1960s lowered the water table and shortened the hydroperiod in cypress strands (Drew and Schomer 1984). Reductions in both the water table and the soil surface have modified the relationship between the ocean and the freshwater terrestrial systems of south Florida, resulting in saltwater intrusion (Klein et al. 1974).

It is clear that the boundary between freshwater and saltwater vegetation in south Florida has changed in both the distant and recent past. There is stratigraphic evidence of mangrove

replacing freshwater marsh in the coastal reaches of south Florida (Gleason et al. 1974 and references therein, Willard et al. 1999). Recent inland expansion of mangrove, and mangrove colonization of other forest and nonforest vegetation types has been attributed to salt water intrusion (e.g., Craighead 1974, Alexander and Crook 1974). Vegetation changes that appear to have occurred during this century are frequently attributed to freshwater diversions or a combination of freshwater diversion and sea-level rise. Thomas (1974) thought sea-level rise played a minor role in historical salt intrusion in south Florida, linking it instead to human consumption and diversion of fresh water, periodically exacerbated by drought. Where sea-level rise might have affected swamp forest through increased hydroperiod and/or peat accretion in the natural system, south Florida swamps have been subjected to decreased hydroperiods, peat loss, and, potentially, increased salinities. Thus, as in many deltaic systems, human modifications have reduced the freshwater supply to the coastal margin, changing the interaction between rising seas and coastal forest.

Coastal swamp forests of Texas

As noted previously, coastal swamp forest in Texas was very limited in extent even prior to coastal development due to high evapotranspiration and relatively low freshwater outflows (Shew et al. 1981). Some global change scenarios predict both increased warming and decreased rainfall for this coast (Kattenberg et al. 1996, Longley 1995). Additionally, sea-level rise and decreased runoff are expected to decrease inflow/volume ratios of south Texas lagoons (Longley 1995), a change that would promote hypersaline conditions in these lagoons (Shew et al. 1981). Thus, factors limiting the occurrence of bottomland and swamp forests in south Texas are expected to strengthen.

Forest change and retreat on marshy coasts with lesser freshwater outflows

Along marshy coasts with relatively small freshwater outflows the forest edge generally abuts salt marsh. Often there is a narrow zone of salt-tolerant shrubs (e.g., *Iva frutescens*, *Baccharis halimifolia*) between the forest and the herbaceous salt marsh. These types of forest marsh boundaries typify much of the Big Bend coast of Florida and occur throughout the Gulf coast where forest islands exist on raised areas surrounded by salt marsh. These raised areas that support coastal forest include the cheniers of western Louisiana's Chenier Plain, topographic highs in the limestone bedrock along Florida's Gulf coast, and shell mounds (Indian middens) throughout the Gulf Coast. These shell mounds support small islands of live oak forest in the saline marsh

of the Mississippi Delta, far from the influence of the freshwater lens and the swamp forest/marsh boundary (Brown 1936).

In contrast to forests of high-volume estuaries, the most coastward forests in these areas are not swamp forests, but pine flatwoods, hardwood forests, often dominated by live oak (*Quercus virginiana*), or, in south Florida, tropical hardwood hammocks. In south Florida, these forests often occur next to mangrove forest, rather than salt marsh.

Studies of historical rates of forest loss are rare. Ross et al. (1994) studied reduction in *Pinus elliottii* var *densa* stands in the Florida Keys. The forested area on Sugarloaf Key decreased from 46 ha to 30 ha between 1935 and 1991, and the distribution of dead pines indicated that live pine occupied at least 88 ha at some time prior to 1935. The authors linked stand decline to low elevations and high salinity, patterns expected to occur as a result of sea-level rise. Earliest pine mortality occurred at the lowest elevations studied, in locations now occupied by halophytic vegetation, and pine stands exhibiting decline had higher groundwater salinity, higher soil salinity, lower predawn xylem water potential, and higher $\delta^{13}\text{C}$ values than stands showing little change over time (Ross et al. 1994). They suggest that the presence of a freshwater lens on one side of their study area slowed forest decline there.

Brinson et al. (1985) studied gradients in forest structure in an estuary in North Carolina, where bottomland forest (dominated by *Fraxinus pennsylvanica*, *Quercus nigra*, *Nyssa sylvatica* var. *biflora*, *Acer rubrum* and *Ulmus rubra*) met *Juncus roemerianus* marsh. Three of the four forest stands studied had intertidal soil. Declining stands (those with low ratios of living-to-dead trees) were more frequently flooded and had higher groundwater salinities than healthier stands. Effects of upstream development on freshwater supply to these stands could not be evaluated, but effects of a two-year drought were pronounced. Brinson et al. (1985) emphasized the potential importance of these periodic intrusions in structuring forest transitions at the coast.

Williams et al. (1999) studied changes in coastal hardwood forest in Waccasassa Bay, Florida, ca. 5 km from the mouth of the Waccasassa River. This forest was on low lying, gradually sloping topography due to antecedent geology, rather than patterns of floodplain sedimentation. The area was underlain by a limestone platform characteristic of much of northwest Florida Big Bend coast (Terrell 1979) and topographic highs in the limestone supported forest stands surrounded by salt marsh. The forest, characterized as hydric or mesic hammock (Vince et al. 1989) contained many species in common with bottomland forests of floodplains around the Gulf, and abutted saline, *Juncus roemerianus* marsh. The forest fringe was dominated by *Sabal palmetto*, *Juniperus virginiana* var. *silicicola*, *Quercus virginiana* and *Celtis laevigata*. Williams et al. (1999) found that progression of forest decline (as indicated by species composition changes and tree recruitment) correlated with frequency of tidal flooding, but was not associated with a reduction in soil redox potential, an indicator of potentially stressful flooding conditions. Because the order in

which tree species were eliminated from stands corresponded roughly to the relative salt-tolerance of their seedlings (Williams et al. 1998), and because regeneration failure occurred long before a species was eliminated from a stand, they concluded that forest retreat was caused primarily by seedling exposure to salt through tidal flooding.

In other areas, as well, local rainfall and drainage from the topographic highs that support forest appear responsible for supplying freshwater to the forest edge. Sternberg et al. (1991) studied water use patterns across zones in a hardwood hammock/mangrove transition in the Florida Keys. They found that, although groundwater salinity beneath hardwood hammock was fairly high (14.7 ppt), soil water there was fresher (salinity $<6.1 \pm 3.6$ ppt). They concluded, based on measurements of plant predawn water potential, that hammock species were not utilizing the groundwater. In a follow-up study, Ish-Shalom et al. (1992) studied tropical hardwood hammocks in the Lower Florida Keys, ca. 0.7-1.1 m above mean sea level, and showed that these hardwoods tapped fresh rainfed soil water, rather than the saline groundwater that underlay some of the hammocks. Because these forests seemed not to tap the relatively shallow water table (<1 m below the surface), the authors suggest that sea-level rise would affect these forests first through changes in tidal flooding frequency, rather than through salt intrusion into groundwater. All of these low-lying forests experience occasional storm surges. Craighead (1974) noted that hardwood hammocks on Indian mounds in south Florida may be surrounded by saline, tidal vegetation. Hurricane tides may overrun these hammocks, but Craighead suggested that copious rains accompanying the hurricanes rapidly wash the salt from the shallow peaty soil.

Hmielski's investigations of hydrological relationships at a salt marsh/forest boundary in Virginia yield insights into factors that affect freshwater supply to the forest edge on these types of coasts (Hmielski 1994). The transition he studied was similar to many along the Gulf coast, with slash pine (*Pinus elliottii*) grading into a redcedar (*Juniperus virginiana*) and a shrub zone (*Iva frutescens*), then into *Juncus roemerianus* marsh. Hmielski suggested that forest margins on steep coastlines may receive substantial inputs of groundwater and that this groundwater may aid in flushing salt from soil. This groundwater flushing at the forest/marsh transition sharpens the transition from forest to marsh, may protect the forest from sulfide toxicity by carrying iron, which precipitates the sulfide, and may help flush salt introduced in the occasional high tide or storm surge (Hmielski 1994, Brinson et al. 1995). Because of the low hydraulic gradient on flatter coastlines, however, forest margins and stands on slightly elevated hummocks in marsh were likely dependent on rainfall and local drainage (i.e., from hummock to marsh) for freshwater supply and salt flushing, rather than groundwater. While channelized flow through faults in limestone in areas where forest rests on a shallow limestone platform (i.e., over much of coastal Florida) may provide exceptions to generalizations about freshwater supply to coastal forest stands (Williams et al. 1999), most evidence to date suggests that forest stands adjacent to salt marsh on the Gulf coast

utilize shallow rainfed lenses of water.

Because the marsh/forest transition occurs in the intertidal zone, factors that reduce tidal exposure affect the elevation at which this transition occurs. Most notably, salt marsh protects forest edges from tidal flooding by interfering with the movement of tidal water. Because of this, forest exists at lower elevations as one moves inland along tidal creeks (Williams et al. 1999), and inland from tidal creeks (Hmielski 1994, Brinson et al. 1995).

Forest change and retreat on sandy shorelines

On sandy shorelines and beaches forest loss has generally been associated with shoreline erosion or burial by sand. However, plant zonation has been linked to variation in tolerance of salt spray and, consequently, some researchers have suggested that forest retreat may be caused by a moving salt-spray zone that advances as beach erosion occurs (Bellis 1995). In either case, shoreline erosion has been implicated as the direct or indirect cause of forest retreat.

Erosion of sandy shorelines has been recognized as one consequence of sea-level rise. French et al. (1995) distinguished effects of sea-level rise on sandy, clastic shorelines from effects on other shorelines, based on the tendency for sandy shorelines to respond to sea-level rise with lateral erosion. Bruun (1962) described the manner in which sandy shorelines should retreat in the face of sea-level rise, eroding to maintain an equilibrium bottom profile offshore. Such erosion, however, may come sporadically (i.e., during storms) and be modified by locations of inlets, channels, and various coastal structures (e.g., Walton 1978, Mehta and Cushman 1988). A review of the literature dealing with effects of sea level rise and other factors on coastal erosion is beyond the scope of this report, but may be found in reviews and texts such as Carter and Woodroffe (1994).

Erosion on these shorelines that exposes roots or topples trees has long been noted. Writing of the black mangrove (*Avicennia germinans* = *A. nitida*) on the Gulf side of large barrier islands along the coast of Louisiana, Brown (1936) stated: "Wave action in several instances has undermined these ridges and the Black Mangrove is tumbling into the Gulf." These islands have been retreating at rates up to 50 m/yr (Mendelssohn 1982). Cooke (1939) and Kurz and Wagner (1957) photographed pine stumps on the eroded shoreline of St. George Sound, near Apalachicola Bay, Florida. Similar observations of pine stumps on eroding beaches were made by Martens (1931) on Dog Island just east of St. George Sound. Alexander and Crook (1974) noted the undercutting of Australian pines (*Casuarina* sp.) growing on beaches "north of Cape Sable" on the southwest corner of Florida.

Tree death has been associated with erosion on sandy shores of the Atlantic U.S. coast, as well. Kurz (1942) noted eroding dune cliffs with uprooted cabbage palms, and Kurz and Wagner (1957) took such beach erosion as evidence of sea-level rise. On the Atlantic coast of Florida, Alexander and Crook (1974) noted that the beach shoreline of Hobe Sound National Wildlife Refuge had retreated 250 yards (229 m) between 1940 and the early 1970's where "...the mangrove forest is being covered by sand, killed, and finally washed out to sea." [p. 65]

The implication of burial by sand, as a mechanism for forcing forest retreat has been suggested by others. Penfound and O'Neill (1934) attribute tree failure on barrier islands of Mississippi to burial by shifting sands, stating that moderate deposition of sand usually kills slash pine and saw palmetto (*Serenoa repens*, identified by Penfound and O'Neill as *S. serrulata*). They note that "sand live oak [(*Quercus geminata*)] remains alive and prosperous long after its compatriots have succumbed to sand invasion". Johnson (1900) described coastal sand dunes advancing on the forest of Shackleford Bank, North Carolina, and burying forest. Although many trees died before the advancing dune touched them, species such as *Juniperus virginiana* and *Ilex* sp. survived to be buried green by the advancing sand. No mention was made of the distribution of seedlings in relation to the advancing dunes. It should be noted that the ability to spread vegetatively, rather than by seed, has long been recognized as a major factor in the success of herbaceous species of sand dunes (e.g., Barbour et al. 1985). Woody plants are generally restricted to more stable regions of coastal dunes and sandy shorelines, but the relationship between their seedlings and sand movement has received little formal attention.

Several researchers have tried and failed to correlate plant distribution to soil salt content in coastal dune systems. Much of our knowledge of ecological relationships on barrier islands comes from the Atlantic coast, where barrier islands of Virginia and North Carolina support many of the same species found in the northern Gulf of Mexico. Oosting and Billings (1942), studying the zonation in herbaceous coastal dune communities in North Carolina, found surprisingly low salt concentrations in soil water above the water table. They concluded that, because of the heavy salt-spray load in those communities, leaching must be very rapid. Martin and Young (1997) found that soil salinity and groundwater salinity varied both temporally and spatially across Hog Island, a barrier island on the coast of Virginia. However, they concluded that the distribution of *Juniperus virginiana* could not be explained by patterns of soil salinity: greenhouse experiments revealed that seedlings of *Juniperus virginiana* tolerated higher salinities (at least on a soil dry weight basis) than any that were found in the field. Boyce (1954) studied soil salinity in transects from beaches inland. He found that salinity at the soil surface was frequently elevated, but salinity right below the surface of the sand was fairly low, a pattern that other researchers had also found. He attributed the higher salt concentration at the surface to salt-spray accumulation.

Soil salinity may be temporarily elevated by storm surges, but generally has not been observed to change vegetation. Soil salinities on Hog Island were elevated by a storm surge that occurred in 1991 (Young et al. 1995b). Although ground water salinity was still 6 ppt one week after the storm, Young et al. (1995b) observed little damage to *Myrica cerifera* in the island's swales. Stopp and O'Neal (1996) described effects of Hurricane Opal's storm surge on vegetation of Santa Rosa Island, Florida. Browning of some plants (e.g., *Pinus elliottii*, *Ilex vomitoria*, *Quercus hemisphaerica*, *Serenoa repens*, *Vitis* spp., and several herbaceous species) was particularly pronounced in areas where wracklines and other evidence indicated exposure to surge water. This survey was conducted 3 weeks after the storm, and the authors did not know whether effects were permanent or temporary. Temporary leaf loss is a common response of trees in hurricanes (see sections on hurricanes), and some of the species surveyed by Stopp and O'Neal (*Quercus hemisphaerica* and *Serenoa repens*) were producing new leaves within 2 weeks of the storm.

Exposure to salt-spray has been recognized as an important factor controlling both the morphology and zonation of coastal shrubs and trees. Studies of salt-spray influence are generally traced to the seminal work of Wells and Shunk (1937, 1938). Wells and Shunk (1938) demonstrated that the sculpted forms of shrubs on exposed coasts of North Carolina were caused by salt-kill of terminal buds on the windward side of plants. They showed that minor shielding, such as that afforded by slight depressions in the canopy of exposed shrubs, was sufficient to protect the young shoots from salt spray damage. Furthermore, they demonstrated that plant zonation correlated with susceptibility to salt spray damage. Injury of young tissue following experimental exposure to salt spray yielded a tolerance ranking. They found that *Baccharis halimifolia* was most tolerant of salt spray. *Myrica cerifera* and *Ilex vomitoria* were somewhat less tolerant, followed by *Quercus virginiana* then *Pinus taeda*. Species that typically occurred inland of the spray zone (persimmon, turkey oak, and grape) exhibited injury even to mature foliage.

Following the research by Wells and Shunk (1938), other researchers related zonation near the ocean to salt spray exposure. Oosting and Billings (1942) studied transects with herbaceous and shrubby vegetation on the sandy banks of North Carolina. Variation in most environmental factors studied (soil moisture, soil temperature, soil pH, soil salt content, air temperature, relative humidity, and evaporation) did not relate well to vegetation zonation. Oosting and Billings (1942) found that species distribution best correlated with salt-spray exposure and they related the distribution of herbaceous dune species to experimentally determined differences in tolerance of salt-spray. The greatest drop in spray deposition has been found to occur immediately behind the foredunes (Oosting and Billings 1942, Boyce 1954). The forest typically occurs in the sheltered areas behind these dunes (e.g., Bellis 1995) where both salt spray and other factors, such as sand stability, tend to be more favorable for plant growth.

Boyce (1954) examined patterns of salt-spray deposition and injury at several sites on the Atlantic coast. He made detailed observations of effects of salt spray on the growth and morphology of several woody plants characteristic of both the south Atlantic and Gulf coasts. He investigated mechanisms for differential susceptibility to salt-spray injury. Differences in wettability of leaf surfaces did not appear to explain differences in salt-spray tolerance but differences in susceptibility to mechanical injury seemed to correlate with salt-spray tolerance. Boyce (1954) found that species with flexible leaves (*Phytolacca americana*, *Sassafras albidum* and *Diospyros virginiana*) or deep sinuses in the leaves (*Acer rubrum* and *Quercus laevis*) showed numerous abrasions and lacerations. In contrast, species with short, stiff petioles and small unlobed leaves (*Quercus virginiana*, *Ilex vomitoria*, and *Iva imbricata*) showed fewer abrasions. He postulated that salt might enter through cracks in tissue, and that resistance to mechanical injury may confer resistance to salt spray injury.

Tyndall et al. (1987), however, questioned the role of salt spray in determining the seaward limit of shrubs in North Carolina. They grew potted seedlings of *Myrica pensylvanica* in sand flats just behind the foredune, and moved them to the beach during 3 windy periods to expose them to even higher levels of salt spray. Although seedlings of *Myrica* never naturally occurred in the grass or forb zone, 1-year-old potted seedling survived salt-spray exposure that was at least as intense as that occurring in the grass and forb zone, and exhibited no symptoms of salt stress. Tyndall et al. (1987) concluded that some factor other than salt spray limited the seaward distribution of *Myrica* seedlings.

Vegetation changes and ecological relationships have been intensively studied on Hog Island, a barrier island on the coast of Virginia. Hog Island is very dynamic, eroding at the southern tip and accreting at the northern tip (Hayden et al. 1991). Loblolly pine forests of the southern part of the island died as that part of the island eroded and the freshwater lens disappeared (Hayden et al. 1991). Anthropogenic factors may have affected vegetation patterns and processes on this island. The island was occupied by Europeans in the 1600's, and the last cows were not removed until the 1980's (Hayden et al. 1991). The role of herbaceous vegetation in stabilizing dunes and barrier islands is a well recognized (e.g., Mendelsohn 1982), and Oosting and Billings (1942) suggested that grazing "has indirectly transformed several of the banks [in North Carolina] into almost barren seas of shifting sand".

Despite the potential contributions of humans to the deterioration of Hog Island, many patterns of vegetation change are consistent with effects of sea-level rise and storms. Marshes on the bay side of the island are retreating where no overwash occurs to supply more sand (Hayden et al. 1991). Current stands of loblolly pine (*Pinus taeda*) have apparently experienced poor recruitment for ca. 20 years (Johnson and Young 1993). These declining stands are at lower elevation (<2 m vs. 5-7 m elevation) and experienced more frequent overwash than healthy stands

on nearby Parramore Island.

The dynamics of *Myrica cerifera* populations on Hog Island have been studied and may affect loblolly pine fates. *Myrica cerifera* has colonized the younger parts of the island and formed relict, nonregenerating stands on older soils (Young et al. 1995a). Interactions with a saline water table on the bay (marshy) side of the island and erosion on the seaward side of the island have been shown to affect *Myrica's* distribution (Young et al. 1994, Young et al. 1995b). The distribution of *Frankia*, the nitrogen-fixing nodule-forming symbiont of actinorhizal *Myrica cerifera* roots, was not found to limit *Myrica's* distribution (Young et al. 1992). However, VAM colonization of *Myrica* roots was absent in declining stands, present in healthy stands, and the potential for colonization appeared low in young soils where salinity was highest (Semones and Young 1995). Many dune plants are endomycorrhizal (Koske and Halvorson 1981), potentially benefiting plants both through increased nutrient acquisition and through binding sand near the root (Sutton and Sheppard 1976). It is not clear, however, what role (if any) the ability to form mycorrhizal associations plays in coastal forest retreat.

Johnson and Young (1993) suggested that the presence of *Myrica* may limit loblolly pine recruitment, noting that, in addition to elevational differences between healthy pine stands on Parramore Island and declining stands on Hog Island, *Myrica* stands were more dense in pine stands of Hog island. Tolliver et al. (1995) carried out greenhouse experiments that suggested that *Myrica* may inhibit seed germination and seedling growth in loblolly pine through canopy shading and allelopathic effects, although litter from wax myrtle appeared to benefit pine seedlings. Based on the findings of Wells and Shunk (1938) it seems plausible that *Myrica* could also benefit tree seedlings by protecting them from salt spray. More work is required to determine which of these relationships represent controlling factors, causing vegetation change.

Despite the long history of research on causes of species zonation and retreat on sandy coastlines, few generalizations can be drawn about mechanisms of forest retreat and interactions with sea-level rise. Many of the factors considered important in forest zonation and change (salt-spray exposure, erosion, burial by sand, storm surges) occur primarily, or are intensified, during hurricanes and other storms. Where forest on the leeward side of sandy barriers meets salt marsh, sea-level rise may eliminate forest through increased salinity and/or flooding. However, on the seaward or windward edges of sandy shorelines, sea-level rise may eliminate coastal forest primarily by increasing erosion. As shorelines retreat and seaward shrubs and trees disappear, salt-spray may penetrate farther into the forest, eliminating sensitive species and causing shifts in vegetation zones behind the forest edge (Bellis 1995). Changes in storm intensity or frequency, changes in sand supply, either through natural geomorphic processes or human constructs, and destruction of sand-binding vegetation may all have a greater effect on the rate of retreat of coastal forest on sandy shorelines than on other types of shorelines.

HURRICANES: EFFECTS ON COASTAL FOREST AND POTENTIAL INTERACTIONS WITH SEA-LEVEL RISE

Hurricanes and violent frontal storms produce a variety of apparently destructive effects. However, their role in coastal forest retreat may be minor in some coastal systems, and their effect beneficial in some coastal communities on the Gulf of Mexico (Conner et al. 1989). These storms produce high winds that may cause damage to trees through wind-throw and breakage. They often expose inland plants to salt through salt spray and storm surges. Storm surges may alter substrate elevations by causing erosion or sedimentation. Such changes in elevation would obviously alter the interaction of coastal vegetation with sea-level rise, and have been shown to be important in maintaining marshes in the face of rising seas (e.g., Baumann et al. 1984, Cahoon et al. 1995, Goodbred and Hine 1995, Guntenspergen et al. 1995, Leonard et al. 1995). Differential susceptibility to storm effects influences the species composition of coastal forest. However, present coastal forests have been exposed to storms throughout their history, and the role of storms in coastal forest retreat is not well understood. The role of storms in coastal forest retreat may differ depending on characteristics of the coastline and associated forest. Storm effects on different types of coastal forests are considered below.

Hurricane effects on swamp forest

Swamp forests appear fairly resistant to wind damage. Touliatos and Roth (1971) examined forest damage in Mississippi after Hurricane Camille (August 17, 1969 with winds >320 km/h and tidal surges >6.7 m). They ranked trees in resistance to storm damage and found cypress and tupelo gum to be second only to live oak and palm in resistance to breakage and uprooting (Table 2). Species typical of bottomland and pine forests were more susceptible. Doyle et al. (1995) found similar patterns in the Atchafalaya Basin of Louisiana after Hurricane Andrew (August 26, 1992, sustained winds of 220 km/h). Only 1% of stems >2.5 cm dbh were lost in their swamp forest plots, and none of the dominant species (*Taxodium* and *Nyssa*) uprooted. In contrast, plots dominated by bottomland hardwood forest lost 21.5% of stems >2.5 cm dbh. Many snapped or uprooted trees, however, subsequently resprouted. Hurricane Hugo (September 22, 1989, with sustained winds of 222 km/hr) caused less wind damage in swamp forests than in bottomland forests in South Carolina (Gresham et al. 1991, Putz and Sharitz 1991). Gresham et al. (1991) found that most baldcypress suffered only light crown damage after Hurricane Hugo hit the coast of South Carolina. Their data

show that ca. 10% of the baldcypress trees surveyed suffered broken tops or more severe damage. Putz and Sharitz (1991) found that 49% of bottomland trees and 19% of swamp forest trees > 20 cm dbh suffered major damage in Congaree Swamp National Monument, South Carolina. They defined major damage as uprooting, snapped trunk or loss of >25% of the tree crown. Loope et al. (1994) reported observations of much more extensive baldcypress damage (46% with “major damage”) in South Carolina after Hurricane Hugo, but this may have been related to storm surge damage (see below). Gresham et al. (1991) concluded that “tree species commonly found in the lower coastal plain (longleaf pine, baldcypress, and live oak) suffered less damage than species with larger natural ranges”. Hurricane Andrew (24 August 1992, with winds of 242 km/hr; Pimm et al. 1994) caused only minor damage to cypress of south Florida. Only 1-4% of the cypress trees near the eye suffered broken stems or were uprooted, and many trees suffered only partial defoliation, even though autumn leaf senescence had already begun (Loope et al. 1994, Armentano et al. 1995, Noel et al. 1995).

Touliatis and Roth (1971) attributed the variation in susceptibility to damage to depth of rooting, buttressing, and wind-resistance of crowns, noting that live oak and cypress are deeply rooted, and cypress and palm canopies offer little wind resistance. The resistance of swamp forest trees to hurricane damage suggests that wind-damage from storms plays little, if any role in the retreat of the forest/marsh edge in these systems. The greater susceptibility of bottomland forest species to damage, however, may facilitate movement of swamp forest into higher, less frequently flooded reaches of the forest as sea-level rises by reducing competition from bottomland species.

Leaf loss during hurricanes is common and has posed difficulties for using remote imaging techniques to assess forest loss directly after hurricanes (Cablak et al. 1994). Day et al. (1976) found that Hurricane Carmen (with high wind and torrential rains) caused premature leaf drop in both a bottomland hardwood site and a cypress-tupelo swamp at Lac des Allemands near New Orleans, Louisiana. The bottomland hardwood site contained species such as red maple (*Acer rubrum* var. *drummondii*), water tupelo (*Nyssa aquatica*), boxelder (*Acer negundo*), and cottonwood (*Populus heterophylla*). The swamp forest was dominated by baldcypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*). In both sites, litterfall peaked in early September, 2 months earlier than normal winter leaf drop and litter production. Defoliation is noted in most studies of hurricane impact, but has been attributed variously to high winds, salt spray, or effects of salt introduced in surge water.

Storm surges in swamp forest may cause greater tree mortality, but do not appear to permanently eliminate the forest. Conner (1995b) found that *Taxodium distichum* and *Nyssa* sp. suffered high mortality in two South Carolina stands exposed to the 3-m storm surge that accompanied Hurricane Hugo. A third stand, not exposed to surge water, suffered only minor wind damage. Natural seedling regeneration of canopy species was present but low 1.5 years

Table 2. Relative susceptibility of tree species to hurricane damage. Species listed in descending order of resistance (based on Touliatos and Roth 1971).

<u>Breakage</u> ¹	<u>Uprooting</u>	<u>Salt</u> ²	<u>Insect and disease</u>
palm	live oak	palm	live oak
live oak	palm	red cedar	palm
baldcypress	baldcypress	live oak	sweetgum
pond cypress	pond cypress	sugarberry	water oak
sweetgum	tupelo gum	slash pine	sycamore
tupelo gum	red cedar	longleaf pine	baldcypress
mimosa	sweetgum	pond cypress	pond cypress
dogwood	sycamore	loblolly pine	southern red oak
magnolia	longleaf pine	baldcypress	magnolia
sweet bay	mimosa	tupelo gum	tupelo gum
southern red oak	southern red oak	sweetgum	sweet bay
water oak	magnolia	water oak	hickory
sycamore	slash pine	sycamore	pecan
longleaf pine	loblolly pine	sweet bay	red cedar
slash pine	sweet bay	southern red oak	red maple
loblolly pine	water oak	hickory	mimosa
red cedar	red maple	mimosa	dogwood
hickory	dogwood	pecan	longleaf pine
red maple	hickory	magnolia	slash pine
pecan	pecan	red maple	loblolly pine
		dogwood	

¹ Modified from Touliatos and Roth (1971) based on observations by Loope *et al.* (1994).

² Modified based on Pezeshki (1990), Hmielski (1994), Conner (1995a), McLeod *et al.* (1996), Tolliver *et al.* (1997), Williams *et al.* (1998, 1999).

after the hurricane and experimental plantings of *Taxodium* seedlings indicated that regeneration was possible in the affected stands. Poor height growth of planted seedlings in the stand that was not subjected to saline surge waters was attributed to the good survival of canopy trees there with rapid canopy recovery and consequent shading of the forest floor. Conner (1995b) concluded that the storm surge severely altered species composition in the swamp forest stands and that intervention (plantings) might be necessary to speed recovery of pre-hurricane composition.

It should be noted that storm surges differ in their effects, depending on water tables prior to the surge and the rainfall that accompanies the surge. In flooded soil, no pore space is available for salt water infiltration, and soil salinization is slowed (Gardner *et al.* 1992, Allen *et al.* 1996). During most hurricanes, storm surges are accompanied by heavy rainfall that help wash salt from the soil. Hurricane Hugo, which caused salt-kill in the swamp forests of South Carolina, was accompanied by

very little rain (ca. 21 - 65 mm; Gardner et al. 1992). Elevated salinities were noted in forest soil for at least 2 months until the winter rains of December and early January came. The following spring was abnormally dry, though, and Gardner et al. (1992) observed fairly long-term effects of the storm surge on forest soil salinity.

Little information is available on hurricane effects on the elevation of the swamp forest floor. Due to the low position of swamp forests in the landscape, it is unlikely that hurricanes would lower the swamp forest floor. Increased sedimentation may be possible. Conner and Day (1991), however, did not find elevated sedimentation rates in swamp forests of the Lake Verret Basin during seasons with hurricanes.

Hurricane effects on pine forest

Touliatos and Roth (1971), examining effects of Hurricane Camille in Mississippi, ranked slash pine and loblolly pine more susceptible to breakage than swamp forest dominants and many bottomland hardwoods. Hurricane Andrew caused high mortality among mature slash pines in the pine rocklands of south Florida (Armentano et al. 1995). Large (<17.8 cm dbh) slash pine on shallow soil (shallow limestone with deep solution holes) in the Long Pine Key area of Everglades National Park suffered ca. 32% mortality due primarily to bole breakage (Loope et al. 1994). South of the Big Cypress, where the limestone has fewer solution holes (and, presumably less opportunity for deep root development) 41 % of trees were downed (Loope et al. 1994).

Such overstory removal may simply affect age structure of hurricane-damaged pine stands. Loope et al. (1994) suggested that canopy openings created by Hurricane Andrew in the Pine rocklands of south Florida would allow recruitment of pine saplings into the overstory. Stoneburner (1978) examined tree rings in slash pines of barrier islands off the coast of Mississippi. He found evidence that slash pine growth increased following hurricanes, but that this response was delayed, occurring 3-5 years after a hurricane. In contrast, Alden (1993) found that slash pine growth on Cape St. George Island, Florida, exhibited reduced growth for several years after Hurricanes Eloise (1975), and Elena and Kate (1985). Johnson and Young (1992) found similar decreases in loblolly pine growth following storms on the Atlantic coast. Doyle and Gorham (1996) examined tree rings in slash pine in Mississippi ca. 20 years after Hurricane Camille struck the coast. They found two different growth responses to the Hurricane. Radial stem growth was not affected the year of the hurricane because, as Doyle and Gorham (1996) point out, hurricanes generally occur toward the end of the growing season. However, some trees showed increased growth in years following the hurricane and some showed reduced growth. The authors speculated that canopy trees sustained damage and suffered reduced growth following hurricanes, whereas subcanopy trees were released

by hurricane damage to canopy trees. (This type of pattern has been observed in Puerto Rico, where Hurricane Hugo killed mature trees and very young seedlings, but greatly speeded the recruitment of surviving seedlings into the sapling size class (You and Petty 1991)). Differences among studies on pines, therefore, may be partly due to differences in sizes of the trees studied. Alden (1993) selected large trees to obtain long growth records. According to predictions of Doyle and Gorham (1996) and observations that larger trees generally sustain the most hurricane damage (e.g., Loope et al. 1994), these individuals would suffer damage and growth reduction, whereas shorter individuals might experience growth enhancement.

Pines are susceptible to salt-spray damage (Wells and Shunk 1938). Most obvious salt-spray damage is associated with storms. These storms blow salt aerosols farther inland than normal, even on the relatively windy Atlantic coasts (e.g., Hall 1933, Wallace and Moss 1939, Moss 1940). Little et al. (1958) speculated that damage may be more severe after dry storms than after storms with large amounts of rainfall, because rain should wash salt from needles. However, they noted severe salt-spray damage to foliage after a wet hurricane in New England, attributing this damage to salt carried by wind that continued after the heavy rains had ceased.

The soil salinization caused by the storm surges may cause leaf drop or mortality in pines. Gardner et al. (1992) noted that pine mortality after Hurricane Hugo in South Carolina was greatest near swales and depressions where trapped surge water had caused extensive mortality among hardwoods. Hmielski (1994) noted that the Halloween Storm (Oct 31, 1991) and a subsequent January storm raised the salinity in the groundwater of a Virginia coastal pine forest zone to 20 ppt. Salinity remained elevated (5-15 ppt) for 4 months. In this instance, needles of loblolly pine (*Pinus taeda*) turned yellow, but plants dropped them and recovered.

In pine forest killed by Hurricane Hugo's storm surge, Gardner et al. (1992) noted subsequent pine regeneration. Survival of the first seedling cohort following Hurricane Hugo was poor, but the second year's cohort appeared to fare better. Gardner et al. (1992) attributed improved seedling survival the second year to increased rainfall and a progressive flushing of salt from soils. Thus, as in nearby swamp forest (Conner 1995b), the extreme salinization caused by this storm surge/low rainfall event caused forest death but apparently did not prevent subsequent tree seedling regeneration.

Southeastern pine species are relatively susceptible to insect damage following hurricanes (Touliatos and Roth 1971). Gunter and Eleutris (1973) noted outbreaks of bark beetle (*Ips* spp.) on downed pines a year after Hurricane Camille. Gardner et al. (1992) noticed bark beetle attacks on pines were concentrated on broken trees or trees near swales where salinization had occurred following Hurricane Hugo. Fredericksen et al. (1995) investigated effects of hurricane wind damage on susceptibility to bark beetle damage in loblolly pine. Their bending and pruning treatments, simulating wind effects of hurricanes, increased beetle density near stressed trees only

slightly, and no successful beetle attacks occurred. They did not test effects of soil salinization. Gardner et al. (1992) pointed out that they could not determine whether beetle attacks after Hurricane Hugo increased mortality, or whether infested trees would have died from primary effects of the hurricane anyway.

Pine forests occur on sandy coastlines, elevated areas of bottomland forests, and sediment-poor limestone coastlines. Effects of wind, salt-spray, and storm surges associated with hurricanes may be similar in these different forests. However, pine forest on sandy coastlines experience greater erosion and/or burial by sand during hurricanes.

Hurricane effects on hardwood hammocks

Tropical hardwood hammocks of south Florida have been considered fairly resistant to hurricane damage by many researchers. The stature and profile of a stand appears to affect its susceptibility to hurricane wind damage. Craighead (1974) attributed hurricane resistance of these stands to the streamlined outline of their canopy, noting that damage usually only occurred at the edge of the stand or in areas where hammocks have been opened up for roads, paths or boardwalks. Loope et al. (1994) reported that Hurricane Andrew caused extensive damage in these forests, downing 20-30% of the large trees in tropical hammock forests of Elliott Key, Biscayne National Park, Florida. They also noted, however, that “stands of shorter, smaller-diameter trees survived with much less damage, often with loss of only minor branches.” Thus, stature and stand form appear to affect wind protection within a stand, and consequently, susceptibility to hurricane damage.

Hurricane Andrew completely defoliated all hardwoods except oaks, but new leaf production was noted within 3-4 weeks of the hurricane (Loope et al. 1994). Although oaks were only partially defoliated, they were slower to produce new leaves. Loope et al. (1994) observed that “Andrew hit live oaks particularly hard”, causing major branch loss. This conclusion contrasts with observations along other parts of the Gulf and Atlantic coasts, where live oak (*Quercus virginiana*) has generally been noted for its resistance to hurricane damage (e.g., Touliatos and Roth 1971, Bellis 1995). This apparent contradiction may stem from differences among researchers in their evaluation of damage, or may reflect differences in hurricane resistance between the tropical hardwood species that co-occur with live oak in south Florida and other hardwood species that co-occur with live oak at more temperate latitudes.

Wind damage from hurricanes is not necessarily fatal in these tropical hardwood hammocks. Loope et al. (1994) noted that large individuals of lignum vitae (*Guaicacum sanctum*) “have been repeatedly windthrown by hurricanes but resprouted”. Resprouting in tropical trees following hurricane damage is a common response that has been noted throughout the Caribbean

(e.g., Bellingham et al. 1994, Zimmerman et al. 1994). Mortality of damaged trees may be delayed months or years, however, as has been observed in the tropical forests of Puerto Rico (Walker 1995) and the Yucatan Peninsula (Whigham et al. 1991).

Even where hurricanes have caused tree mortality, stand recovery has generally been noted. Alexander and Crook (1974) noted that Hurricane Donna (September 1960, winds of 290-320 km/h, and a storm surge of ca. 4 m; Williams and Duedall 1997) selectively killed hardwood hammock species, resulting in mangrove invasion. However, they also noted that tropical hammock species were recovering. Loope et al. (1994) noted that seedlings and saplings in hammocks fared well during Hurricane Andrew, most retaining at least part of their foliage. In general, hurricanes have not been observed to effect permanent changes in hardwood hammocks. However, fires following hurricanes may slow recovery, and hurricanes may increasingly facilitate invasion of hardwood hammocks by non-native species (e.g., Horvitz et al. 1995).

Fires following hurricanes have been reported in tropical forests (Whigham et al. 1991, Furley and Newey 1979). Whigham et al. (1991) suggested that fires following hurricanes might be especially important in areas with shallow organic soils. However, despite the combination of direct hurricane damage and subsequent fire damage to their study site (a dry tropical forest on the Yucatan Peninsula), Whigham et al. (1991) concluded that forest composition was unlikely to change.

Effects of hurricanes on the soil surface elevation of tropical hardwood hammocks has not been well studied. Although Hurricane Andrew was accompanied by a large storm surge (>5 m high at Miami, Florida; Williams and Duedall 1997), little erosion was noted in the tropical hardwood hammocks of south Florida (Loope et al. 1994). Loope et al. (1994) did not mention sedimentation deposition in hardwood hammocks, as was noted in mangrove swamps of south Florida following Hurricane Andrew (Risi et al. 1995). Catastrophic peat fires that followed the Yankee Hurricane of 1935 were at least partially attributed to hurricane-produced fuel loads (Craighead 1974). Peat fires can cause long-term vegetation changes in south Florida by lowering the surface elevation and changing the flooding regime at a site (Wade et al. 1980). Those following the Yankee Hurricane temporarily destroyed hardwood hammocks and destroyed cypress heads (Craighead 1974).

Farther north on the west coast of Florida, hurricanes can cause extensive damage to coastal subtropical hardwood hammocks. In some low lying areas of this coast, stands of forest exist on topographic highs in the underlying limestone, surrounded by salt marsh (Hine and Belknap 1986, Hine et al. 1988). Tree blow-down on these forested islands was photographed in Citrus County after Hurricane Elena in 1985 (Hine et al. 1987), and noted at Waccasassa Bay, in Levy County, after the “Storm of the Century”, an extratropical storm that occurred in 1993, (Williams et al. unpublished data).

Observations made by Williams et al. on effects of the “Storm of the Century” suggest that such storms may affect species composition of the forest edge, but may be more likely to affect forest retreat through effects on soil surface elevation than through direct damage to trees. Of the trees in 13 long-term monitoring plots at Waccasassa Bay, only southern red cedar (*Juniperus virginiana* var *silicicola*) experienced significant uprooting and mortality. Other trees of the forest edge (*Sabal palmetto*, *Quercus virginiana*, and *Celtis laevigata*) experienced little fatal damage, and wind damage from this storm did not extend far inland. The storm did not appear to permanently affect seedling recruitment. In those heavily damaged stands where tidal flooding was sufficiently infrequent to permit seedling establishment (Williams et al. 1999), new southern red cedar recruitment occurred within 4 years. Destruction of canopy trees represented permanent tree loss only in stands where sea-level rise had already eliminated recruitment (Williams et al., unpublished data).

Effects of storms on soil surface elevation in these systems may be important in how the stands interact with sea-level rise. Deposition of sediment in coastal forest stands was noted after the “Storm of the Century” and after subsequent storms at Waccasassa Bay (Williams et al., unpublished data). The amount of sediment deposited was less than that reported for nearby marshes (Goodbred and Hine 1995). The net effect of storm-induced erosion, deposition, and changes in the forest floor wrought by tree tip-ups has not been evaluated, but may influence the susceptibility of the forest edge to rising seas.

As in other forest systems, salt water introduced in storm surges can cause leaf drop among forest trees. Effects of the salt water are often obscured by the fact that these surges often are accompanied by strong winds that physically damage leaves and often occur late in the growing season, sometimes only weeks before winter-deciduous species begin normal leaf drop. Hurricane Allison (5-6 June 1995) was the earliest hurricane to strike Florida during this century (Williams and Duedall 1997). Although Hurricane Allison struck the panhandle of Florida, she generated a surge that, pushed by westerly winds, flooded forest along the Florida peninsula at the height of the growing season. At Waccasassa Bay, Florida brackish water (14.5 ppt sea salt) was pushed 100’s of meters into the forest beyond the normal reach of the tides. No rain was received for over a week after the surge. During the week following the surge, leaves of winter-deciduous species (e.g., mulberry, fig, sweetgum, elm and maple) yellowed or turned brown and dropped (S.A. McDonald, Yankeetown, Florida, personal communication). Grass and freshwater marsh vegetation that occurred in pockets in the forest understory browned. No visible damage occurred to leaves of evergreen species (e.g., cabbage palm, southern red cedar, live oak, magnolia). Deciduous trees began to releaf 2-3 weeks after the surge, following an episode of heavy rainfall (S.A. McDonald, personal communication). Thus, as in other forested systems in the southern United States, salt intrusion associated with infrequent storm surges does not appear to cause permanent

change in low-lying hardwood hammocks.

Hurricane effects on sandy shorelines

Hurricanes, through their effects on erosion, are considered a major force in the transgression of sandy shorelines (e.g., Tedesco et al. 1995, Dingler and Reiss 1995). Most of the forces shaping coastal forests on sandy shores (e.g., surges, salt spray, and sand movement) are associated with hurricanes, as discussed above (see section on “Forest change and retreat on sandy shorelines”). Hurricanes often cause acute exposure to salt spray and saline surge water, as previously discussed. They may also directly erode the coastal forest edge, as Hurricane Camille (1969) did, uprooting and eroding soil from the roots of live oaks on mainland and barrier island beaches of Mississippi (Gunter and Eleuterius 1973).

Some researchers have suggested that hurricanes may expose mineral soil on sandy coasts, providing opportunity for pine regeneration and, thus, favoring pine dominance (Stoneburner 1978, Vogel 1980). Although there is evidence for increased growth in established pine seedlings following hurricanes (see above), there is little published evidence for increased seedling establishment.

The role of hurricanes in coastal forest retreat

Coastal forests on the Gulf of Mexico have been repeatedly exposed to hurricane damage throughout their history. It is, therefore, not surprising that species characterizing the coastal edge of forests (e.g., *Taxodium distichum*, *Quercus virginiana*) appear very resistant to hurricane damage. Even in instances where wind damage or soil salinization by storm surges has killed trees, subsequent tree regeneration has generally been observed. Thus, direct impacts of hurricanes on forest trees may simply serve to reinforce existing zonation patterns near the coast. (Exceptions may occur where forest stands are surrounded by invasive exotics (Horvitz et al. 1995)).

Permanent effects of hurricanes on coastal forest retreat or advance are more likely to occur through the influence of hurricanes on erosion and sedimentation (Conner et al. 1989). On sandy coasts, hurricanes appear to play a major role in forest retreat through their erosive action. On low-lying coastlines, effects of hurricanes on soil elevation is not so clear. Hurricane deposition of sediment in mangrove forests of south Florida has been repeatedly noted and measured. The degree to which this sedimentation counteracts effects of sea-level rise has not been fully analyzed. Sediment deposition associated with storms has also been observed at the coastal edge of other low-lying forests. The quantity of deposition, the spatial distribution of sedimentation and erosion

and, thus, the effect of these storms on the forest's interaction with sea-level rise have been even less well studied than in mangroves.

It has been suggested that storm frequency and strength may change as a consequence of global warming. Modelling efforts by Emanuel (1987) yielded predictions that a doubling of atmospheric CO₂ would lead to a 40-50% increase in the destructive potential of hurricanes, due to increased maximum wind speeds. Models by Bengtsson et al. (1996) suggested that, although maximum wind speeds in hurricanes may increase somewhat, hurricane frequency will decrease. Overpeck (1990) predicted that changes in disturbances such as hurricanes would significantly alter forest composition. The impact on the forests of the Gulf of Mexico, however, is unclear; the composition of these forests has historically been shaped by repeated hurricane impact. Changes in storm frequency and strength may affect interactions between coastal forest and sea-level rise by modifying rates of sediment deposition and erosion.

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Chapter 2
SEA-LEVEL RISE AND MANGROVES

Zuleika S. Pinzon

Mangroves constitute an important ecosystem in the Gulf of Mexico and south Florida. Their location at the interface between marine and terrestrial habitats makes mangroves vulnerable to any change in sea level. Due to their susceptibility to changes in duration and amplitude of flooding which lead to changes at different levels of the ecosystem, mangroves have been suggested as good indicators of coastal changes (Blasco et al. 1996). A framework for monitoring the response of Florida's mangrove forests to global change has been established (Davis et al. 1994).

RESPONSES OF MANGROVE FORESTS TO SEA-LEVEL RISE

Predictions of possible responses of mangroves to sea-level rise were made as early as in the 1950s (Egler 1952). Nevertheless, literature defining detailed responses of mangroves to sea-level rise conflicts. Parkinson et al. (1994) gave a good comprehensive discussion on some of these contradictions. We review apparent contradictions, predictions, and factors that may affect mangrove response to sea-level rise.

Predictions and recent data

Changes expected to occur at the seaward and landward margins of mangroves have led scientists to identify different potential responses to sea-level rise. Mangroves may retreat at the shoreline. This retreat could be either accompanied by compensatory mangrove expansion on the landward margin (relocation), or without any replacement, yielding net mangrove loss and shoreline recession. Alternatively, there could be some expansion of the seaward margin (progradation) or on the landward side, producing a net gain in mangrove extent.

Retreat of the coastal margin would be due to submergence or to erosion (lost of sediment or peat from around the roots) of seaward margin due to sea-level rise and/or the disappearance of protective barriers in the seaward front. Erosion rates may increase in certain areas worldwide, including some where mangroves grow (Hanson and Lindh 1993, Wells 1995). This erosion would exacerbate effects of sea-level rise. Wanless et al. (1994) predicted that with sea-level rise of about 3mm/yr nearly all south Florida coastlines would retreat. Seaward mangrove margins would erode and the landward margin should continue to build upward. Current relative rates of sea-level rise

(since 1930) are even higher than those during the 5500-3200 years BP period for this region, and are about 10 times the rate during the past 3200 years. However, since these current rates followed a period of growth of coastal sediment bodies, which was not the case during the mid-Holocene, we could expect that erosional rates would not be as high as during that previous period (Wanless et al. 1994).

Ellison (1993) illustrated a case of mangrove retreat due to sea-level rise accompanied by erosion, in Bermuda. The rate of sediment accretion was lower than the rate of sea-level rise and sheet erosion occurred at the seaward edge forming a small cliff. As a consequence, some mangrove trees collapsed because they could not stand effects of the wind since their root support was weakened. The seaward edge had died back in the last century approximately 80 m from its previous position, which had apparently been stable for at least 1000 years (Ellison 1992). This erosion weakened the trees support making them more susceptible to windthrow. In this case mangroves could not migrate landward because of steeper contours in the surroundings.

Erosion might not be limited to the seaward edge of mangroves. Wolanski and Chappell (1996) predicted that the channel of the Norman River estuary, in Australia, would widen throughout its length as a consequence of bank erosion due to sea-level rise. Mangroves on eroded banks along that channel would presumably be lost.

When there is shoreline retreat but simultaneous expansion on the landward side, researchers have termed this change "relocation". Mangroves would retreat inland as a slow rate of sea-level rise induces changes in salinity gradients and flooding regimes, resulting in mangrove encroachment into inland areas. Migration landward might be prevented, however, by steep slopes, as has occurred in Bermuda (Ellison 1993), or human barriers such as embankments or sea walls (Bird 1993, Snedaker 1993). Under this scenario, a shift in species composition along the flooding gradient could also occur, leading to a change in mangrove forest structure. Specific responses of mangrove species will be discussed further below.

Mangroves may expand landward or seaward by colonizing current salinas (bare sand or mud flats in the center of mangrove ecosystems, where salinities are extremely high), increasing its abundance in current scrub mangrove sites, and/or colonizing new inland zones due to saline water inundation. This will depend on the rate of sedimentation and on the species-specific characteristics of propagules (e.g., size, buoyancy). Based on a very low rate of sea-level rise (1 mm/year), and analyzing case studies in Western Australia where natural processes and industrial impacts simulated a sea-level rise, Semeniuk (1994) predicted mangrove encroachment of tidal creeks and colonization of salt flats or up-slope habitats. Park et al. (1989a) used a simulation model to predict the response of U.S. coastal wetlands to future sea-level rise. Their model predicts that mangroves would increase in some areas of the Gulf of Mexico with sea-level rises up to approximately 1.5 m by the year 2100, if dry land areas are not protected by levees or similar structures. For highest

rates of sea-level rise predicted, mangroves decline. Although the model has some limitations (see Titus and Greene 1989), like generalizing an accretion rate for all the sites studied, it gives some insights of the possible responses of mangroves and wetlands in general to sea-level rise.

Snedaker (1993, 1995) included another scenario where precipitation and fresh-water runoff play the major roles in defining the fate of mangroves. This scenario is more applicable to peat forming mangrove environments, typical of southern Florida, than to non-peat-forming environments (Snedaker 1993). According to Snedaker, if reductions occur in the input of fresh water to mangrove forests, results could be similar to those of subsidence observed for areas of salt marshes in the eastern coast of U.S. Mangrove productive potential would decrease, and the increased availability of sulfate from sea water could accelerate anaerobic decomposition with subsequent loss of peat mass. In this regard, Maul (1993) pointed out that in arid areas, where peat production rates are lower than in rain-fed humid areas, mangroves might be more vulnerable to be overstepped or abandoned, implying too that precipitation and catchment runoff may be more important factors than the sea-level rise itself.

Ellison and Stoddart (1991) studied stratigraphy records from low, limestone islands, from deltaic environments and continental margin. Based on the responses of mangroves during the Holocene, and the absence of mangroves during the period of rapid sea-level rise, they predicted collapse of modern mangals in areas where the rates of sediment accumulation are low under current predictions of sea-level rise. They stated that "...in the absence of significant allochthonous sediment input, mangrove ecosystems... are under stress at rates between 9 and 12 cm/100 cal years, and cannot persist in their expansive modes at rates above this." Snedaker et al. (1994), however, indicated that some mangrove islands in the Florida Keys have expanded seaward and landward with a sea level rise of 23 cm/100 yr. (i.e., have been able to keep up with rates of sea-level rise above those predicted to cause ecosystem collapse by Ellison and Stoddart (1991)). Storms may deposit large amounts of sediment in the mangrove forests of southwest Florida, however, and the role of this deposition in mangrove response to sea-level rise has not been fully evaluated (see sections on Accretion and Hurricane damage). Bacon (1994) assessed possible mangrove responses to sea-level rise on 233 sites along 20 islands in the Eastern Caribbean without using stratigraphy records, and concluded that the ecosystem collapse predicted by Ellison and Stoddart (1991) in those islands is unlikely. He analyzed site characteristics of the islands and the conditions of the wetland margin to estimate the probability of mangrove reduction.

Callaway et al. (1997) studied sediment accretion rates in low tidal-range sites along the Gulf of Mexico by taking cores along transects in the low, mid and high intertidal zone and measuring the ^{137}Cs activity. They included three marsh areas (Aransas and San Bernard National Wild Refuges, in Texas, and Biloxi Bay in Louisiana) and one mangrove area in the Florida Keys. Net accretion was positive for the Florida Keys, meaning that mangroves there have been keeping

up with recent rates of relative sea-level rise. They also found that the organic accumulation rates in the sediments of the mangrove areas in the Florida Keys were higher than rates of mineral accumulation, with the latter extremely low when compared with other sites along the Gulf coast. Enos and Perkins (1979) described how parts of south Florida have prograded seaward more than 8 km during the last 4500 years through lateral accretion of lime mud and peat. According to them most of the islands in Florida Bay developed from mud banks, apparently assisted by mangrove colonization.

Mangrove responses to sea-level rise can not be generalized. Bacon (1994) and Semeniuk (1994) have highlighted the importance of considering local environmental settings, such as geomorphology, sedimentology, hydrology, and also the biological nature of the species involved when predicting these responses. Even the type of mangrove affected (fringe, estuarine, basin or scrub) and the windward/leeward aspect can also affect the kind of response (Bacon 1994).

Stratigraphy records seem to indicate that mangroves will be able to keep pace with sea level rise, as long as the rates of sediment accretion or mangrove peat formation balance that change. Some coastal wetlands will depend on sediment supply from adjacent river catchments (Bijlsma et al. 1996), i.e., allochthonous sediment (see Ellison 1992) to keep up with sea-level rise. Historical studies on the development of mangroves under sea-level rise conditions seem to indicate that high islands and continental coastlines will be more prepared to cope with rising sea-level than low carbonate coastlines. Macrotidal and river-dominated deltaic mangrove systems are expected to persist with sea-level rise, although erosion of the seaward margin is also expected. In the case of low islands, in carbonate settings, where sedimentation is mainly autochthonous (from calcareous sediment or mangrove peat), mangroves are most vulnerable to sea-level rise (Woodroffe 1990, Ellison and Stoddart 1991, Parkinson et al. 1994). Nevertheless, Snedaker et al. (1994) suggested that carbonate production in some oceanic islands might compensate for the lack of significant inputs of allochthonous sediment. High islands and continental coasts with relatively fast accretion rates might be less affected by sea-level rise (Ellison and Stoddart 1991).

Past Analogues

In northern Australia, with macrotidal conditions and dominance of allochthonous sediments, mangroves have persisted for about 8000 yrs (Woodroffe 1990). Mangroves became established during a transgressive phase between 8000 and 6000 years BP, when sedimentation rate should have been about 6 mm per year (Woodroffe 1990). During the period 6800-5300 years BP sea level was relatively stable and mangroves flourished covering extensive areas (Woodroffe et al. 1985). However, since then, mangroves have become reduced in area as sediments progressively

built up to a level at which tidal flooding ceased, eliminating the intertidal environment and forming in many cases bare, high-tidal flats (Woodroffe et al. 1985, Woodroffe 1990). With the estimates of future sea level rise of 2-9 mm/yr (Warrick et al. 1996), re-establishment and expansion of mangroves on formerly tidal floodplains might be expected in northern Australia and other tidally dominated systems (Crowley 1996), as long as vertical accretion rates keep up with those rates.

In tropical Australia, macro and mesotidal mangrove areas exposed to similar sea-level rise during the Holocene responded in different ways. This region experienced a rapid post-glacial sea-level rise until 6000 years BP. Wolanski and Chappell (1996) compared the response of three Australian tidal estuaries with different hydrodynamics and geomorphic features to sea-level rise during the period about 7000 to 6000 years BP. In one of them, South Alligator, sedimentation on the mangrove tidal plain kept pace with the sea-level rise, and mangroves expanded throughout most of the valley that existed before inundation took place. In the Norman River estuary sedimentation did not keep pace with sea level and mangroves were drowned and overtaken by lower intertidal and subtidal sedimentation, and the shoreline changed as mangroves migrated further inland. In the third case, Coral Creek, which does not receive any terrigenous sedimentation, mangroves moved upslope during sea-level rise and subtidal marine sediments buried the transgressive mangrove facies. Wolanski and Chappell (1996) modelled the effect of instantaneous sea-level rises of 0.1-0.5 m on these estuaries, using current hydrodynamic settings, and predicted similar responses as those that occurred during the late stages of post-glacial sea-level rise.

There seem to be indications that in other areas characterized by autochthonous sediment deposition mangroves have persisted since before 6000 years BP (Woodroffe 1990). These findings suggest that in some cases mangroves might keep up with sea-level rises as high as 10-15 mm/yr (Woodroffe 1990). Mangroves have persisted throughout the Holocene in the Guyanas, in northern South America, where the sediment supply from the Amazon mouths apparently allowed vertical accretion to keep pace with rates of sea-level rise as high as 60 cm/100 years during several centuries (Jelgersma 1994). In Jamaica, palynological evidence suggests that mangroves have persisted there for the past 6500 years, although with a reduction of *Rhizophora* areas (Hendry and Digerfeldt 1989). Bacon (1990, 1994) indicated that preliminary investigations supported the existence of mangroves throughout the Holocene in Trinidad. This persistence, however, may have been as mangrove patches, in a refuge mode (sensu Bloom 1970).

Several authors (e.g., Scholl 1964a, b, Parkinson 1989, Ellison 1996) agree that mangrove forests in the Wider Caribbean Region established expansively just after about 3000 YBP, when the rate of sea-level rise dropped to 4 - 7 cm/100 years. Ellison (1996), using pollen analysis, showed that wide establishment of mangroves in Belize has only occurred in the last 3000 years.

On the southwestern coast of Florida, biological sediment production and accumulation in man-

groves outpaced the transgressive effects of sea-level rise after 3500 - 3200 YBP (Parkinson 1989). Prior to this time mangroves seem to have existed in reduced areas that served as refugia. Nevertheless, there are indications that in areas with autochthonous sediment accretion mangroves have been able to persist for short periods during the Holocene with rates of sea-level rise of up to 8-10 mm/yr (Woodroffe 1990).

Accretion rate

Parkinson et al. (1994) indicated that any conceptual model attempting to predict the fate of mangrove forests due to a sea level rise will depend on whether historical or geological data of accretion rates are used. Historical studies use the activity of ^{137}Cs and ^{210}Pb radionuclides to assess time of sediment deposition; geological studies use ^{14}C analysis of peat samples to assess time of organic sediment origin. They pointed out that peat accretion rates on geological time scales tended to be lower than historical rates, and that both displayed high geographic variability. These authors, using a conceptual model, predicted unstable (=submergence) mangrove forest conditions within carbonate settings of the Wider Caribbean Region for most projections of sea-level rise over the next century (1.0 - 9.1 mm/yr). They predicted stability of mangrove forests at rates of sea-level rise ≤ 1.6 mm/yr (potentially up to 4.9 mm/yr), but only if historical sediment accretion rates were used. Comparisons of their model's predictions with data on mangrove submergence on Bermuda over the past few centuries, led them to conclude that fates of mangrove forests were more accurately predicted when geological data on accretion rates were used, rather than historical rates. In general, therefore, they concluded that loss of mangroves can be expected to occur in carbonate settings, such as the Wider Caribbean Region, but not in the large river-dominated deltaic mangrove systems of the major tidally-dominated systems of the world.

Ross et al. (1991) compared aerial photography from the 1935-1991 period for some islands in the Florida Keys, and found landward migration of mangroves. Snedaker et al. (1994) also indicated that those same authors found seaward colonization of mangroves in these islands, despite the rise in sea-level. Though they mentioned that these areas colonized by mangroves are historically accreting carbonate shoals, specific rates of sediment accretion were not provided.

A recent historical study in marshes and mangroves of the Gulf of Mexico reveals vertical accretion rates of 1.8 to 8.9 mm/year (Callaway et al. 1997). In the mangroves areas of the Florida Keys, average rates were 1.9 to 4.2 mm/year. These rates are higher than the 1.4 to 2.0 mm/year that Lynch et al. (1989) estimated for Rookery Bay, Florida, using historical data too. Even their original (without consolidation-correction) rates were lower: 2.2. to 2.9 mm/year. Callaway et al. (1997) apparently did not use consolidation correction in their data.

Accretion in the Florida Keys may have been modified by human activities, such as dredging and construction. Parkinson et al. (1994) showed that rates of historical mangrove forest peat accretion were relatively high in one area of Florida when compared with other areas in the Wider Caribbean Region due to human intervention. In Hutchinson Island, an average of 9.5 mm/yr was estimated. This relatively high value apparently resulted from dike construction for mosquito control impoundments.

In south Florida, catastrophic events affect sedimentation processes too. There is evidence that hurricanes influence sedimentation and morphological modifications in the coastal environments of southwest Florida (Craighead and Gilbert 1962, Craighead 1964, Ball et al. 1967, Craighead 1971, Risi et al. 1995). Hurricane Donna removed about 60 cm of mangrove peat from some of the Ten Thousand Islands (Craighead 1971). On the other hand, this hurricane deposited mud as far as 8 km inland from Florida Bay shoreline (Ball et al. 1967). Craighead (1971) also described how this mud formed layers up to about 12 cm thick and extending over 15 km inland. A mud layer up to 20 cm thick and covering over 110 km² was deposited by Hurricane Andrew in 1992, and mangrove seedlings have become established on some of the exposed mud deposits so created (Risi et al. 1995). Such episodic sedimentation may partially explain perceived conflicts between Ellison's predictions of mangrove retreat in the absence of allochthonous sedimentation and observations of mangrove expansion in south Florida (e.g., Snedaker et al. 1994).

Maul and Martin (1993) estimated a rate of sea-level rise of 1.3 mm/yr for Key West, Florida, during the years 1846-1992. They also showed that the mean trend in the rate of sea-level rise for several areas in the peninsular Florida is 2.2 mm/yr. These rates of sea-level rise falls into the range for which the conceptual model of Parkinson et al. (1994) predicts stability using historical peat accretion rates. Other estimates for relative sea-level rise along Florida's shorelines, based on tide gauge records are: 2-4 mm/yr (Wanless et al. 1994), and 1.7-2.3 mm/yr (Penland and Ramsey 1990). Other states in the Gulf of Mexico have higher rates of relative sea-level rise, mainly due to subsidence (Penland and Ramsey 1990, Turner 1991).

Management strategies

Ellison (1992) suggests some management strategies to assist mangroves during sea-level rise. These strategies include: protecting eroding edges from further erosion; assisting in leaf litter retention to enhance peat production; and some prohibitive management strategies, such as limiting the access of motor propellers to mangrove areas. Titus and Greene (1989) suggested implementing policies limiting coastal development in areas currently undeveloped, so mangroves and other wetlands could expand into these areas as sea-level rises. Another alternative that

those authors favored was a policy of what they called presumed mobility, vacating some areas surrounding current wetlands, so these could migrate inland as sea level rises. Lewis (1992) has suggested subsidizing accretion rates by the controlled application of dredged material. Wanless et al. (1994) have also suggested that careful planning is needed now, when regional and local zoning and policies could help prepare for the forthcoming modifications to the environment due to sea-level rise. All these authors seem to agree that the sooner these management strategies are adopted, the better we will be able to cope with consequences of sea-level rise.

Despite changes in sea-level, mangrove forests have persisted through the Quaternary. Nevertheless, conditions now are not the same as earlier in the Holocene, so responses of mangroves to sea-level rise might be different. Even though mangroves have kept pace with some rates of sea level rise in the past, their responses to those same rates could now be different because humans have altered so much of the surrounding area (Parkinson et al. 1994, Ong 1995). In many places, mangrove will retreat landward if sea level rises, but barriers created by humans could interrupt this process. More immediate and localized anthropogenic impacts might affect the response of the ecosystem to global climate change (Edwards 1995). Presently, mismanagement and land use/abuse of mangrove areas appear to be more major threats to mangrove forests than sea-level rise (Maul 1993, Edwards 1995).

COMMUNITY ECOLOGY AND PHYSIOLOGICAL ECOLOGY OF MANGROVES: POTENTIAL PREDICTORS OF RESPONSE TO GLOBAL CHANGE

Mangrove Forest Zonation

Because mangrove forest zonation has typically been linked to gradients in elevation or proximity to the ocean, it seems reasonable to expect encroaching seas to shift mangrove zones landward. Such expectations are complicated, however, by inconsistencies in zonation patterns and uncertainties regarding causes of mangrove zonation. The classical zonation pattern for south Florida described by Davis (1940) depicts *Rhizophora mangle* dominating the seaward zone, with *Laguncularia racemosa* and *Avicennia germinans* dominating at higher elevations inland. His theory that zonation represented successional stages, although widely accepted for many years, was later contradicted by several authors (e.g., Thom 1967). Lewis et al. (1985) compared zonation in three different localities in Florida and showed that no single representation could accurately describe mangrove forests in Florida. None of the areas portray the classical zonation pattern described by Davis (1940). Detweiler et al. (1975), however, found mangrove distribution having the classical pattern in an area in Tampa Bay. Zonation does occur in the mangrove forests, including the classical one, but the sequence of species seems to change within and among locations.

Mechanisms to explain zonation patterns in mangrove forests have not been well elucidated. Thom (1967, 1975) proposed that zonation responds to geomorphological processes. Abiotic factors such as frequency of tidal inundation (Watson 1928) and salinity (Ball 1988) have been correlated with mangrove zonation. Macnae (1968) included another factor, waterlogging of the soil, determined by rainfall, drainage patterns, and evapotranspiration rates. Tidal sorting of propagules (Rabinowitz 1978), propagule predation (Smith 1987), and interspecific competition (Ball 1980) are other hypotheses proposed to explain mangrove zonation. Soil sulfide concentrations, being lower in stands of *A. germinans* than in stands of *R. mangle*, have been thought to influence mangrove zonation (Carlson et al. 1983, Nickerson and Thibodeau 1985). This variation in sulfide concentration, however, appears to result from differential abilities of the two species to oxidize their rhizospheres (Thibodeau and Nickerson 1986), and its role in zonation is unclear. Snedaker (1982) reviewed mechanisms causing zonation and emphasized potential differences in competitive ability across salinity gradients, driven by differential abilities to maintain high photosynthetic rates and low respiration rates at different salinities.

There are contradictory results in the literature regarding the roles of propagule dispersal and seed predation in zonation. The seed predation hypothesis predicts dominance of species with smaller propagules in the high intertidal and of species with larger propagules in the low intertidal zone. *Avicennia*, however, is the dominant genus in the low intertidal zone of mangrove forests in Australia, despite the small size of its propagules. Similarly, tests of the seed predation hypothesis, which predicts that the rarity or absence of any species in any zone is due to predation of its propagules by crabs, have yielded contradictory results. Smith et al. (1989) could not find a relation between *R. mangle* distribution in south Florida and its seed predation by crabs.

Transplant experiments challenge the contention that zonation among species is caused by physiological adaptation to different conditions along environmental gradients in the intertidal zone. Rabinowitz (1978) did a reciprocal planting experiment with seedlings of *R. mangle*, *A. germinans*, *L. racemosa*, and *Pelliciera rhizophorae*, in Panama, and found that, at least during the first year, seedlings grew about equally well in each other's adult habitat (i.e., in any of the mangrove zones). Similarly, in Costa Rica, Jimenez and Sauter (1991) found that *A. bicolor* survived and grew best in *R. racemosa* dominated stands. *R. racemosa*, although it grew and survived best in its "home" stand, also grew and survived in the *A. bicolor* stands in the higher intertidal zone. Snedaker (1982), indicated that first-year seedlings could apparently grow anywhere, implying that the importance of differential physiological performance during later life stages in determining zonation could not be totally disregarded. Ellison and Farnsworth (1993) suggested that the lower elevational limit would be determined by edaphic or physiological factors while the upper elevational limit would be determined by biotic interactions, in a manner similar to that in some temperate salt marsh zones.

Shifts in species composition may occur in some areas as a result of sea-level rise, implying changes in zonation. Jimenez and Sauter (1991) attributed the increase colonization of *R. racemosa* in forests dominated by *A. bicolor* as a result of increasing mean sea level in that area of Costa Rica they studied. Unfortunately, the relative importance of the different factors affecting seedling dynamics is not well understood, complicating predictions in this regard.

Mangrove Response to Freezing

Freezing temperatures in the Gulf and Atlantic coasts of the U.S., caused by cold polar air masses frequently invading during the winter time, prevent mangrove formations to thrive in these areas (West 1977). Periodic freeze events cause mortality of mangrove populations (Davis 1940, Lugo and Patterson-Zucca 1977, West 1977, Sherrod et al. 1986). The northern limit for the distribution of *Rhizophora* has been reported as Cedar Keys (29°N), Levy County, on the Gulf coast of Florida (Davis 1940, Graham 1964), and Flagler County on the Atlantic coast (Little 1978). In 1996, we observed *Rhizophora* successfully established in Seahorse Key (29°8'N), where it seems to be recovering after the 1989 freeze. Its propagules have been observed along the Texas coast (McMillan 1971, Gunn and Dennis 1973, Markley et al. 1982), but they do not establish naturally (McMillan 1971). However, the northernmost occurrence of well-developed *Rhizophora* and *Laguncularia* trees in the 1960s was around the Tamiahua Lagoon, Mexico, at 21°40'N (Ayala-Castañares 1969). *Avicennia* grows in shrubby form along different parts of the Gulf of Mexico, through Louisiana and Texas coasts (Sherrod and McMillan 1985, McMillan and Sherrod 1986). It grows up as far north as Seahorse Key, 29°8'N (McMillan and Sherrod 1986), even after the last severe freezing event of 1989 (pers. obs.). Little (1978), however, recorded *Avicennia* in the Apalachee Bay in the Gulf of Mexico at about 30°N. This location and St. Augustine, on the Atlantic coast of Florida, at 29°53'N, mark its northernmost distribution (West 1977, Little 1978). The Coastal Coordinating Council (1973, cited in Lewis et al. 1985) reported mangroves for Nassau County in Florida, which is at a higher latitude than these limits. The cold conditions on the Mississippi coasts, and not the lack of suitable habitat, prevent mangrove from growing there (Sherrod and McMillan 1985).

Freezing temperatures may produce aboveground damage or mortality in mangrove plants (Sherrod and McMillan 1985). Chilling (nonfreezing temperatures) may also cause injury or physiological dysfunction to mangrove plants. Bending of stem apex and/or wilting of apical leaves are some of the responses of *Avicennia germinans* seedlings to chilling conditions (McMillan and Sherrod 1986). Mortality due to freezing conditions have been reported for Florida (Davis 1940) and Louisiana (West 1977). *Avicennia germinans* were among the most severe native woody

plants damaged by the cold fronts of 1983 and 1989 in the southern part of Texas (Lonard and Judd 1985, 1991). Leaf death and twig damage up to the base of the plants were reported. The 1983 freeze caused a reduction of 80-85% in the mangrove populations in Texas (Sherrod and McMillan 1985), although in some locations population had recovered four years later, with individuals producing flowers and fruits (Everitt and Judd 1989). A remote sensing assessment of black mangrove on the Texas Gulf Coast indicated, however, that in some areas populations were even more reduced after the 1989 freeze (Everitt et al. 1996). According to Sherrod and McMillan (1985) recovery time depends on local climatic conditions and coastal management policies.

Apparently, there is a latitudinal gradient in chilling tolerance for the three species: *Avicennia germinans*, *Laguncularia racemosa*, and *Rhizophora mangle*. McMillan (1975) and Markley et al. (1982) found that populations from lower latitudes appeared less chilling tolerant than those from higher latitudes. Chilling tolerance decreased from Texas > Florida > Caribbean. Within the Gulf of Mexico, eastern and western populations have different responses to chilling temperatures. Populations from the Texas coast have greater chilling tolerance than those from Louisiana and Florida. This differential response may be a consequence of a combined effect of evolutionary divergence among populations and differences in winter temperature patterns across the northern Gulf of Mexico (McMillan and Sherrod 1986). McMillan (1986) also showed isozyme differentiation between populations of Texas and Mexico and those of south Florida and the eastern Caribbean. This divergence apparently resulted from a process of natural selection, as a response to the dramatic changes in regional climate during the Pleistocene (Sherrod and McMillan 1985). A similar adaptive latitudinal gradient for seagrasses has been showed in the Gulf of Mexico and Caribbean (McMillan and Phillips 1979).

Field (1995) suggested that mangroves would move further poleward if the average air temperature increases, and some models of impacts of global climate change on coastal vegetation have included northward expansion of mangroves (e.g., Park et al. 1989a, b). According to Snedaker (1995) the northern distributional limit of mangroves was reduced after the 1970s due to the occurrence of severe freezes. This observation led him to reject the hypothesis that mangroves on the Gulf of Mexico would expand northward with global warming. Factors controlling the latitudinal distribution of mangroves are complex and not completely understood (Woodroffe and Grindrod 1991). Temperature is indeed a key factor, but other factors such as ocean currents and biological characteristics of the propagules seem to be important too. Even when discussing temperature, some authors refer to air temperature (e.g., Chapman 1976) while others to sea surface temperature (e.g., Duke 1992) as regulating mangrove distribution. Some experimental plantings suggest that mangroves can flourish at higher latitudes than their current distribution (see Woodroffe and Grindrod 1991).

Hurricane Damage

Hurricanes may cause mangrove mortality, sedimentation, subsidence and changes in species composition. Seedlings may be killed (Smith et al. 1994, Baldwin et al. 1995), and larger trees may experience immediate or delayed mortality. Delayed mortality has been observed in individuals of *A. germinans* and *L. racemosa* that resprouted after hurricanes and in individuals of *R. mangle* that had bark damage or cracking stems, with death occurring months and even years after the hurricane (Craighead and Gilbert 1962, Smith et al. 1994, Baldwin et al. 1995).

In south Florida, susceptibility to damage appears to be related to size of individuals. Large trees are more likely to be damaged by hurricanes, but it is a non-linear relationship (Smith et al. 1994, Armentano et al. 1995, Baldwin et al. 1995, McCoy et al. 1996). Roth (1992) studied mangrove forests on the Atlantic side of Nicaragua struck by Hurricane Joan in 1988 and also found that damaged trees were significantly larger than unbroken ones. Similarly, Doyle et al. (1995) concluded that taller dominant trees are more susceptible to damage than subcanopy trees, which usually get damaged by felled and snapped trees. One extreme and particular situation described by Craighead (1971) on the impact of Hurricane Donna in 1960, is what he called “floating islands”. Pieces of red mangrove peat were lifted with the trees intact on it, and transported some distance away.

There is also a differential response to damage among mangrove species. Among the mangroves of south Florida, *R. mangle* experienced higher mortality rates than *A. germinans* and *L. racemosa* due to the impact of Hurricane Andrew in 1992 (Smith et al. 1994, Baldwin et al. 1995). A similar trend was found by Roth (1992) in mangroves of Nicaragua impacted by Hurricane Joan in 1988. Nevertheless, *R. mangle* seems to be the species with higher resistance to breakage (Roth 1992, Baldwin et al. 1995) but more prone to lean and branch damage (Baldwin et al. 1995). Resistance to windthrow follows this pattern too: *R. mangle* > *A. germinans* > *L. racemosa* (Roth 1992, Doyle et al. 1995).

Regeneration patterns are also different among the three species. Baldwin et al. (1995) assessed mangrove damage and recovery after Hurricane Andrew in south Florida. *R. mangle* re-established mainly through seedling recruitment while the other two species did via epicormic sprouting. About 50% of the trees that snapped, were leaned, or had branch damaged resprouted after the hurricane. Baldwin et al. (1995) also assessed regeneration in areas impacted by Hurricane Betsy in 1965 and indicated similar pattern of regeneration. Since their study was concentrated on the middle to lower intertidal zone, they suggested that results might differ in zones with different hydrologic regimes.

Apparently, catastrophic disturbances such as hurricanes may result in some shifts in species composition and forest structure. Craighead (1971) found that *Rhizophora* invaded *Avicennia*

-dominated areas that were devastated by the storm of 1935, and increased further in abundance after Hurricane Donna in 1960. *Avicennia* did not recolonize those areas. McCoy et al. (1996) predicted alteration in the forest structure at the site they studied (the mouth of Lostman's River) as a consequence of Hurricane Andrew. Large trees of *L. racemosa* were severely damaged, with just a few small individuals remaining. Recovery of the *L. racemosa* stands from seedlings was not expected due to the low number and sizes of *L. racemosa* in comparison to other species. Smith and Whelan (1999), tracking recovery in the 7 years following Hurricane Andrew, however, found that *L. racemosa* dominated recruitment at many sites.

Hurricanes in south Florida have frequently deposited sediment in mangrove forests (see section on accretion). However, due to an apparent increase in sulfide levels and more reducing conditions (lower redox potentials) in areas devastated by a hurricane, anaerobic decomposition may increase (Smith et al. 1994). This would result in reduction of the surface levels of peat soils and, together with rising sea-level, may interfere with the reestablishment of propagules in these areas (Smith et al. 1994). Some mangrove stands destroyed by Hurricane Donna in 1960 have since eroded and subsided, becoming deep intertidal and subtidal areas, uncolonized by mangroves (Wanless et al. 1994). Effects of hurricanes on soil elevation may differ depending on the position of the site relative to the eye of the hurricane. On the southwest coast of Florida, Hurricane Andrew deposited large amounts of sediment in mangroves with an onshore storm surge along the south eye wall of the hurricane, but merely destroyed mangroves without depositing sediment north of that wall (Risi et al. 1995). Swiadek (1997) suggested that erosion might continue long after Hurricane Andrew where uprooting and death of mangroves had left sediments unprotected from wave action. The net effect of hurricanes on soil elevation in the mangrove stands of south Florida is unclear.

The frequency for hurricanes in Florida is about 20 - 24 years, which agrees with the time these forests reach maturity (Lugo et al. 1974). If the frequency or strength of storms and hurricanes affecting south Florida change, as has been predicted by some authors (e.g., Emanuel 1987, Bengtsson et al. 1996), this change might affect regeneration cycles, forest composition, and interactions of the mangrove forest with sea-level rise.

Salinity, Flooding, and Sedimentation

Mangroves can tolerate up to 90 ppt of salinity (Snedaker 1982). They are able to utilize freshwater or ocean water depending on availability (Sternberg and Swart 1987). Nevertheless, there are differential responses of the species to salinity levels (Naidoo 1985, Pezeshki et al. 1990) with a possible optimum level for growth (see Ball 1988, Upkong 1991). For the species in the

northern Gulf of Mexico relative tolerance seems to be: *A. germinans* > *L. racemosa* > *R. mangle* (Odum et al. 1982).

Increased salinity in some areas may result as sea-level rises and precipitation levels are reduced (Ellison 1994). Rising sea-level could be one of the causes leading to saline water intrusion in the south Florida's porous and shallow water table (Sternberg and Swart 1987), although most researchers attribute the bulk of salt water intrusion in south Florida to groundwater pumping and diversions of fresh water (e.g., Klein et al. 1974, Thomas 1974). Increased salinity decreases net primary productivity and reduces growth in mangroves (Ball 1988, Lin and Sternberg 1992), affecting interspecific competition (Ellison 1994). On the other hand, it might give some advantage to the mangroves in their inland migration (see Snedaker 1993).

Mangroves can also tolerate various intensities of waterlogging, and species appear to react to flooding differentially (Naidoo 1985). However, when subjected to prolonged periods of floodings, like from the impoundments for mosquito control in Florida, mangroves may die (Harrington and Harrington 1982). Impoundments may vary in their effects on flooding and salinity. Rey et al. (1990) reported mangrove death in a closed impoundment in the Indian River Lagoon, Florida where, isolated from tidal water exchange, evaporation raised salinity to >100 ppt. Hatton and Couto (1992) found increased mortality in mangroves in Mozambique, Africa, due to a reduction in tidal exchange. Odum and McIvor (1990) pointed out that permanent flooding of the aerial root system due to diking or impounding has been an important factor causing the death of many mangrove areas.

The growth of mangrove plants may be influenced by sedimentation. Ellison and Farnsworth (1996) recently studied sedimentation rates around saplings in Belizean mangrove cays, a carbonate setting. Sediment accretion beneath saplings was 3-6 mm/year. Growth of saplings was depressed in the cay with lower sedimentation rates. The authors hypothesized that the sedimentation regime affected sapling growth. Undoubtedly, more studies on the responses of the different mangrove species to sedimentation, especially the early life stages, are needed.

CONCLUSIONS

Effects of sea-level rise on mangrove communities can not be generalized. Responses seem to be very site-specific. Relative sea-level rise over long time periods and sedimentation rates are key information required for predictions. It is obvious from the literature that we need more long term data on seedling and forest dynamics in mangrove vegetation, as well as more information on seedling responses to combinations of factors, to make more precise and detailed predictions. Nevertheless, past analogies have proven very useful in helping to understand the possible directions of mangrove changes due to sea-level rise.

We discussed the effects of sea-level rise without taking into account other factors that might be altered as a consequence of global climatic change. Changes in the frequency of storms and hurricanes, temperature, and atmospheric CO₂ concentration will act concomitantly with sea-level rise, but predicting the interactive effect of these factors is an even more difficult task. Changes in hurricane frequency may affect accretion rates, thereby affecting mangrove response to sea-level rise. Increasing CO₂ may increase growth and productivity of mangroves (Farnsworth et al. 1996), potentially contributing to peat formation and partially counteracting effects of sea-level rise. While existing evidence seems to indicate that overall existence of mangroves will not disappear as consequence of sea-level rise, it also indicates that they will be lost in many places.

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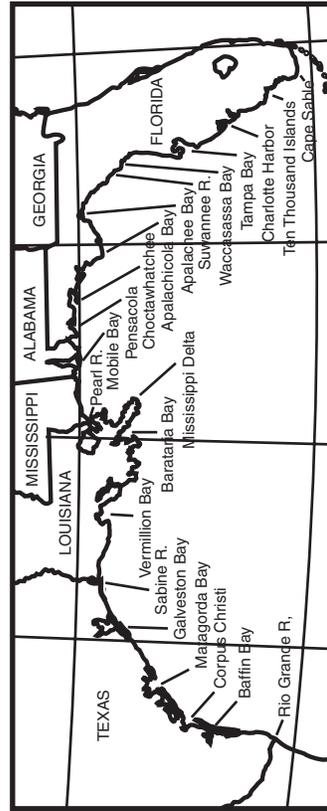
APPENDICES

Appendix 1.

Geographical Distribution of Trees and Shrubs along the Coast on the Gulf of Mexico (after Little, 1971, 1977).

For each species:

- = areas where distribution maps indicate a species exists on the coast
 - ▨ = areas where distribution maps indicate a species is within 60-100 km of the coast, but not on the coast.
- Species that occur within 10 km of the coast are listed.



Landmarks shown on species distribution records.

Codes following species name indicate flooding tolerance (after McKnight et al. 1981, Hook 1984), and/or zone of occurrence (after Wharton et al. 1982)

Flooding tolerance

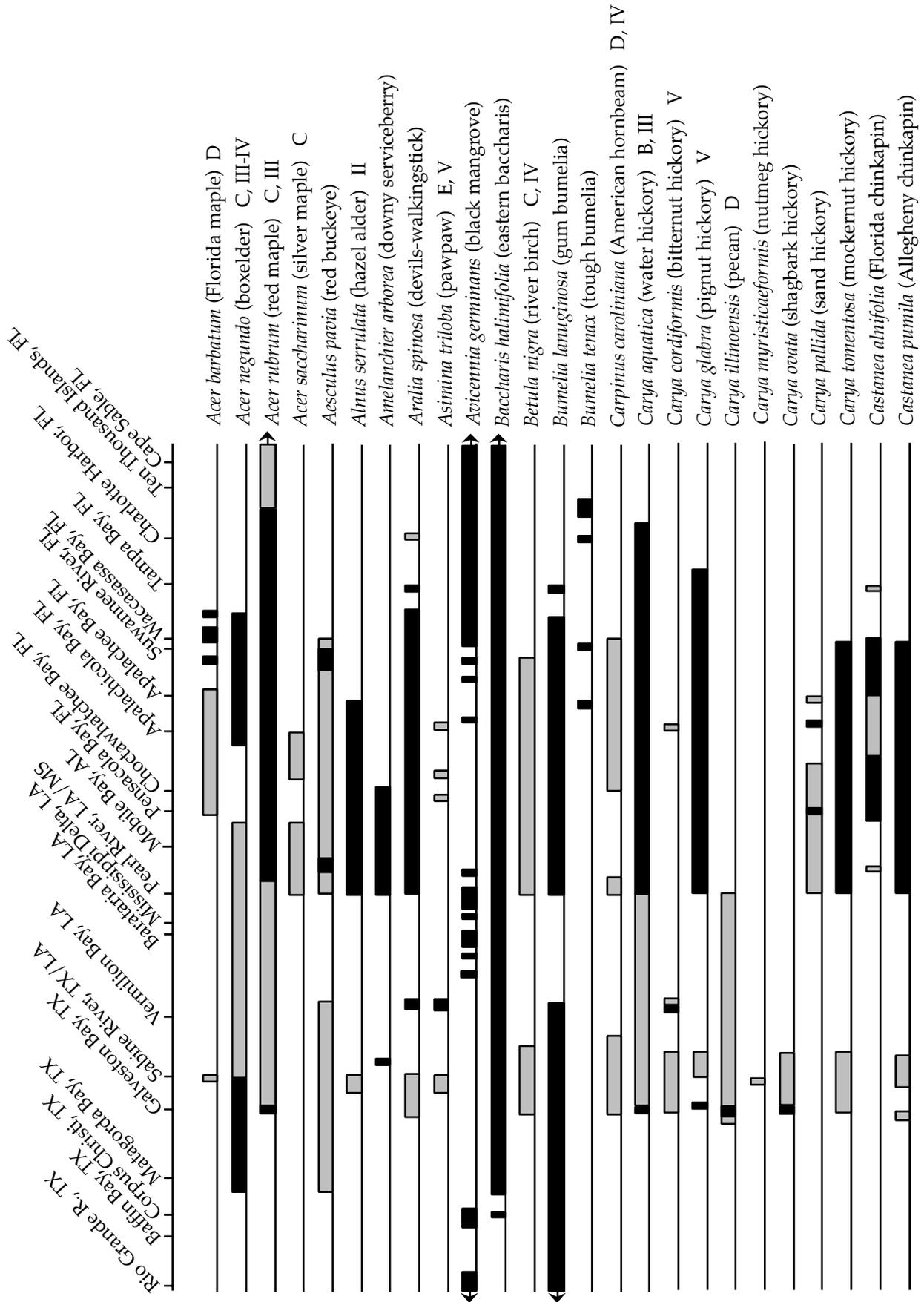
- A = most tolerant
- B = highly tolerant
- C = moderately tolerant
- D = weakly tolerant
- E = least tolerant

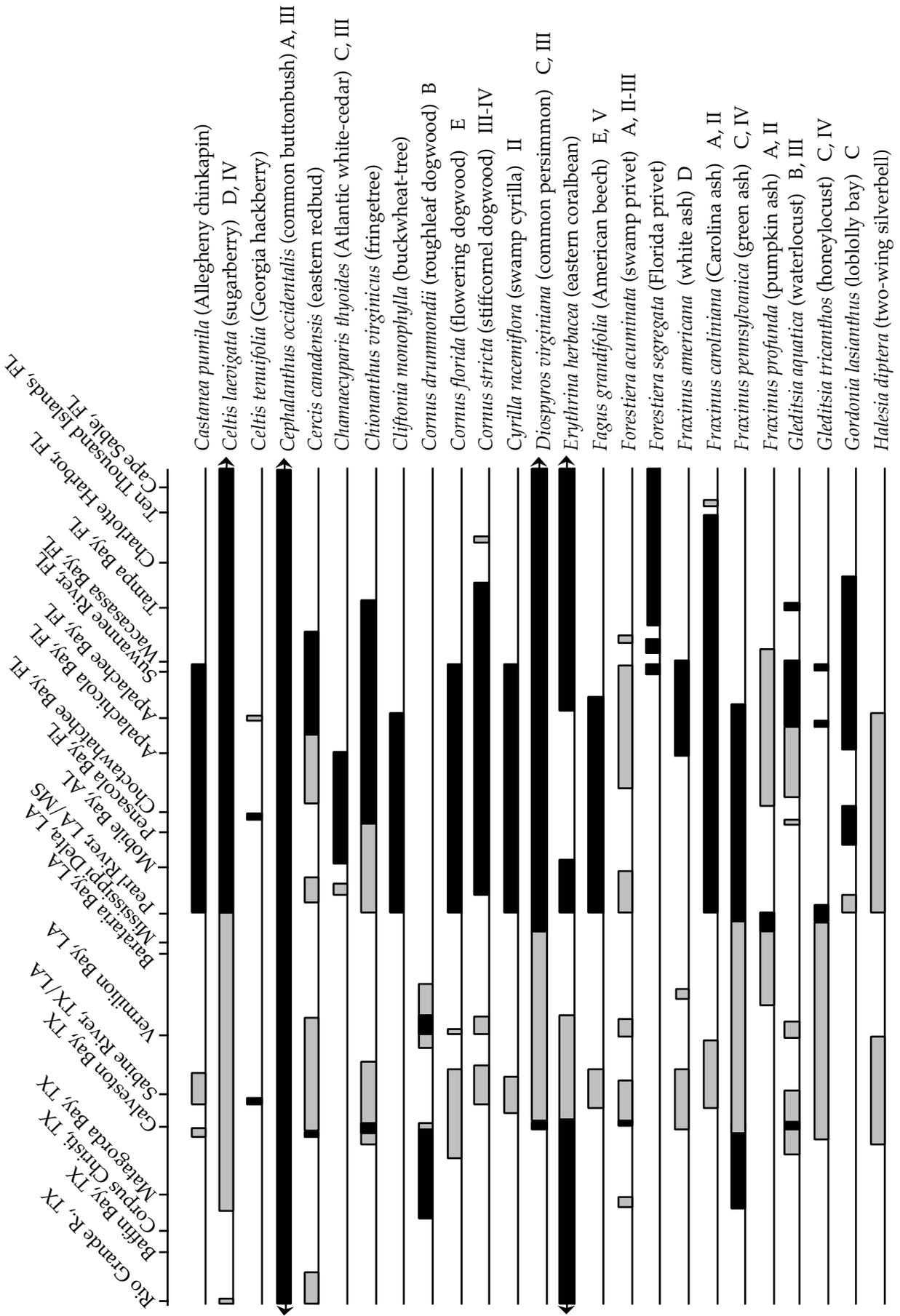
Zones of occurrence

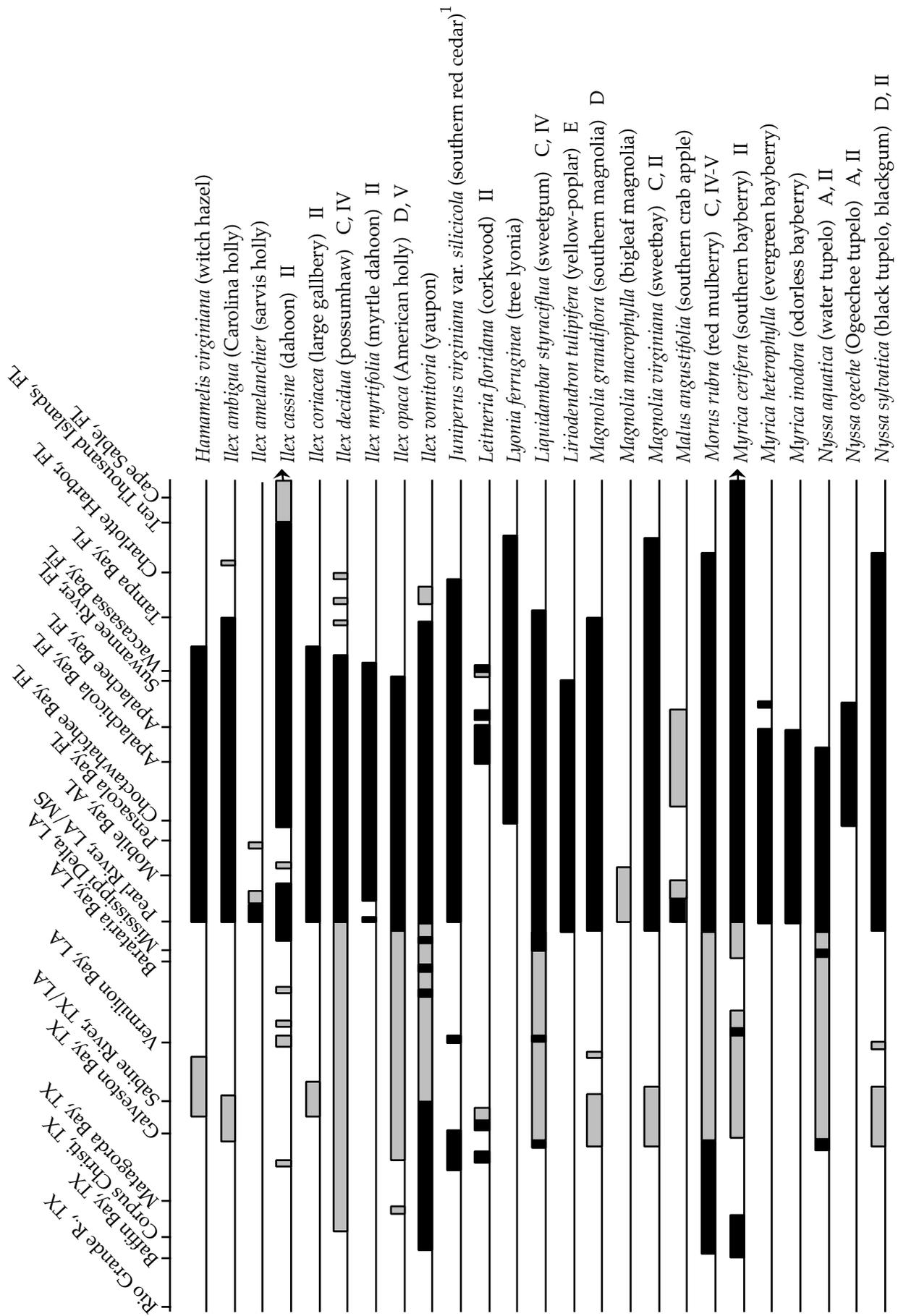
- II = flooded all year
- III = flooded >25% of the growing season (spring and summer)
- IV = flooded 12.5-25% of the growing season (spring)
- V = flooded 2-12.5% of the growing season
- VI = flooded <2% of the growing season

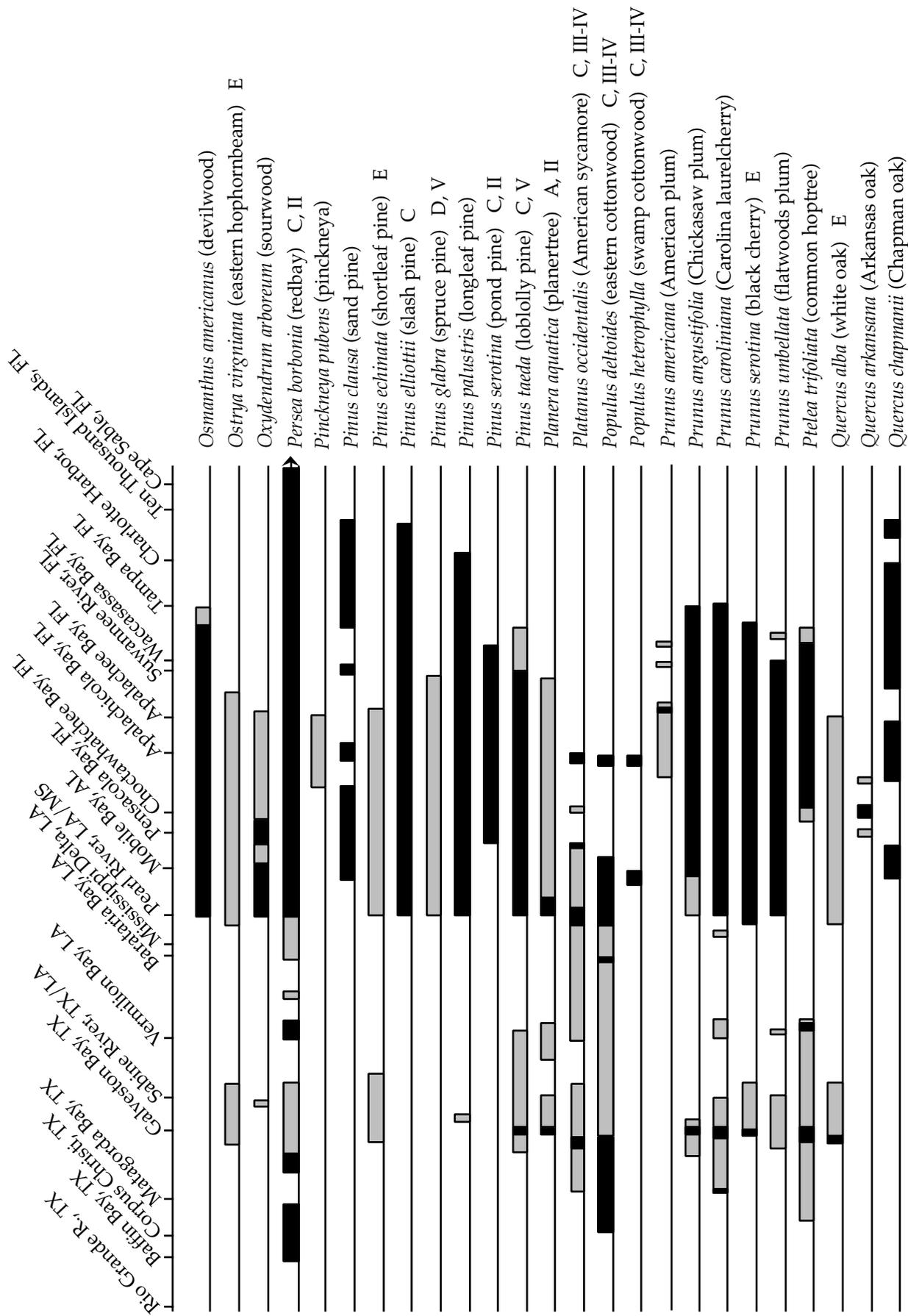
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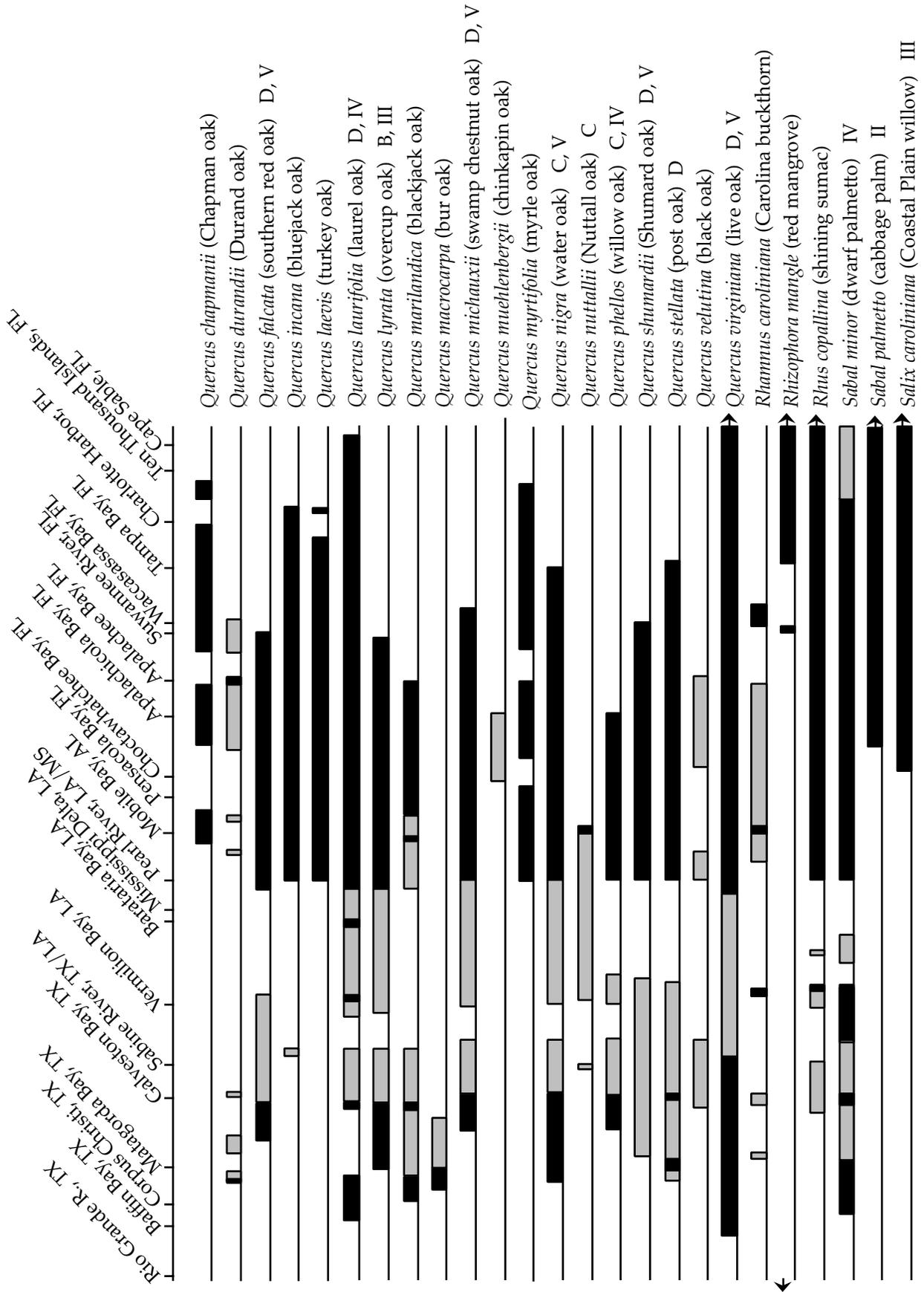
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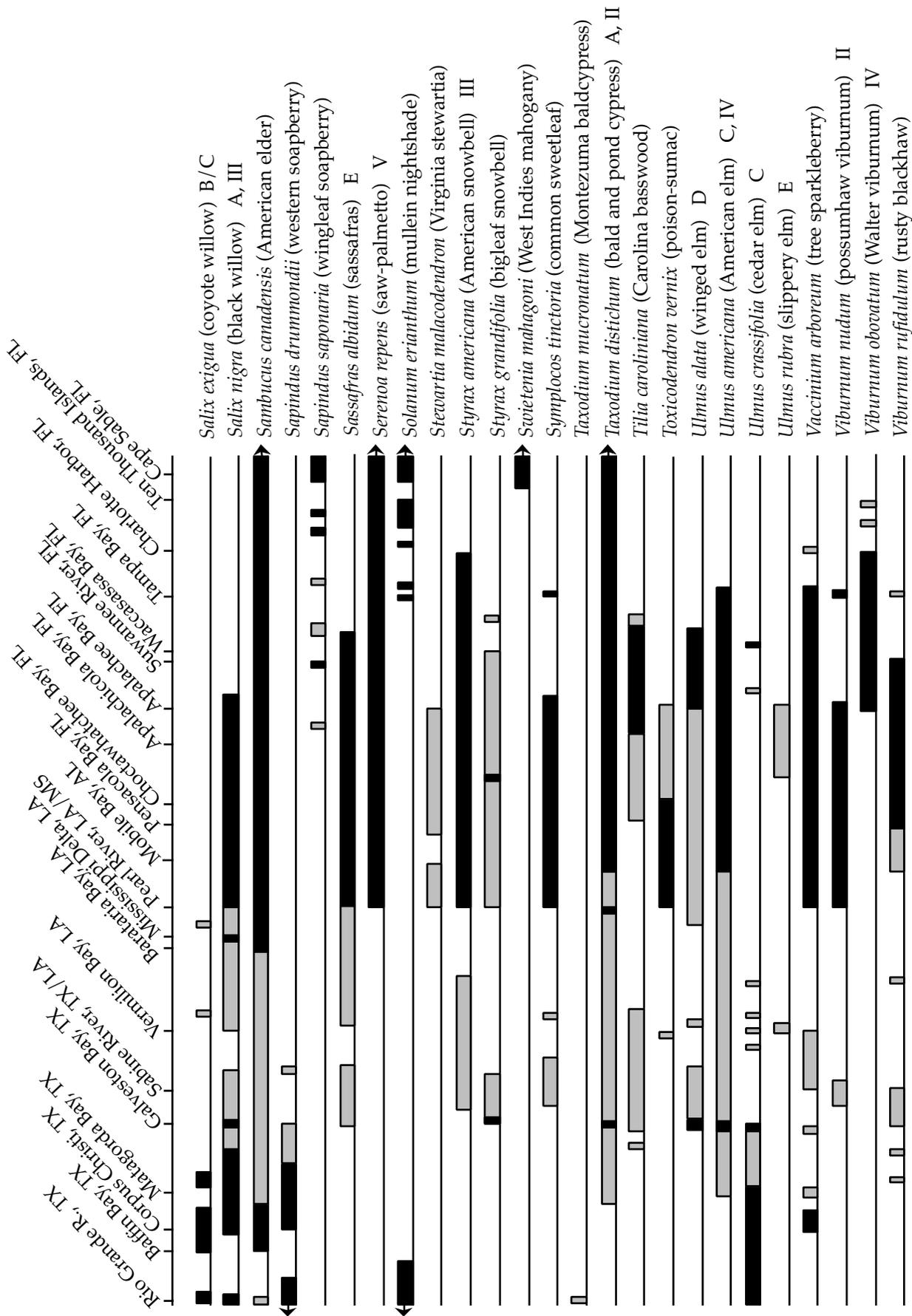


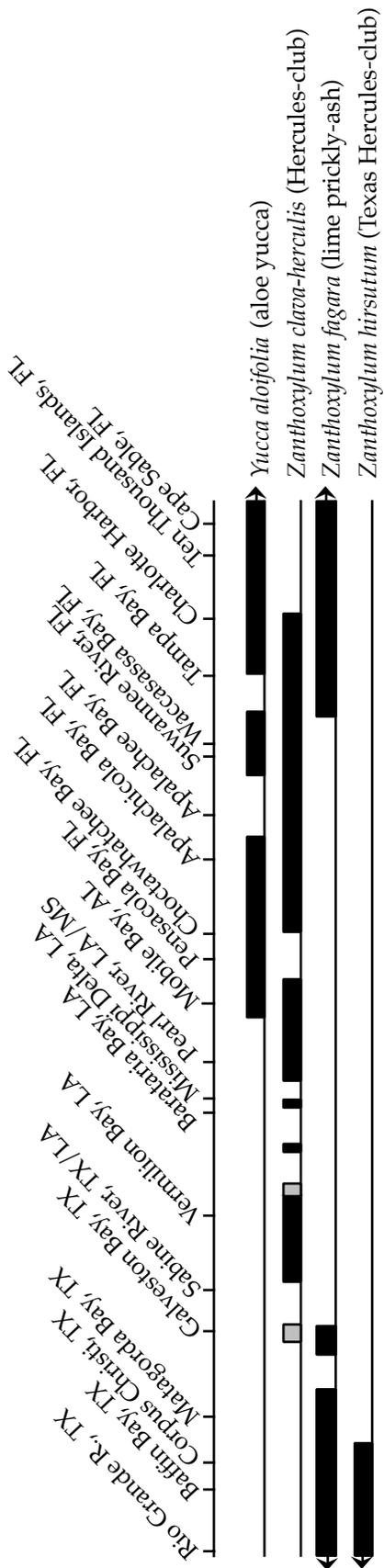












Footnotes to Appendix 1:

¹ Eastern red cedar (*Juniperus virginiana*) listed as least tolerant (E)

Appendix 2.

Bibliography of tree species' responses to flooding and salinity.

List includes research on woody plants of the Gulf of Mexico and a few general resources.

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.

Demonstrates intraspecific variation in salt-tolerance of *Taxodium distichum*. Seedlings from seed sources in brackish-water areas had higher biomass and leaf area than seedlings from freshwater sources. (Greenhouse/controlled environment experiments. Seed source Louisiana and Alabama.)

Allen, J.A., J.L. Chambers and M. Stine. 1994. Prospects for increasing the salt tolerance of forest trees: A review. *Tree Physiology* 14 (7-9): 843-853.

Review of evidence for intraspecific variation in salt-tolerance; discussion of mechanisms (physiological and genetic) controlling salt tolerance.

Allen, J.A., S.R. Pezeshki and J.L. Chambers. 1996. Interaction of flooding and salinity stress on baldcypress (*Taxodium distichum*). *Tree Physiology* 16 (1-2): 307-313.

Review of studies of effects of flooding and salinity on baldcypress. Discusses interactions between flooding and salinity and possible mechanisms for these interactions.

Alpha, C.G., D. Drake and G. Goldstein. 1996. Morphological and physiological responses of *Scaevola sericea* (Goodeniaceae) seedlings to salt spray and substrate salinity. *American Journal of Botany* 83 (1): 86-92.

Young seedlings of *Scaevola sericea* were subjected to combinations of substrate salinity (1, 3, and 10 ppt sea salt) and salt spray (0, ca. 200 mg m⁻² d⁻¹, and 1200-1500 mg m⁻² d⁻¹) in a factorial design. Substrate salinity reduced seedling growth and leaf area. Salt spray had similar, but less pronounced effects. With exposure to either substrate salinity or salt spray, cell sap osmolarity increased, leaf thickness increased and leaf carbon isotope ratios became more positive, indicating an increase in water-use efficiency.

Angelov, M.N., S.J.S. Sung, R.L. Doong, W.R. Harms, P.P. Kormanik and C.C. Black. 1996. Long-term and short-term flooding effects on survival and sink-source relationships of swamp-adapted tree species. *Tree Physiology* 16 (5): 477-484.

One-year-old seedlings of swamp tupelo (*Nyssa sylvatica* var. *biflora*), sweetgum (*Liquidambar styraciflua*), swamp chestnut oak (*Quercus michauxii*), and cherrybark oak (*Quercus falcata* var. *pagodifolia*) were subjected to continuous root flooding for 2 years. 95% of the swamp tupelo and sweetgum survived; the oaks did not survive one year. Flooding reduced leaf size in the oaks, but not swamp tupelo. Death of oaks occurred after periods of seasonal growth. Flooding increased ADH activity and starch concentrations in swamp tupelo. Patterns in photosynthesis and soluble sugar concentration were also investigated.

Ball, M. 1988. Ecophysiology of mangroves. *Trees* 2: 129-142.

Broad review of responses of mangroves to waterlogging and salinity.

Ball, M.C. and G.D. Farquhar. 1984. Photosynthetic and stomatal responses of two mangrove species, *Aegiceras corniculatum* and *Avicennia marina*, to long term salinity and humidity conditions. *Plant Physiology* 74: 1-6.

Seedlings exposed to NaCl for 3 months had lowered photosynthetic rates. Reductions in stomatal conductance and photosynthetic capacity co-limited photosynthesis.

Ball, M.C. and G.D. Farquhar. 1984. Photosynthetic and stomatal responses of the grey mangrove, *Avicennia marina*, to transient salinity conditions. *Plant Physiology* 74: 7-11.

Temporary exposure to elevated NaCl caused a reduction in the capacity to assimilate CO₂ which recovered after plants were returned to initial salinity levels. Reductions in stomatal conductance and photosynthetic capacity co-limited the rate of photosynthesis.

Boules, A. 1974. Effects of flooding on hardwood trees. *Miss Farm Res* 37 (7): 3-5.

Briscoe, C.B. 1957. Diameter growth and effects of flooding on certain bottomland forest trees. PhD, Duke University. 91 p.

Seedlings of northern red oak (*Quercus rubra*), cherrybark oak (*Quercus falcata* var. *pagodaefolia*), slash pine (*Pinus elliotii*), water tupelo (*Nyssa aquatica*) and swamp tupelo (*Nyssa sylvatica* var. *biflora*) were tested for tolerance of soil flooding, and complete submersion, and effects of seedling age and water temperature were examined. Species differences in tolerance of soil flooding and submersion was consistent with the species distribution: northern red oak was least tolerant, water tupelo and swamp tupelo were most tolerant, and cherrybark oak and slash pine were intermediate. Submersion of seedlings reduced growth more than soil flooding. Fungal and larval damage following submersion was noted. However, some slash pine and water tupelo that were submerged briefly grew more rapidly than control seedlings. As seedling age increased from 4 to 33 days, tolerance to flooding and submersion increased. Growth in water at 68°F was optimal, while growth was stopped at 41°F and 95°C produced severe injury.

Burton, J.D. 1971. Prolonged flooding inhibits growth of loblolly pine seedlings [*Pinus taeda*]. U S Forest Serv Res Note So 124: 4p.

Busch, D.E. and S.D. Smith. 1995. Mechanisms associated with decline of woody species in riparian ecosystems of the southwestern U.S. *Ecological Monographs* 63 (3): 347-370.

Water relations and competitive interactions among shrubs and trees of noncoastal riparian areas of the Colorado River were investigated. *Tamarix ramosissima*, a naturalized species, had higher osmotic potential and higher water-use efficiency than native species (*Populus fremontii*, *Salix gooddingii*, and *Tessaria sericea*). *Salix* appeared more tolerant of salt- and water stress than *Populus*, potentially explaining the persistence of *Salix* in areas where *Populus* has died or become senescent.

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): 1045-49.

Four-month-old baldcypress (*Taxodium distichum*) and Chinese tallow (*Sapium sebiferum*) seedlings were exposed to continuous flooding at 3 salinities for 3 months and acute, temporary exposure to 21 ppt sea salt (see McLeod et al. 1996). Chinese tallow was more tolerant of salinity than baldcypress, but baldcypress was more tolerant of flooding. Flooding reduced growth in Chinese tallow, but increased diameter growth (but not biomass gain) in baldcypress. All seedlings survived to the end of the experiment, except those flooded with 10 ppt sea

salt. When flooded with 10 ppt sea salt, baldcypress died in 2 weeks and Chinese tallow survived 6 weeks.

Conner, W. 1995. Response of forested wetland species to flooding and increased salinity. Clemson University. Final report 14-16-0009-15659.

Responses of baldcypress, water tupelo, green ash, Chinese tallow, swamp blackgum, buttonbush, Nuttall oak, overcup oak, swamp chestnut oak, and water oak to flooding and salinity were examined. Treatments included continuous exposure, and exposure designed to simulate a storm surge. Additionally, effects of seedling age in baldcypress were examined by comparing 1-year-old and 4-year-old seedlings. Swamp blackgum and the four oak species died when flooded with 2 ppt water. All species died at 10 pp. Pot size had an effect on the outcome of the saltwater surge experiment; it was suggested that the freshwater volume in large pots retarded saltwater infiltration.

Conner, W.H. and G.R. Askew. 1992. Response of baldcypress and loblolly pine seedlings to short-term salt water flooding. *Wetlands* 12 (3): 230-233.

Baldcypress and loblolly pine seedlings were exposed to simulated storm surges (30 ppt seawater salinity). Seedlings were 6-month-old and 18-month old. Length of seawater exposure varied from 0 to 5 days. Seedlings were followed for 9 weeks after seawater exposure for signs of resprouting. Baldcypress died back then resprouted. Young baldcypress survived 1 day of seawater exposure well but none survived >2 days of exposure. Older baldcypress survived longer exposures. Baldcypress tended to die back and resprout upon exposure to seawater. Young pine seedlings were more tolerant of seawater flooding than baldcypress, but still no seedlings survived more than 2 days of exposure. Older pines survived up to 3 days of exposure. Resprouting was not observed in loblolly pine.

Conner, W.H. and G.R. Askew. 1993. Impact of saltwater flooding on red maple, redbay, and Chinese tallow seedlings. *Castanea* 58 (3): 214-219.

Young (4-month-old) seedlings of *Acer rubrum* (red maple), *Persea borbonia* (redbay), and *Sapium sebiferum* (Chinese tallow) were subjected to flooding with seawater (27 ppt salinity) for 0-5 days (see Conner and Askew, 1992). Some seedlings of *Acer rubrum* and *Persea borbonia* survived one day of seawater exposure; none survived <1 day of exposure. Mortality occurred within 2-3 weeks of exposure. Many seedlings of *Sapium sebiferum* (>50%) survived 5 days of exposure. Data on biomass partitioning is given.

Cornelius, V.R. 1980. Synergistic effects of NaCl and SO₂ on net photosynthesis of trees. *Ange wandte Botanik* 54: 329-335.

Coutts, M.P. and W. Armstrong. 1976. Role of oxygen transport in the tolerance of trees to waterlogging. In *Tree Physiology and Yield Improvement*, ed. M. G. R. Cannell and F. T. Last. pp 361-385. London: Academic press.

General review of oxygen transport in trees and tree response to flooding.

Day, F.P., Jr. 1987. Effects of flooding and nutrient enrichment on biomass allocation in *Acer rubrum* seedlings. *American Journal of Botany* 74 (10): 1541-1554.

Seedlings (<1-year old) were subjected to 3 flooding treatments (continuously flooded, intermittent flooding and no flooding) and four fertilization treatments (no fertilization, +P, +N, and +N & P) in a factorial design. Root/shoot ratios decreased in continuously flooded plants. Plants fertilized with a combination of N and P had the greatest mass, and fertilization appeared

to compensate for effects of flooding.

DeBell, D.S., D.D. Hook, W.H.J. McKee and J.L. Askew. 1984. Growth and physiology of loblolly pine roots under various water table level and phosphorous treatments. *Forest Science* 30: 705-714.

Loblolly pine seedlings were exposed to 3 flooding treatments (drained, flooded and flooded seasonally), with and without phosphorus fertilizer for 2 years. Root development was best in the seasonally flooded treatment, worst in the continuously flooded treatment, and improved by phosphorus addition. Measurements of metabolites suggested that seedlings could accelerate glycolysis under anaerobic conditions, enhancing production of nontoxic products at the expense of ethanol production.

DeLaune, R.D., S.R. Pezeshki and W.H. Patrick, Jr. 1987. Response of coastal plants to increase in submergence and salinity. *Journal of Coastal Research* 3: 535-546.

General review of environmental changes that occur with flooding and saltwater intrusion, and responses of plants to these stresses. Responses of bottomland tree species are reviewed.

Demaree, D. 1932. Submerging experiments with *Taxodium*. *Ecology* 13: 258-262.

A variety of greenhouse studies and field plantings demonstrated that seeds of *Taxodium distichum* could not germinate underwater. Some, however, remained viable underwater for up to 30 months, germinating when drained. Germination in natural stands proceeded as the water receded. Seedlings and saplings could not withstand total submersion for more than a few days.

Dickson, R.E. and T.C. Broyer. 1972. Effects of aeration, water supply and nitrogen source on growth and development of tupelo gum and bald cypress. *Ecology* 53: 626-634.

Young (4-6 week old) seedlings were subjected to 5 watering regimes: (1) saturated soil with air slowly bubbled through it, (2) saturated soil, (3) watering to maintain soil near field capacity, (4) watering at 1/2 the days required for a plant to wilt, and (5) rewatered when plants began to wilt. Growth was better in treatments 1-3 than in treatments where soil water was allowed to drop below field capacity. Growth reductions were related to water stress. Fertilization experiments showed that fertilization with urea produced more growth than fertilization with nitrate.

Dionigi, C.P., I.A. Mendelssohn and V.I. Sullivan. 1985. Effects of soil waterlogging on the energy status and distribution of *Salix nigra* and *Salix exigua* (Salicaceae) in the Atchafalaya River Basin of Louisiana. *American Journal of Botany* 72 (1): 109-119.

Field studies in the Atchafalaya Basin showed that *Salix exigua* dominated higher elevation sites, and *S. nigra* tended to be found in lower waterlogged sites. Energy status of leaves (adenylate energy charge was lower for *S. exigua* in lower field plots than in other plots. *S. nigra* exhibited the opposite pattern. Flooding under controlled conditions showed *S. exigua* to have lower leaf conductance than *S. nigra*, regardless of flooding treatment. *S. nigra* was better able to oxidize its rhizosphere. The distribution patterns of the two species was constant with their relative abilities to withstand waterlogging and water deficits.

Donovan, L.A., K.W. McLeod, K.C.J. Sherrod and N.J. Stumpf. 1988. Response of woody swamp seedlings to flooding and increase temperatures. I. Growth, biomass, and survivorship. *American Journal of Botany* 75: 1181-1190.

Seedlings of bald cypress (*Taxodium distichum*), water tupelo (*Nyssa aquatica*), black willow (*Salix nigra*) and button bush (*Cephalanthus occidentalis*) were subjected to 3 levels of flooding and 3 water temperatures in a factorial experiment (see McLeod et al. 1986). Flooding at high temperature reduced growth and survivorship of all species, although survivorship of button bush was still quite high (87%).

Drew, M.C. 1988. Effects of flooding and oxygen deficiency on plant mineral nutrition. *Advances in Plant Nutrition* 3: 115-159.

Most reviewed work is research on herbaceous plants.

Ernst, W.H.O. 1990. Ecophysiology of plants in waterlogged and flooded environments. *Aquatic Botany* 38: 73-90.

General review of environmental chemical changes and metabolic changes that occur with flooding. Brief reference is made to reactions of *Salix* and *Nyssa*.

Erstad, J.L.F. 1994. Adaptation of woody plants to weather and climate in a maritime environment II. Salt and water stress. *Norsk Landbruksforskning* 8 (3-4): 249-270.

Review of literature on defenses against wind, salt and water stress. Common defenses against different stressors are noted. The heritability of resistance mechanisms is discussed.

Ewing, K. 1996. Tolerance of 4 wetland plant-species to flooding and sediment deposition. *Environmental and Experimental Botany* 36: 131-146.

Seedlings of *Alnus rubra* and *Fraxinus latifolia*, wetland trees of the Pacific Northwest were exposed to flooding and sedimentation. Continuous soil flooding killed both species in less than a week. Sediment addition to the soil surface resulted in an immediate drop in photosynthesis for *Alnus rubra*.

Farnsworth, E.J., A.M. Ellison and W.K. Gong. 1996. Elevated CO₂ alters anatomy, physiology, growth, and reproduction of red mangrove (*Rhizophora mangle* L.). *Oecologia* 108: 599-609.

Seedlings of *Rhizophora mangle* were grown at 350 and 700 ppm CO₂ for over one year. Seedlings grown under elevated CO₂ grew faster, had higher photosynthetic rates, and had lower stomatal conductance than those grown at ambient CO₂. Mangroves grown in high CO₂ were reproductive after only 1 year of growth (2 years before they typically reproduce in the field), and showed other signs of accelerated maturation.

Francois, L.E. 1982. Salt tolerance of eight ornamental tree species. *Journal American Society of Horticultural Science* 107(1): 66-68.

Field plantings of trees (>2 yr old) were watered with 1, 2, and 4 ppt salt (NaCl and CaCl₂) for ca. 30 months. *Liquidambar styraciflua* (sweetgum) suffered growth reductions of 33% and 81% at high and low salinity, respectively. *Magnolia grandiflora* (southern magnolia) suffered growth reductions of 46% and 69% at low and high salinity. *Liriodendron tulipifera* (tulip tree) in salt treatments all died. The study also included 5 tree species not native to the Gulf coast (*Prunus cerasifera*, *Bauhinia purpurea*, *Lagerstroemia indica*, *Pinus pinea* and *Pyrus kawakamii*). Data are presented on leaf injury and salt concentrations in leaves.

Gardiner, E.S. and J.D. Hodges. 1996. Physiological, morphological and growth-responses to rhizosphere hypoxia by seedlings of North-American bottomland oaks. *Annales Des Sciences Forestieres* 53 (2-3): 303-316.

Very young seedlings of *Quercus lyrata*, *Q. laurifolia*, *Q. phellos* and *Q. nigra* were subjected to root-zone hypoxia in a hydroponic system. All species exhibited similar reductions in net photosynthesis and slight reductions in carbon isotope ratios. Hypoxia increased leaf/weight ratios (LWR). *Q. nigra* had the highest LWR under hypoxic conditions. Changes in diurnal patterns of stomatal conductance and possible roles of stomatal vs. nonstomatal limitations to photosynthesis are discussed.

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

Review of physiological mechanisms of salt tolerance (mostly studies of herbaceous species).

Harms, W.R. 1973. Some effects of soil type and water regime on growth of tupelo seedlings. *Ecology* 54: 188-193.

Two-year-old swamp tupelo (*Nyssa sylvatica* var *biflora*) and water tupelo (*Nyssa aquatica*) were grown in two types of soil (a sandy loam from a headwater swamp and a silty clay loam from a river swamp) and three flooding regimes (20 cm deep with moving water, 20 cm deep with stagnant water, and to the soil surface with moving water). Water tupelo grew better in soil from the river swamp. Soil type had no effect on swamp tupelo growth. Growth of both species was poorest in stagnant water.

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

Review of factors that influence waterlogging. Reviews previously published classifications of flood tolerance of tree species and offers a new ranking classification.

Hook, D.D. 1984. Adaptations to flooding with fresh water. In *Flooding and Plant Growth*, ed. T. T. Kozlowski. pp 265-294. New York, NY: Academic Press.

General review of flooding effects on seed germination, growth and dormancy, morphological characteristics (including stem hypertrophy), anatomical characteristics, oxidation of the rhizosphere, metabolic adaptations, mineral relations and mycorrhizae. Tree species of swamp and bottomland forests are reviewed well.

Hook, D.D. and C.L. Brown. 1973. Root adaptations and relative flood tolerance of five hardwood species. *Forest Science* 19: 225-229.

Associations between the relative flood-tolerance of different species and various root responses were examined. The relative flood-tolerance of seedlings of 5 species, determined based on survival and growth reduction under flooded conditions was: water tupelo (*Nyssa aquatica*) > green ash (*Fraxinus pennsylvanica*) > sycamore (*Platanus occidentalis*) = sweetgum (*Liquidambar styraciflua*) > yellow poplar (*Liriodendron tulipifera*). Yellow poplar did not display any of the traits hypothesized to be associated with flood tolerance. The other 4 species displayed different sets of traits. Water tupelo and green ash displayed similar types of adaptations, but to differing degree.

Hook, D.D. and J.R. Scholtens. 1978. Adaptations and flood tolerance of tree species. In *Plant Life in Anaerobic Environments*, ed. D. D. Hook and J. R. Schlotens. pp 299-331. Ann Arbor, MI: Ann Arbor Science Publishers.

Review of anatomical, morphological and physiological characteristics promoting flood tolerance in trees. Many species of the southeastern United States are mentioned.

Hook, D.D. and T. Shear. 1987. The nature of waterlogging tolerance of loblolly pine. In *Southern Forest Tree Improvement Conference* in edited by the Southern Forest Tree Improvement Committee, p. 51-57.

Hook, D.D., C.L. Brown and P.P. Kormanik. 1970. Lenticels and water root development of swamp tupelo under various flooding conditions. *Botanical Gazette* 131: 217-224.

Seedlings of *Nyssa sylvatica* var. *biflora* were subjected to several combinations of flooding with moving or stagnant water, and continuous vs intermittent flooding. Lenticel hypertrophy and number of closing layers was greatest under surface saturation and intermediate flooding; lowest under continuous flooding. Water roots developed primarily under continuous flooding in moving water.

Hook, D.D., C.L. Brown and P.P. Kormanik. 1971. Inductive flood tolerance in swamp tupelo. *Journal of Experimental Botany* 22: 78-89.

Functions of unflooded roots and newly initiated flood roots were compared. Flood roots produced more ethanol, and oxidized their rhizosphere better than unflooded roots. Roots could tolerate 10% CO₂, but 31% CO₂ adversely affected new root initiation.

Hook, D.D., D.S. DeBell, W.H.J. McKee and J.L. Askew. 1983. Responses of loblolly pine (mesophyte) and swamp tupelo (hydrophyte) to soil flooding and phosphorous. *Plant and Soil* 71: 383-394.

Flooding of young (7-week-old) potted seedlings of loblolly pine caused reduced growth, increased Fe concentrations and caused other nutrient imbalances in shoots. Flooding of swamp tupelo did not. Loblolly pine leaked more of the ethanol it produced from its roots than did swamp tupelo. Fertilization with P improved loblolly pine performance under flooded conditions.

Hunt, F.M. 1951. Effects of flooded soil on growth of pine seedlings. *Plant Physiology* 26: 363-368.

Seedlings of shortleaf pine (*Pinus echinata*), loblolly pine (*Pinus taeda*), and pond pine (*Pinus serotina*) were subjected to 4 flooding treatments: continuous flooding with standing water, continuous flooding with flowing water, alternately flooded for two weeks and drained for two weeks, and drained. After 12 weeks, little effect was observed beyond a slight reduction in growth in stagnant water. After 12 weeks, seedlings were exposed to cycles of drying and watering for 7 months. Seedlings from all four initial flooding treatments survived these cycles well.

Jackson, M.B. 1990. Hormones and developmental change in plants subjected to submergence or soil waterlogging. *Aquatic Botany* 38: 49-72.

General review of hormonal responses to waterlogging.

Jackson, M.B., P.A. Attwood, R.W. Brailsford, D. Coupland, M.A. Else, P.J. English and J.E. Summers. 1994. Hormones and shoot relationships in flooded plants - an analysis of methods and results. *Plant and Soil* 167 (1): 99-107.

Review of methods for studying hormone responses to flooding. Includes mention of some woody plants, including species of pine and willow.

Janiesch, P. 1991. Ecophysiological adaptations of higher plants in natural communities to waterlogging. In *Tasks for Vegetation Science*, pp 50-60. 22. Dordrecht: Kluwer Academic Publishers.

Jefferies, R.L. 1981. Osmotic adjustment and the response of halophytic plants to salinity. *BioScience* 31 (1): 42-46.

General review, primarily discussing herbaceous halophytes.

Jones, R.H. and R.R. Sharitz. 1990. Effects of root competition and flooding on growth of Chinese tallow tree seedlings. *Canadian Journal of Forest Research* 20 (5): 573-578.

The effect of root competition in bottomland forest on seedlings of Chinese tallow (*Sapium sebiferum*) and green ash (*Fraxinus pennsylvanica*) was investigated by burying pots in a closed canopy forest, half designed to allow invasion by roots of surrounding trees and half designed to discourage root access. Root competition reduced seedling growth ca. 30% in both species. In a second experiment, responses of seedlings of Chinese tallow and water tupelo (*Nyssa aquatica*) to flooding were investigated. Seedlings were grown in flooded and drained pots at two light levels (20% and 100% full sun). Chinese tallow produced adventitious roots and hypertrophied lenticels under flooded conditions. Flooding reduced growth in both species, but Chinese tallow survived flooding better than water tupelo.

Kawase, M. 1981. Anatomical and morphological adaptation of plants to waterlogging. *Horticulture Science* 16: 8-12.

General review of responses to waterlogging. Includes references to woody plants.

Keeland, B.D. and R.R. Sharitz. 1995. Seasonal growth-patterns of *Nyssa sylvatica* var *biflora*, *Nyssa aquatica*, and *Taxodium distichum* as affected by hydrologic regime. *Canadian Journal of Forest Research* 25 (7): 1084-1096.

Diameter growth of *Nyssa sylvatica* var *biflora*, *Nyssa aquatica*, and *Taxodium distichum* was studied in 5 sites in South Carolina that varied in hydroperiod and water depth. *Nyssa* spp. grew best in sites that experienced deep, periodic flooding. *Taxodium distichum* grew best with shallow permanent flooding. In an impounded area, *Taxodium* diameter growth increased for several years following impoundment, then began to decline.

Keeley, J.E. 1979. Population differentiation along a flood frequency gradient: Physiological adaptations to flooding in *Nyssa sylvatica*. *Ecological Monographs* 49: 89-108.

The responses to flooding of one-year-old seedlings from upland, floodplain, and swamp plants were compared. Upland plants were intolerant of flooded soil: roots deteriorated and survival was poor. Swamp plants were tolerant of flooding, producing new roots with increased capacity for alcoholic fermentation. After a year, fermentation in roots had dropped and internal oxygen transport to roots had increased. Floodplain plants produced a flood-tolerant phenotype, but transported less oxygen to roots under drained conditions, produced fewer succulent roots and did not accelerate alcoholic fermentation, as swamp plants did.

Kennedy, H.E., Jr. 1970. Growth of newly planted water tupelo seedlings after flooding and siltation. *Forest Science* 16 (2): 250-256.

Seedlings were exposed to different depths and durations of flooding in a field study. Some were also exposed to increased siltation. Submersion of seedlings, flooding until late in the growing season, reflooding during the growing season and moderate siltation all reduced growth.

Kozlowski, T.T. 1982. Water supply and tree growth. *Forestry Abstracts* 43: 145-161.

Review of tree response to flooding. Information for many tree species of the southeastern United States is included.

Krause, C.R. 1982. Identification of salt spray injury to *Pinus* species with scanning electron microscopy. *Phytopathology* 72 (4): 382-386.

Scanning electron microscopy revealed salt-spray damage to leaf cuticles before macroscopic foliar injury was visible.

Land, S.B.J. 1974. Depth and genetic influences on injury caused by artificial sea water in floods to loblolly pine and slash pine seedlings. *Canadian Journal of Forest Research* 4: 179-185.

Seedlings of loblolly pine and slash pine from families of full-sib progenies were flooded with a 75% solution of artificial seawater for 2-4 days. Salt exposure caused a decrease in tissue water potential and osmotic potential, and an increase in Na and Cl concentration. Injury and Cl concentration were greater when seedlings were flooded with saltwater to greater depths. Slash pine seedlings were more tolerant of saltwater flooding than loblolly pine seedlings, but substantial variation among families was observed.

Lin, G. and L.d.S.L. Sternberg. 1992. Effect of growth form, salinity, nutrient and sulfide on photosynthesis, carbon isotope discrimination and growth of red mangrove (*Rhizophora mangle* L.). *Australian Journal of Plant Physiology* 19: 509-517.

Responses of tall and scrub forms of red mangrove to salinity, nutrients, and sulfide were compared. Seedlings were subjected to 12 treatments, combinations of 3 salinities (100, 250, and 500 mM NaCl), 2 nutrient levels, and 2 sulfide concentrations (0 and 2 mM Na₂S). Growth forms responded similarly. High salinity, low nutrients and high sulfide all decreased net photosynthesis, stomatal conductance and plant growth. Only salinity reduced intercellular CO₂ concentration, and carbon isotope discrimination. Results suggest that the high transpiration-use efficiency observed for scrub mangroves in the field is caused by high salinity.

Lin, G. and L.d.S.L. Sternberg. 1993. Effects of salinity fluctuation on photosynthetic gas exchange and plant growth of the red mangrove (*Rhizophora mangle* L.). *Journal of Experimental Botany* 44 (258): 9-16.

Young plants were grown under constant levels of salinity (0, 100, 250, 500 and 750 mol m⁻³ NaCl) and three levels of fluctuating salinity: 0-200 (mean of 100 mol m⁻³), 100-400 (mean of 250 mol m⁻³), and 250-750 (mean of 500 mol m⁻³). Seedlings generally grew better and had higher photosynthetic rates under constant salinity conditions than under fluctuating conditions with the same mean salinity. At a mean salt concentration of 500 mol m⁻³, however, constant salinity levels produced higher photosynthetic rates than fluctuating salinity levels, and no differences were observed in growth.

McKee, W.H., Jr., D.D. Hook, D.S. DeBell and J.L. Askew. 1984. Growth and nutrient status of loblolly pine seedlings in relation to flooding and phosphorus. *Soil Science Society of America Journal* 48 (6): 1438-1442.

2-month-old seedlings were subjected to 3 flooding treatments (continuously flooded, flooded during the dormant season, or not flooded) for 20-25 months. Growth was best under dormant-season flooding, and poorest under continuous flooding. P fertilization increased growth in the flooded treatment, but not the other treatments.

McKee, W.H., Jr. and M.R. McKevlin. 1993. Geochemical processes and nutrient uptake by plants in hydric soils. *Environmental Toxicology and Chemistry* 12: 2197-2207.

General review of geochemical changes that occur with flooding and plant responses.

McKevlin, M.R. and D.D. Hook. 1995. Morphological and physiological differences between rooted Cuttings of Atlantic white cedar grown in continuously flooded or moist peat. In *Proceedings of the Eighth Biennial Southern Silvicultural Research Conference*, Auburn, Alabama, edited by M. Boyd, USDA Forest Service General Technical Report SRS-1, p. 311-320.

Flooding reduced survival, growth, ADH activity, and foliar Mn, Mg, and Ca concentrations when compared to cuttings grown in moist peat moss. Flooding increased foliar K and Na concentrations after two seasons. Oxygen uptake rates were not affected. Stecklings that died earlier had lower foliar Ca and higher P than those that survived.

McKevlin, M.R., D.D. Hook, W.H. McKee, Jr., S.U. Wallace and J.R. Woodruff. 1987. Phosphorous allocation in flooded loblolly pine seedlings in relation to iron uptake. *Canadian Journal of Forest Research* 17: 1572-1576.

Newly germinated and 1-year-old seedlings of loblolly pine were grown in flooded and drained pots for 24-28 weeks. Flooding reduced P concentrations in shoots, increased P concentrations in roots and increased Fe concentrations in all seedling components. The authors suggest that Fe interferes with the movement of P into stems and foliage.

McKevlin, M.R., D.D. Hook, W.H. McKee, Jr., S.U. Wallace and J.R. Woodruff. 1987. Loblolly pine seedling root anatomy and iron accumulation as affected by soil waterlogging. *Canadian Journal of Forest Research* 17 (10): 1257-1264.

Loblolly pine seedlings were subjected to flooded and drained soil conditions. Fe accumulated on the epidermis and outside the endodermis, but also occurred elsewhere. A detailed description of the aerenchyma system is given. The authors suggest that loblolly pine seedlings have a limited aeration system, and that diffusion of oxygen may be responsible for the presence of oxidized Fe within the stele.

McKevlin, M.R., D.D. Hook and W.H. McKee, Jr. 1995. Growth and nutrient use efficiency of water tupelo seedlings in flooded and well-drained soil. *Tree Physiology* 15 (11): 753-758.

Young seedlings of water tupelo were subjected to flooded and drained soil conditions for 28 weeks in a greenhouse experiment. Flooding increased growth, and the concentrations of Fe, P, and K in roots. In leaf tissue, K concentration decreased, but Fe and P concentrations were unchanged. N concentration was reduced in all seedling tissues. Seedlings in flooded soil produced more biomass per unit nutrient absorbed.

McKevlin, M.R., D.D. Hook and W.H. McKee, Jr. 1997. Tolerance of loblolly pine (*Pinus taeda* L.) families to soil waterlogging stress. *Trees* (draft to be submitted)

Ten open-pollinated families and one general seed source were investigated for tolerance of waterlogging. Families differed in their growth in a hydric field site. Continuous flooding of soil in controlled soil tanks resulted in higher CO₂ and ethylene production by roots than in seasonally flooded tanks. Oxygen uptake rates and ADH activities did not differ. Families differed in root P concentration and Fe concentration. All families produced aerenchyma zones in the stele.

McKevlin, M.R., D.D. Hook and A. Rozelle. 1997. Adaptations of plants to flooding and soil waterlogging. In *Ecology and Management of Southern Forested Wetlands*, ed. M. Messina and W. Conner. pp Lewis Publishers, CRC Press.

Review of responses to flooding (metabolic, morphological, anatomical, etc) with extensive reference to swamp and bottomland forest trees of the southeastern United State.

McLeod, K.W., L.A. Donovan, N.J. Stumpff and K.C. Sherrod. 1986. Biomass, photosynthesis and water use efficiency of woody swamp species subjected to flooding and elevated water temperature. *Tree Physiology* 2: 341-346.

Seedlings of water tupelo (*Nyssa aquatica*), bald cypress (*Taxodium distichum*), button bush (*Cephalanthus occidentalis*) and cuttings of black willow (*Salix nigra*) were subjected to 3 water levels (+6, 0, and -6 cm from the soil surface) at 3 water temperatures (30, 35, and 40°C) for ca. 3 months. At 30°C, flooding reduced growth in all species except water tupelo. At 40°C flooding reduced growth of all species. High temperature reduced stomatal conductance and photosynthesis in water tupelo and black willow, but not bald cypress or button bush. The combination of high temperature and flooding reduced water-use efficiency in all species except button bush.

McLeod, K.W., J.K. McCarron and W.H. Conner. 1996. Effects of flooding and salinity on photosynthesis and water relations of four Southeastern Coastal Plain forest species. *Wetlands Ecology and Management* 4 (1): 31-42.

First-year seedlings of green ash (*Fraxinus pennsylvanica*), water tupelo (*Nyssa aquatica*), Chinese tallow (*Sapium sebiferum*) and baldcypress (*Taxodium distichum*) were exposed to chronic salt and flooding in one experiment and temporary exposure in a second. Chronic exposure consisted of ca. 2.5 months exposure to 6 treatments: flooded vs not flooded, and 0, 2, 10 ppt synthetic sea salt in a factorial design. Temporary, or acute, exposure seedlings were exposed to flooding or watering with 21 ppt sea salt for 48 hours, followed by gradual dilution. Continuous freshwater flooding reduced net photosynthesis in all species except baldcypress. Flooding with 10 ppt sea salt killed all four species; but 10 ppt was not fatal under nonflooded conditions. Temporary watering with 21 ppt salt reduced photosynthesis in only green ash and water tupelo. Temporary flooding with 21 ppt salt reduced photosynthesis in all species.

McMinn, J.W. and W.H. McNab. 1971. Early growth and development of slash pine under drought and flooding. [*Pinus elliottii*]. U S Forest Serv Res Pap Se 89: 10p.

Mitsch, W.J. and W.G. Rust. 1984. Tree growth responses to flooding in a bottomland forest in northeastern. *Forest Science*. 30 (2): 499-510.

Tree ring data and water level data from the Kankakee River floodplain in Illinois were compared. Growth cycles for *Quercus bicolor*, *Ulmus americana*, and *Fraxinus pennsylvanica* were similar, and correlated poorly with flooding and streamflow data.

Munns, R. and A. Termaat. 1986. Whole plant response to salinity. *Australian Journal of Plant Physiology* 13: 143-160.

Review of salt effects on plants. Data primarily from herbaceous plants.

Naidoo, G. 1985. Effects of waterlogging and salinity on plant-water relations and on the accumulation of solutes in three mangrove species. *Aquatic Botany* 22 (2): 133.

Seedlings of *Avicennia marina*, *Rhizophora mucronata*, and *Bruguiera gymnorrhiza* were subjected to salinity and waterlogging for 60 days in a 2 x 2 factorial design. Stomatal conductance was lowest under a combination of flooding and salinity. Salinity depressed tissue water potentials. Cation accumulation in roots was high. *Rhizophora* was more tolerant of salinity than *Bruguiera*. The authors suggest that the combination of low stomatal resistance, low tissue water potential, high relative water content and high tissue cation concentration make it a good pioneer in the mangrove association.

Newsome, R.D., T.T. Kozlowski and Z.C. Tang. 1982. Response of *Ulmus americana* seedlings to flooding of soil. *Canadian Journal of Botany* 60: 1688-1695.

Flooding of soil caused stem swelling, production of hypertrophied lenticels, adventitious root formation, and reduced leaf formation and expansion. Ethylene production was increased. Stomatal conductance was permanently reduced in leaves that had completed expansion prior to flooding, but not in leaves that completed expansion under flooded conditions.

O'Leary, J.W. and J.J. Riley. 1970. Physiological Response of Plants to Salinity and Humidity (Research proj. technical completion rept. Jul 67-Jun 68. Arizona Univ., Tucson. Inst. of Atmospheric Physics. Report No.: W70-05119; OWRR-A-016-ARIZ(1) 1970.

Pereira, J.S. and T.T. Kozlowski. 1977. Variation among woody angiosperms in response to flooding. *Physiologia Plantarum* 41: 184-192.

Flooding of young *Populus deltoides*, *Salix nigra*, *Eucalyptus camaldulensis*, *E. globulus*, *Ulmus americana*, *Quercus rubra*, and *Fraxinus pennsylvanica* caused stomatal closure, inhibition of root growth, changes in root and stem morphology, adventitious root formation, and leaf senescence. In amphistomatous species (*Populus deltoides*, *Salix nigra* and *Eucalyptus camaldulensis*) flooding caused rapid stomatal closure on the adaxial leaf surface. Abaxial conductance in *Salix nigra* and *Eucalyptus camaldulensis* did not decrease. Flooding did not increase water stress.

Perry, L. and K. Williams. 1996. Effects of salinity and flooding on seedlings of cabbage palm (*Sabal palmetto*). *Oecologia* 105 (4): 428-434.

First year seedlings of *Sabal palmetto* were exposed to four salt solutions (0, 8, 15, and 22 ppt) and two flooding regimes (continuously flooded vs. flushed and drained) in sand culture in a factorial greenhouse experiment. Photosynthesis declined between 8 ppt and 15 ppt. At high salinity, flooding increased photosynthetic rates. Results of the greenhouse study were related to seedling performance in the field, where survival of transplanted seedlings at the forest edge declined with frequency of tidal flooding, and with salinity of the tidal water.

Peterson, D.L. and F.A. Bazzaz. 1984. Photosynthetic and growth responses of silver maple (*Acer saccharinum* L.) seedlings to flooding. *American Midland Naturalist* 112 (2): 261-272.

Seedlings were subjected a series experimental treatments involving soil flooding and complete seedling submersion. Soil flooding reduced both root biomass and leaf area. Soil flooding reduced photosynthetic capacity after 21 days, and submersion reduced it after 3 days. Timing of flooding (spring vs. late summer) did not affect seedling response. Two-year-old seedlings had a greater capacity for photosynthesis following flooding than newly germinated seedlings.

Pezeshki, S.R. 1987. Gas exchange response to tupelo-gum (*Nyssa aquatica* L.) to flooding and salinity. *Photosynthetica* 21 (4): 489-493.

Seedlings of *Nyssa aquatica* were subjected to two levels of flooding (flooded and drained) and two levels of salt (0 and 50 mol m⁻³ synthetic sea salt) in a factorial design for 3 weeks. Both flooding and salt were found to reduce in photosynthesis primarily through nonstomatal limitations.

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.

Six-month-old seedlings of baldcypress and water tupelo were subjected to soil anaerobiosis (soil redox potential of -160 mV) and salinity (51 mol m⁻³ synthetic sea salt) in a 2 x 2 factorial experiment. Anaerobiosis resulted in a greater reduction of net photosynthesis in baldcypress than in water tupelo. Salinity reduced net photosynthesis in water tupelo. Under combined salt and anaerobiosis, the two species had similar reductions in height growth.

Pezeshki, S.R. 1991. Root response of flood tolerant and flood sensitive tree species to soil redox conditions. *Trees* 5: 180-186.

Roots of seedlings of *Taxodium distichum*, *Quercus lyrata*, and *Quercus falcata* var *pagodaefolia* were subjected to low soil redox potentials. Root growth slowed in *T. distichum* below +200 mV and ceased below +350 mV in the two oak species. Low soil redox potential resulted in root anatomical changes and increased alcohol dehydrogenase activity in *T. distichum*, but not in the oaks.

Pezeshki, S.R. 1992. Response of *Pinus taeda* L. to soil flooding and salinity. *Annales des Sciences Forestieres* 49: 149-159.

Seedlings of loblolly pine were subjected to 3 treatments (control, flooded, flooded with 50 mol m⁻³ NaCl). Flooding alone reduced photosynthesis and growth substantially, while flooding with saltwater reduced them a bit farther.

Pezeshki, S.R. 1994. Plant response to flooding. In *Plant-Environment Interactions*, ed. R. E. Wilkinson. pp 289-321. New York: Marcel Dekker, Inc.

General review of effects of flooding on soils, plant metabolism and growth.

Pezeshki, S.R. 1996. Flood-induced changes in internal oxygen transport in wetland tree species. In *Proceedings: Southern Forested Wetlands Ecology and Management*, Clemson University, edited by K. M. Flynn, pp. 197-202.

Seedlings of baldcypress (*Taxodium distichum*) subjected to root zone hypoxia developed greater root porosity and oxygen flux, but root dry weight was reduced. Leaf gas exchange rates were initially reduced, but recovered substantially.

Pezeshki, S.R. and J.L. Chambers. 1985. Stomatal and photosynthetic response of sweet gum (*Liquidambar styraciflua*) to flooding. *Canadian Journal of Forest Research* 15 (2): 371-375.

Seedlings (ca. 1.5-years-old) were flooded to 20 cm above the soil surface in a growth chamber experiment. Flooding for 9 days induced partial stomatal closure and a reduction in net photosynthesis. Leaf water potential did not fall. Partial stomatal reopening was observed 3 days after cessation of the flooding treatments.

Pezeshki, S.R. and J.L. Chambers. 1986. Effect of soil salinity on stomatal conductance and photosynthesis of green ash (*Fraxinus pennsylvanica*). *Canadian Journal of Forest Research* 16: 569-573.

Seedlings (1-year-old) of green ash were exposed to single applications of salt, followed by freshwater flushing during subsequent days. Exposure consisted of application of 300 mL of solution with 0, 7.3, 14.6, 36.5, an 73.0 g NaCl. Rapid reduction in stomatal conductance and photosynthesis occurred. Leaf injury occurred at all levels of salt exposure. Rapid mortality occurred at the two highest salt concentrations.

Pezeshki, S.R. and J.L. Chambers. 1986. Variation in flood-induced stomatal and photosynthetic response of three bottomland tree species. *Forest Science* 32 (4): 914-923.

Seedlings (ca. 1.5 years old) of *Fraxinus pennsylvanica*, *Quercus michauxii*, and *Taxodium distichum* were flooded (8-10 cm above the soil) for 21 days. Flooding caused stomatal closure in all species. Leaf water potential did not decline with flooding. Photosynthesis was reduced in *Q. michauxii*, but was not substantially reduced in the other two species, despite stomatal closure.

Pezeshki, S.R., R.D. DeLaune and W.H. Patrick, Jr. 1986. Gas exchange characteristics of bald cypress (*Taxodium distichum* L.): evaluation of responses to leaf aging, flooding, and salinity. *Canadian Journal of Forest Research* 16: 1394-1397.

One-year-old seedlings of bald cypress were subjected to 0, 2, 4, 6, and 8 ppt synthetic sea salt for 28 days. Leaves produced after the imposition of the salt treatments had higher rates of net photosynthesis and conductance than older leaves formed prior to the imposition of treatments, suggesting acclimation to salinity. At the higher salt treatments (6 and 8 ppt), rates were very low for both old leaves and those produced after the introduction of salt.

Pezeshki, S.R., R.D. DeLaune and W.H. Patrick, Jr. 1987. Response of baldcypress (*Taxodium distichum* L. var. *distichum*) to increase in flooding salinity in Louisiana's Mississippi River deltaic plain. *Wetlands* 7: 1-10.

One-year-old seedlings of baldcypress were subjected to 6 treatments: flooding with 5 levels of synthetic sea salt (0, 2, 4, 6, and 7 ppt sea salt) and a well-watered, nonflooded control. Stomatal conductance and net photosynthesis declined in all flooding treatments. Stomatal conductance in seedlings flooded with fresh water fully recovered within three weeks, although net photosynthesis did not fully recover. Stomatal conductance of seedlings exposed to 2 ppt sea salt partially recovered. Adventitious root production accompanied recovery of gas exchange rates. Adventitious roots were produced on submerged portions of stems. They were produced first on plants flooded with fresh water (within 1 week), and later on plants subjected to elevated salinity. No adventitious roots were produced at the highest salt concentration studied.

Pezeshki, S.R., R.D. DeLaune and W.H. Patrick, Jr. 1988. Effect of salinity on leaf ionic content and photosynthesis of *Taxodium distichum* L. *The American Midland Naturalist* 119 (1): 185-193.

Potted seedlings of *Taxodium distichum* (>1 yr old) were flooded with different solutions of synthetic sea-salt for 30 days. Saltwater solutions contained 0, 35, 70, 105, and 140 mol m⁻³ NaCl. Salt treatment raised concentrations of Na, K, Ca and Mg in leaf tissue, and reductions in photosynthesis were linearly related to ion concentration, especially Na concentration. Leaf internal CO₂ concentration did not change.

Pezeshki, S.R., R.D. DeLaune and W.H. Patrick, Jr. 1989. Assessment of saltwater intrusion impact on gas exchange behavior of Louisiana Gulf Coast wetland species. *Wetlands Ecology and Management* 1 (1): 21-30.

Review of effects of flooding and salinity on rates of net photosynthesis and stomatal conductance of woody and herbaceous wetland plants of Louisiana. Results of 5 previously published studies are tabulated. Authors note that exposure to salt concentrations >10 ppt caused leaf death in species of freshwater habitat.

Pezeshki, S.R., W.H. Patrick, Jr., R.D. DeLaune and E.D. Moser. 1989. Effects of waterlogging and salinity interaction on *Nyssa aquatica* seedlings. *Forest Ecology and Management* 27: 41-51.

Seedlings of *Nyssa aquatica* were subjected to two levels of flooding (flooded and drained) and two levels of salt (0 and 50 mol m⁻³ synthetic sea salt) in a factorial design for 6 weeks. Both flooding and salt reduced height growth, but some recovery in salt treatments was noted after 3 weeks. The greatest reduction in stomatal conductance, net photosynthesis, and growth occurred in the salt treatment without flooding.

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.

General review of physiological responses of bottomland and swamp forest tree species to flooding and salinity. Includes information on anatomical, morphological, biochemical, and leaf gas-exchange responses.

Pezeshki, S.R., R. DeLaune and W.H. Patrick, Jr. 1990. Differential response of selected mangroves to soil flooding and salinity: gas exchange and biomass partitioning. *Canadian Journal Forest Research* 20: 869-874.

Seedlings of *Avicennia germinans*, *Laguncularia racemosa*, and *Rhizophora mangle* were subjected to flooding (soil redox potential ca -92 mV) and salinity (ca. 342 mol m⁻³) in a factorial experiment. No effects on leaf conductance or net carbon assimilation rates were observed. However, flooding alone reduced total leaf area in plants of *Laguncularia* and *Avicennia*. Salinity, either alone or in combination with flooding, tended to increase seedling dry weight.

Pezeshki, S.R., R.D. DeLaune and H.S. Choi. 1995. Gas exchange and growth of bald cypress seedlings from selected U.S. Gulf Coast populations: responses to elevated salinities. *Canadian Journal of Forest Research* 25 (9): 1409-1415.

Baldcypress seedlings from seed sources at a brackish site and freshwater site were compared for gas-exchange, growth and anatomical responses to flooding and salinity. Seedlings were

exposed to 4 treatments: no flooding or salt, and flooding with 3 levels of salt (0, 68 mol m⁻³ (4 ppt), and 136 mol m⁻³ (8 ppt)). Seedlings from different sources reacted differently, but seedlings from the brackish source did not perform better under saline conditions than those from the freshwater site. Seedlings from the freshwater site had greater rates of net photosynthesis at 4 ppt, and had greater growth and root porosity than seedlings from the brackish site under several treatments.

Pezeshki, S.R., J.H. Pardue and R.D. DeLaune. 1996. Leaf gas exchange and growth of flood-tolerant and flood-sensitive tree species under low soil redox conditions. *Tree Physiology* 16 (4): 453-458.

Effects of soil redox potential (+170 mV vs. +560 mV) on photosynthesis, stomatal conductance, chlorophyll content, ADH activity and ethylene production were studied in young seedlings of *Taxodium distichum*, *Quercus lyrata*, and *Quercus falcata* var *pagodaefolia*. In *Taxodium distichum*, low redox potential reduced increased ADH activity, increased ethylene production, reduced net photosynthesis (which began to recover after 2 weeks), but did not affect stomatal conductance. In the two oak species, low redox potential had no effect on ADH activity or ethylene production, but reduced both photosynthesis and stomatal conductance. No changes in chlorophyll content were observed.

Regehr, D.L., F.A. Bazzaz and W.R. Boggess. 1975. Photosynthesis, transpiration and leaf conductance of *Populus deltoides* in relation to flooding and drought. *Photosynthetica* 9 (1): 52-61.

Soil flooding for 28 days caused a 50% reduction in photosynthesis in potted plants of *Populus deltoides*. Recovery occurred within one week after the end of flooding. Drought (leaf water potential at ca. -11 bar) caused photosynthesis to fall to near zero.

Rhodes, D. and P. Felker. 1988. Mass screening of *Prosopis* (Mesquite) seedlings for growth at seawater salinity concentrations. *Forest Ecology and Management* 24: 169-176.

Prosopis sp. accessions from around the world were exposed to increasing concentrations of NaCl over a ca. 7 months. The study included material from Texas (one accession of *Prosopis glandulosa* var. *glandulosa*). Seedlings were grown in sand culture in the greenhouse. Final salt treatment was 3.3% NaCl (33 ppt). Accessions of *Prosopis* varied in growth and survival responses to salinity. Survival of *Prosopis glandulosa* var. *glandulosa* declined continuously throughout the experiment, and all dead by the end of the study.

Rushton, B.S. and A.E. Toner. 1989. Wind damage to the leaves of sycamore (*Acer pseudoplatanus* L.) in the coastal and non coastal stands. *Forestry* 62 (1): 67-88.

Leaf damage in sycamore in Northern Ireland was related to site exposure. At sites with high levels of damage, the most damaged leaves were smallest. The authors suggest that damage prevented full leaf expansion.

Sande, E. and D.R. Young. 1992. Effect of sodium chloride on growth and nitrogenase activity in seedlings of *Myrica cerifera* L. *New Phytologist* 120: 345-350.

Nodulated seedlings (5-month-old) of *Myrica cerifera* were exposed to sodium chloride (0, 25, 50, 100, and 150 mM) in a growth chamber experiment. Salt exposure decreased growth and photosynthesis, but no plants died during the study. Nitrogen fixation (acetylene reduction) by root nodules was severely reduced by exposure to 100 and 150 mM NaCl, but not eliminated.

Sehmer, L., B. Alaoui-Sosse and P. Dizengremel. 1995. Effect of salt stress on growth and on the detoxifying pathway of pedunculate oak seedlings (*Quercus robur* L). *Journal of Plant Physiology* 147 (1): 144-151.

Seedlings watered with solutions containing 20 mM NaCl produced leaves with elevated NaCl levels and increased superoxide dismutase activity. No changes were detected in activities of ascorbate peroxidase and glutathione reductase.

Sena, G. and T.T. Kozlowski. 1980. Growth response and adaptation of *Fraxinus pennsylvanica* seedlings to flooding. *Plant Physiology* 66: 267-271.

Flooding caused stomatal closure, reduced dry mass gain, hypertrophied lenticels, production of adventitious roots, leaf necrosis, and leaf abscission in 8-10 week old seedlings. Stomata began to reopen after 15 days of flooding, at approximately the same time adventitious root production began.

Shanklin, J. and T.T. Kozlowski. 1985. Effect of flooding of soil on growth and subsequent response of *Taxodium distichum* seedlings to SO₂. *Environmental Pollution* 38: 199-212.

Three-month-old baldcypress seedlings were subjected to flooding with stagnant water and SO₂ in a growth chamber study. Flooding reduced growth more than SO₂ exposure did. SO₂ exposure reduced growth less in flooded seedlings than in unflooded seedlings, which absorbed more S.

Shao, G., H.H. Shugart and D.R. Young. 1995. Simulation of transpirational sensitivity to environmental changes for shrub (*Myrica cerifera*) thickets on a Virginia barrier island. *Ecological Modelling* 78 (3): 235-248.

Modelling transpiration in *Myrica cerifera* suggested that transpiration was sensitive to climate change, landscape change, and sea-level rise. Effects of groundwater patterns and competition with grasses are discussed.

Shear, T.H. and D.D. Hook. 1987. Use of excessive waterlogging and physiological responses to measure genetic variation in loblolly pine waterlogging tolerance. In *Southern Forest Tree Improvement Conference* edited by S. F. T. I. Committee, p. 146-151.

Tang, Z.C. and T.T. Kozlowski. 1984. Ethylene production and morphological adaptation of woody plants to flooding. *Canadian Journal of Botany* 62 (8): 1659-1664.

Seedlings of *Ulmus americana*, *Fraxinus pennsylvanica*, *Melaleuca quinquenervia*, and *Eucalyptus camaldulensis* exhibited greater morphological adaptation to flooding than seedlings of *Eucalyptus globulus* or *Pinus halepensis*. Only flood-tolerant species produced hypertrophied lenticels and adventitious roots on submerged stems. Ethylene production was stimulated in all species except *Pinus halepensis*. In flooded seedlings of *Fraxinus pennsylvanica*, ethylene production and stem hypertrophy were correlated. Gradients in ethylene in *Eucalyptus* suggested production in submerged portions and translocation upward.

Tang, Z.C. and T.T. Kozlowski. 1984. Water relations, ethylene production, and morphological adaptation of *Fraxinus pennsylvanica* seedlings to flooding. *Plant and Soil* 77: 183-192.

5-month-old seedlings were subjected to flooding with stagnant water for 28 days. Flooding increased ethylene production, and caused formation of hypertrophied lenticels and adventitious roots. Early stomatal closure was followed by reopening of stomata.

Theriot, R.F. 1988. Flood tolerance indices for palustrine forest species. In *The Ecology and Management of Wetlands*. Volume 1: Ecology of Wetlands, ed. D. D. Hook, W. H. McKee Jr., H. K. Smith, J. Gregory, V. G. Burrell Jr., M. R. DeVoe, R. E. Sojka, S. Gilbert, R. Banks, L. H. Stolzy, C. Brooks, T. D. Matthews and T. H. Shear. pp 477-488. London: Croom Helm.

Review and ranking of flood tolerance in bottomland species of the southern United States.

Tolliver, K.S., D.W. Martin, and D.R. Young. 1997. Fresh-water and saltwater flooding response for woody species common to barrier-island swales. *Wetlands* 17: 10-18.

Seedlings of *Baccharis halimifolia*, *Myrica cerifera*, *Pinus taeda*, *Juniperus virginiana*, and *Iva frutescens* were subjected to soil flooding and a range of salinities. Flood water contained, 0, 2, 5, 10, 20, or 30 g L⁻¹ synthetic sea salt. After 30 days, salt was flushed from soils and plants were monitored for a 30-d recovery period. Only *Baccharis* was sensitive to freshwater flooding. No plants died at salinities ≤5 g L⁻¹. At midrange salinity, mortality was highest for *Myrica* and *Baccharis* (60%), followed by *Pinus taeda* (40%), *Iva* (25%) and *Juniperus* (20%). All species died at 20 and 30 g L⁻¹ salt. Data on water relations, stomatal conductance and chloride concentration are reported.

Topa, M.A. and K.W. McLeod. 1986. Responses of *Pinus clausa*, *Pinus serotina*, and *Pinus taeda* seedlings to anaerobic solution culture. I. Changes in growth and root morphology. *Physiologia Plantarum* 68: 523-531.

Young seedlings of *Pinus clausa* (sand pine), *Pinus serotina* (pond pine), *Pinus taeda* (loblolly pine) from a wet site and *Pinus taeda* from a dry site were exposed to aerobic (250 μM O₂) and anaerobic (≤23 μM O₂) solution culture for 30 days. No mortality was observed. Anaerobiosis reduced root mass in loblolly and pond pine, but not shoot height, biomass or leaf emergence. Sand pine, however, suffered a reduction in biomass, with root dieback, shoot chlorosis and retarded leaf development. Dry site loblolly pine exhibited some of these symptoms; wet site loblolly pine exhibited none. The ranking found in flood tolerance (pond pine ≥ wet-site loblolly pine > dry-site loblolly pine > sand pine) corresponded to differences among seedlings in the production of adventitious secondary roots and stem or tap-root lenticels.

Townsend, A.M. 1980. Response of selected tree species to sodium chloride. *Journal American Society of Horticultural Science* 105 (6): 878-883.

Seedlings (2-yr old) of 6 tree species (*Quercus palustris*, *Platanus occidentalis*, *Sophora jamponica*, *Cornus florida*, *Gleditsia tricanthos* and *Pinus strobus*) were exposed to salt in hydroponic solution for 5 weeks. Salt concentrations were 0, 2, 4 and 7 ppt NaCl. Exposure to 7 ppt salt limited height growth in *Platanus* and *Cornus*, whereas *Gleditsia* appeared little affected. Data on dry mass, foliar injury and accumulation of Na and Cl are presented. The short length of the study limited the magnitude of the responses measured.

Werner, A. and R. Stelzer. 1990. Physiological responses of the mangrove *Rhizophora mangle* grown in the absence and presence of NaCl. *Plant, Cell and Environment* 13: 243-255.

Young *Rhizophora mangle* grew better when exposed to 200 mol m⁻³ NaCl than when grown in fresh water. Water-use efficiency was higher, leaf water content and succulence was higher, stomatal conductance and photosynthetic rate were higher, and shoot water potential was lower when grown in a salt solution. Organic acid accumulation was observed at night, although no net CO₂ fixation occurred, indicating CAM-cycling. Malic acid accumulation was more pronounced in salt-treated plants. Internal gradients in Na and Cl were studied.

West, D.W. 1986. Stress physiology in trees--salinity. *Acta horticulturae* 175: 321-332.

General discussion of salt stress with emphasis on agronomic problems and some reference to woody species.

Will, R.E., J.R. Seiler, P.P. Feret and W.M. Aust. 1995. Effects of rhizosphere inundation on the growth and physiology of wet and dry-site *Acer rubrum* (red maple) populations. *American Midland Naturalist* 134 (1): 127-139.

Six-week-old seedlings of *Acer rubrum* grown from seed collected on dry sites and wet sites were flooded for 3 months. Flooded seedlings had lower rates of photosynthesis, higher water potential, and lower growth rates than unflooded seedlings. Seedlings from wet-site populations had better shoot growth and lower water potentials than seedlings from wet-site populations. However, no differences were observed in response to flooding, suggesting a lack of ecotypic differentiation.

Yamamoto, F. 1992. Effects of depth of flooding on growth and anatomy of stems and knee roots of *Taxodium distichum*. *IAWA Bulletin* 13(1): 93-104.

Trees of *Taxodium distichum* that had grown in different depths of water were compared. Trees in deeper water were shorter, larger in diameter, and lesser knee root development. Tracheids in submerged parts of deeply flooded trees were shorter, slightly wider, and had thinner walls than tracheids of shallowly flooded trees. The inner bark of deeply flooded trees had wider phloem rays and more intercellular space than that of shallowly flooded trees. Flooding stimulated ethylene production in bark and apical parts of knee roots.

Yamamoto, F. and T.T. Kozlowski. 1987. Regulation by auxin and ethylene of responses of *Acer negundo* seedlings to flooding of soil. *Environmental and Experimental Botany* 27 (3): 329-340.

Auxin produced in shoot apices appeared to play a large role in the formation of adventitious roots, and changes in xylem structure, changes that occur in flooded *Acer negundo* seedlings. Ethylene played a greater role in leaf epinasty, senescence and abscission, production of hypertrophied lenticels and growth of bark tissue under flooded conditions.

Young, D.R. 1992. Photosynthetic characteristics and potential moisture stress for the actinorhizal shrub, *Myrica cerifera* (Myricaceae), on a Virginia barrier island. *American Journal of Botany* 79(1): 2-7.

Sensitivity of stomatal conductance and photosynthesis to leaf water potential and leaf-to-air humidity deficits were quantified. Field studies of gas-exchange and water relations in ca. 3-m tall *Myrica cerifera* shrubs revealed that nonoptimal air temperatures and humidity deficits would have limited photosynthesis on at least 90% of the days during the relatively wet summer of 1989.

Appendix 3.

Field studies of responses of Gulf coast tree species to impoundments, drainage, and reductions in freshwater supply.

Studies of forest response to increased flooding or salinity often address changes that have occurred as a result of human intervention (dam building, levee building, channel construction, etc). Impoundments often increase flood depths as well as hydroperiod. Many studies of tree response to flooding take advantage of these impoundments (e.g., Conner and Day 1992a, b, Conner et al. 1981, Keeland and Sharitz 1995). Coastal forests downstream of dams, levees and other obstructions to water flow may be subjected to salt-water intrusion that results from reduced freshwater outflow (e.g., Kjerfve 1979). They may also be subjected to unnatural flooding regimes, if controlled water releases occur during the growing season (e.g., Sharitz and Lee 1985). Canals may channel saltwater inland, increasing salt exposure (e.g., Hackney and Yelverton 1990). A few of the most widely cited case studies are reviewed below.

Damming of Chicot Bayou in Louisiana, near the inland edge of the coastal Mississippi deltaic floodplain, in 1942-3 formed Lake Chicot (ca. 2-3 m deep) in an area that was previously mostly swamp forest (*Taxodium distichum*, *Nyssa aquatica*, *Planera aquatica*, *Cephalanthus occidentalis*) with more upland forest in marginal shallow areas. Water levels were drawn down almost every year in an attempt to control aquatic weeds (Eggler and Moore 1961). Surveys by Penfound (1949) and Eggler and Moore (1961) documented forest changes in the impounded area over the subsequent 18 years. Baldcypress death in the deepest reaches of the lake was only 3% during the first 4 years of flooding and 50% of the trees survived at least 18 years after the dam was built, though many have dead tops (Eggler and Moore 1961). *Nyssa aquatica* had lower survival, but 28% still survived 18 years. Neither *Planera aquatica* nor *Cephalanthus occidentalis* survived 18 years, but survival of *Planera* was good for at least the first 4 years after flooding. Cypress increased in marginal areas, where yearly draw-downs apparently allowed seedling regeneration. All “true upland” species died in the shallowly flooded margin (*Carpinus caroliniana*, *Hicoria pecan*, *Liriodendron tulipifera*, *Nyssa sylvatica*, *Quercus nigra*, *Ulmus alata*), but a very small number of trees of bottomland species (*Diospyros virginiana*, *Liquidambar styraciflua*, *Quercus lyrata*, *Salix nigra*) survived frequent flooding for at least 18 years (Eggler and Moore 1961). Stem cores suggested that radial stem growth had increased in flooded trees since flooding. Eggler and Moore (1961) speculate that this may have resulted from reduction of competition.

Conner et al. (1981) compared recruitment and growth of trees in cypress swamps in Louisiana that had been impounded (always flooded to an average depth of 20-30 cm), drained from June through August and flooded to 40 cm the rest of the year, or left with a natural

hydroperiod (in this case, flooded except for a few brief periods during the year). They found no seedlings in the continuously flooded plot, and better recruitment in the drained area than in the natural area. They found the best stem diameter growth in trees of the flooded plots, however. This finding agrees with those of Egglar and Moore (1961). Although it has been speculated that this increased growth resulted from decreased competition after impoundment (Egglar and Moore 1961; Conner et al. 1981), it may simply result from the production of lower density wood. Yamamoto (1992) noted that deeply flooded baldcypress produced wood with larger lumens and thinner cell walls than shallowly flooded baldcypress. Whether these anatomical changes are beneficial, or associated in some way with increased oxygen transport in flooded trees, is unknown (Hook 1984).

Drainage often changes forests, as well as increased flooding. Conner et al. (1981) noted that drainage of cypress swamp for three months of the year appeared to result in succession toward bottomland forest.

Damming the Ocklawaha river formed Lake Ocklawaha in north-central Florida in 1968, flooding forested wetlands. Larger trees could withstand deeper water longer (Lugo and Brown 1984). Harms et al. (1980) and Lugo and Brown (1984) found that survival was poorer in deeply flooded areas than in shallowly flooded areas. All species survived <7 years in areas flooded ≥ 1.3 m deep, but survival was much better in shallowly flooded areas (<10% mortality over 7 years at depths <60 cm; Harms et al. 1980). A few larger *Sabal palmetto* trees have survived >25 years after flooding (F.E. Putz, personal communication). Because sea-level rise is expected to raise water tables only slowly in bottomland forests (i.e, a 60 cm rise only achievable over ca. 60 years, even at the highest rates of relative sea-level rise observed along the Gulf Coast; Hanson and Maul 1993), such increased flooding, if fresh water, may speed death of canopy trees but not eliminate the tree canopy for a long period of time.

Season of flooding may affect survival. Sharitz and Lee (1985) found that growing season discharges from a reservoir on the Savannah River floodplain (Georgia) caused 99% mortality among cypress and water tupelo seedlings, whereas the same seedlings had survived natural winter floods well. Around the Gulf of Mexico, tides are highest during the growing season (late spring to autumn). Thus, although swamp forests in the south tend to flood during the winter, due to low evapotranspiration, the contribution of sea-level to the maintenance of high water levels on the coast may be maximal during the growing season, when seedlings are most susceptible.

Dam construction reduces freshwater flow, allowing salt water to intrude farther up into the estuary and often causing tree death. The Santee Cooper Project in South Carolina allowed salinities > 1ppt reached 13-18 km upstream. This saltwater intrusion has been credited with converting coastal swamp forest to salt marsh (Kjerfve 1979).

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Conner, W.H. and J.W. Day, Jr. 1992a. Diameter growth of *Taxodium distichum* (L.) Rich and *Nyssa aquatica* from 1979-1985 in four Louisiana swamp stands. *American Midland Naturalist* 127: 290-299.

Conner, W.H. and J.W. Day, Jr. 1992b. Water level variability and litterfall productivity of forested freshwater wetlands in Louisiana. *American Midland Naturalist* 128: 237-245.

Conner, W.H., J.G. Gosselink, and R.T. Parrondo. 1981. Comparison of the vegetation of three Louisiana swamp sites with different flooding regimes. *American Journal of Botany* 68:320-331.

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