

Chapter 5: Sensitivity of Gulf Coast Forests to Climate Change

by

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

Introduction

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

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

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

The Big Thicket is at the western edge of the Southern Mixed Hardwoods region (Küchler 1964) or the South-eastern Evergreen Forest described by Braun (1950). Recent biogeographic studies place the Big Thicket in the

Coastal Plains and Flatwoods Ecoregion, Western Gulf Section, Subsection 231Fb (Southwest Flatwoods; Keys et al. 1995). The climate is humid subtropical with an average annual rainfall of 1,341 mm/yr (National Climatic Data Center 1994) evenly distributed throughout the year. Average annual temperature is 20.4° C; mean monthly temperature exceeds 10° C for all months. The growing season is long, from March to November, with approximately 240 consecutive frost-free days. Physically, it is mostly within the drainage of the Neches River 50–100 km inland from the Gulf of Mexico and about 75 km west of the Louisiana border.

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

Long-term Study Sites

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

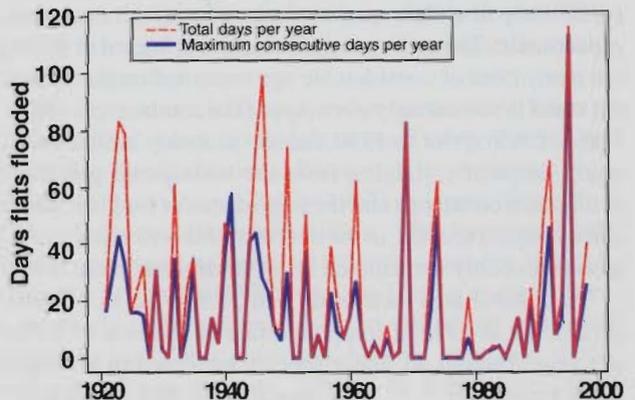


Figure 5-1. Total and maximum consecutive days flooded for the flats at the wet study site, 1920-90.

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

Cross-site Comparisons

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

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

Mortality

At the dry site, mortality loss varied by a factor of three over the period of record (Fig. 5-2), averaging about 0.22 m²/ha per year (0.9% of live basal area). There were no obvious trends or event-related peaks, except that understory trees showed slightly elevated mortality between 1987 and 1993, probably owing to increased canopy density. Much of the year-to-year variation in overall mortality was related to chance death of large trees. Turnover time, the time it would take to replace all the live basal area if new growth were equal to mortality, was 108 years.

At the mesic site, average mortality loss was higher (0.55 m²/ha per year; 1.5% of live basal area) and more variable (eightfold difference between maximum and minimum). Highest mortality (1.59 m²/ha; 4.3% of live basal area) was associated with Hurricane Bonnie (Fig. 5-2), which hit the stand in 1986 (the hurricane actually occurred in 1986, but since it occurred after the mortality survey for that year,

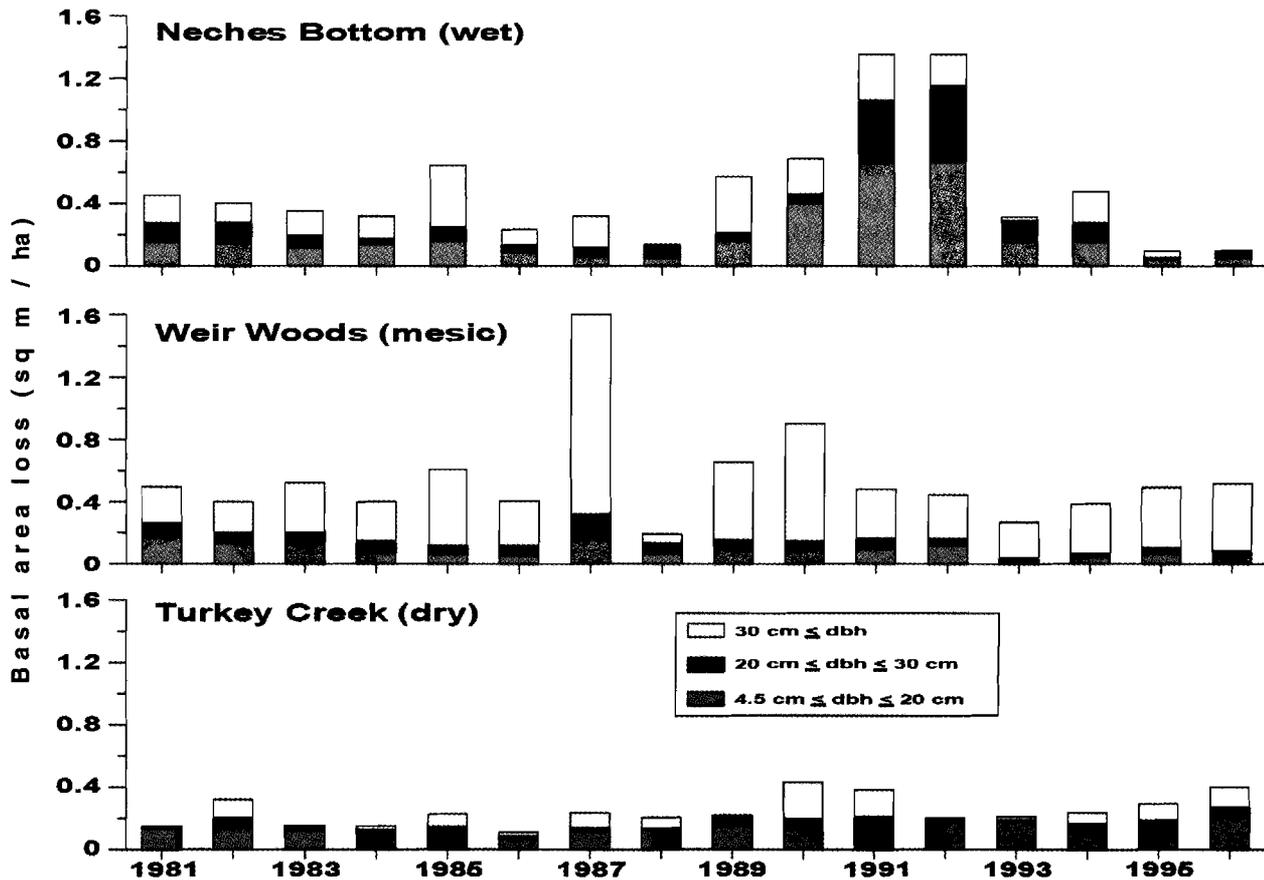


Figure 5-2. Basal area loss by size class for all sites, 1980-96.

the mortality increase is reflected in the 1987 data). Post-hurricane mortality was low in the year following the hurricane; such reductions have been attributed to reduced competition (Waring and Schlesinger 1987). Mortality then showed a mean peak; others have postulated that such peaks are caused by slow death of damaged trees (Putz and Sharitz 1991). To quantify the role of hurricanes, we calculated the overall average basal area loss in nonhurricane years ($0.49 \text{ m}^2/\text{ha}$ per year) and called that normal, or background, mortality. Subtracting that average from the average of all years gave the amount of mortality attributable to the hurricane ($0.06 \text{ m}^2/\text{ha}$ per year), approximately one-eighth of the total mortality. Thus, turnover time was reduced by the hurricane from 69 years for normal mortality alone to 64 years overall. When we consider the likelihood that not all hurricanes will hit this stand and the likely variability of hurricanes, the hurricane effect on stand structure and turnover reported here is probably a high estimate (Bill 1995).

At the wet site, average annual mortality was very high ($0.58 \text{ m}^2/\text{ha}$ per year; 2.1% of live basal area) and intermediate in level of variation (sixfold difference between maximum and minimum). This site may have the highest turnover rate ever reported for a well-developed, mature forest stand in the eastern United States. To quantify the role of flooding, we calculated the overall average basal area loss in nonflood years ($0.38 \text{ m}^2/\text{ha}$ per year) and called that normal, or background, mortality. Subtracting that value from the average over all years gave the amount of mortality attributable to flooding ($0.19 \text{ m}^2/\text{ha}$ per year), approximately one-third of the total mortality. Thus, flooding substantially reduced stand turnover time from 131 years for normal mortality alone to 77 years for all sources of mortality. This estimate of the flood effect must be considered tentative due to the relatively short duration of the record.

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

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

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

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

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

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

Sapling and Seedling Dynamics

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

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

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

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

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

At all three sites, increases in sapling numbers are tied to disturbances in the recent past. At two of the sites (dry and mesic), the disturbance was superimposed upon a pattern of stand recovery from prior logging. Human action appears to have changed natural processes more at the dry site (altered fire regime) and the wet site (altered flood regime) than at the mesic site. Nevertheless, because the disturbances were characteristic for the sites (i.e., fire at the dry site, flooding at the wet site, and a hurricane at the mesic site), some general interpretation is warranted. Most important, fire and flood are similar in that they affect

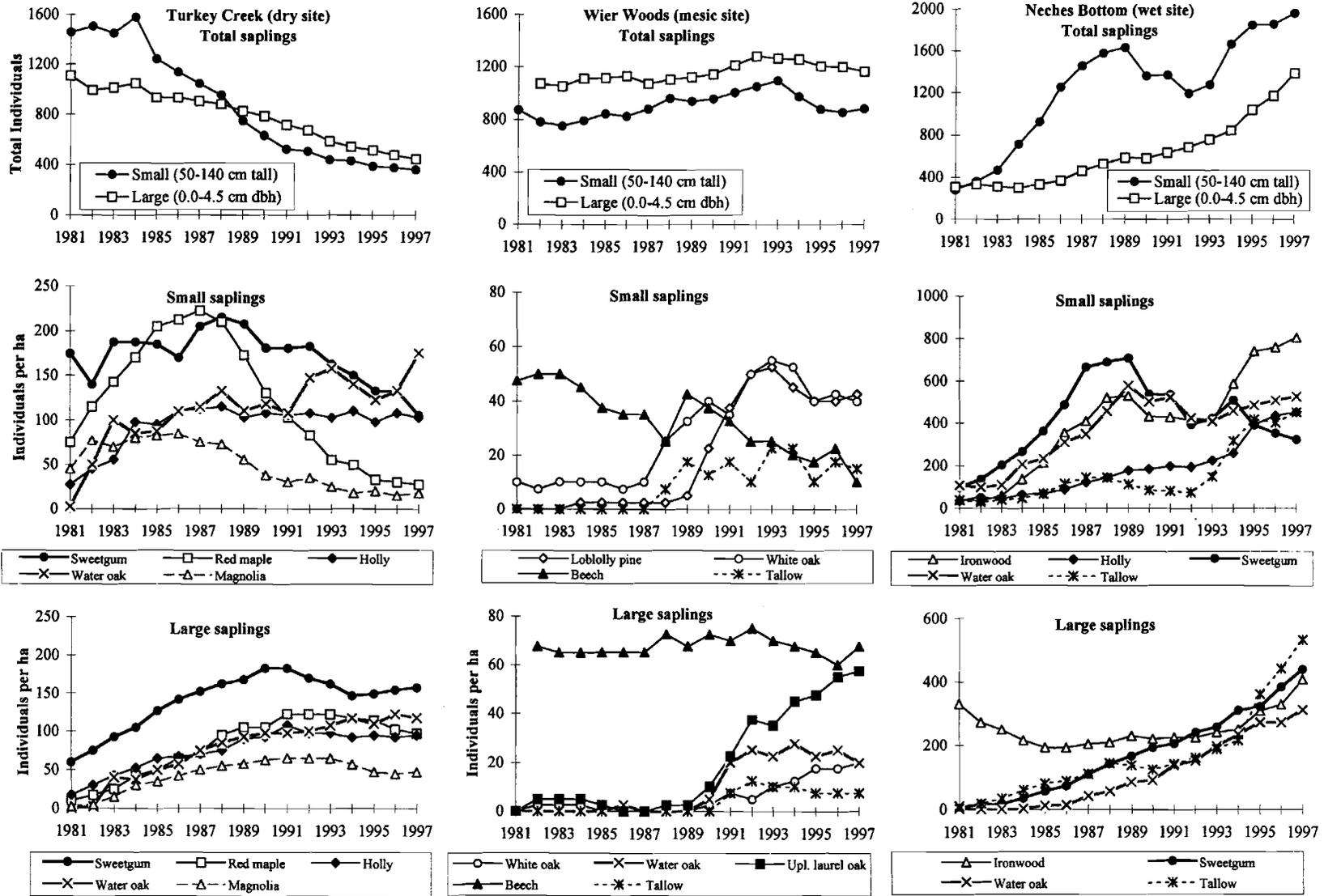


Figure 5-3. Total saplings and density of saplings of selected species at three study sites, 1981-97. Small saplings are individuals between 50 and 140 cm in height. Large saplings are individuals between 0.4 and 4.5 cm dbh.

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

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

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

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

C. Shade tolerant, mostly fire-intolerant species

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

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

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

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

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

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

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

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

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

Overall Stand Dynamics and Vegetation Response Time

Only modest changes in tree basal area, density, and species composition were observed at the three sites; these changes were mostly explainable in terms of successional change following logging or alterations in flood or fire regimes. In contrast, the sapling and seedling layers

varied more, apparently in response to recent disturbances, which suggests strong sensitivity to global warming by way of its effect on the disturbance regime. For the dry stand, autogenic succession is the dominant process, particularly in the subcanopy strata. Nevertheless, the stand may well be sensitive to climate change since the successional process could be accelerated by increased storm activity which could kill canopy trees and thereby accelerate succession to a mesic, less fire-dependent community type (Glitzenstein and Harcombe 1988; Liu et al. 1997). On the other hand, succession could be reversed by increased drought severity; drought could kill mesic juveniles directly via water stress or indirectly via increased fire frequency (e.g., Glitzenstein et al. 1995). The indirect effects could equal or exceed the magnitude of the direct effects.

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

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

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

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

Pattern and Process

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

Flood and Shade Tolerance

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

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

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

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

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

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

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

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

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

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

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

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

Growth Responses

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

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

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

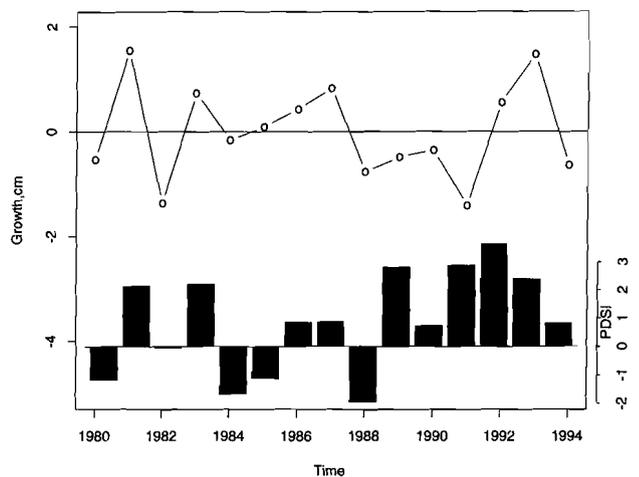


Figure 5-4. Pooled residual sapling growth for three study sites compared to Palmer Drought Severity Index, 1980-93.

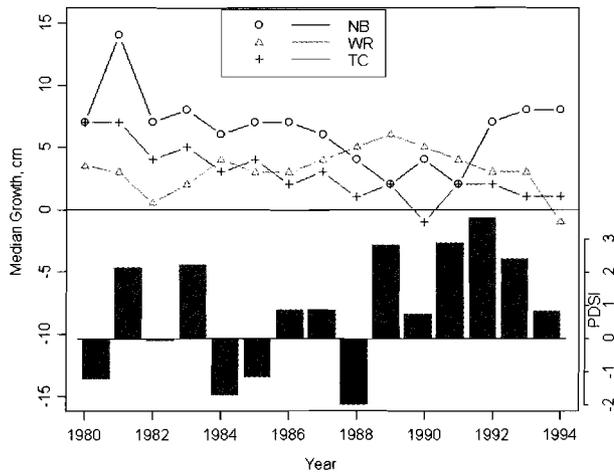


Figure 5-5. Comparison of median residual sapling growth by site with Palmer Drought Severity Index, 1980-93.

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

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

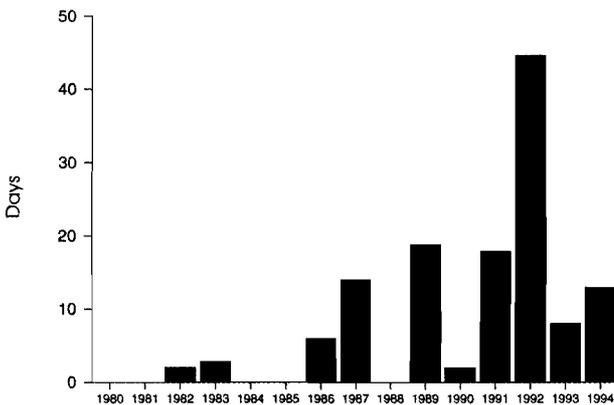


Figure 5-6. Maximum consecutively flooded growing-season days for flats at wet site, 1980-94.

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

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

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

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

We used stepwise linear least-squares regression to model growth as a function of several site variables (percent sand, percent clay, relative elevation, and weighted percent sky; details on estimation of environmental variables can be found in Hall 1993). The following predictor variables were also included in the analysis: size of the individual at the beginning of the period of growth, species-specific growth ranking, total density of individuals

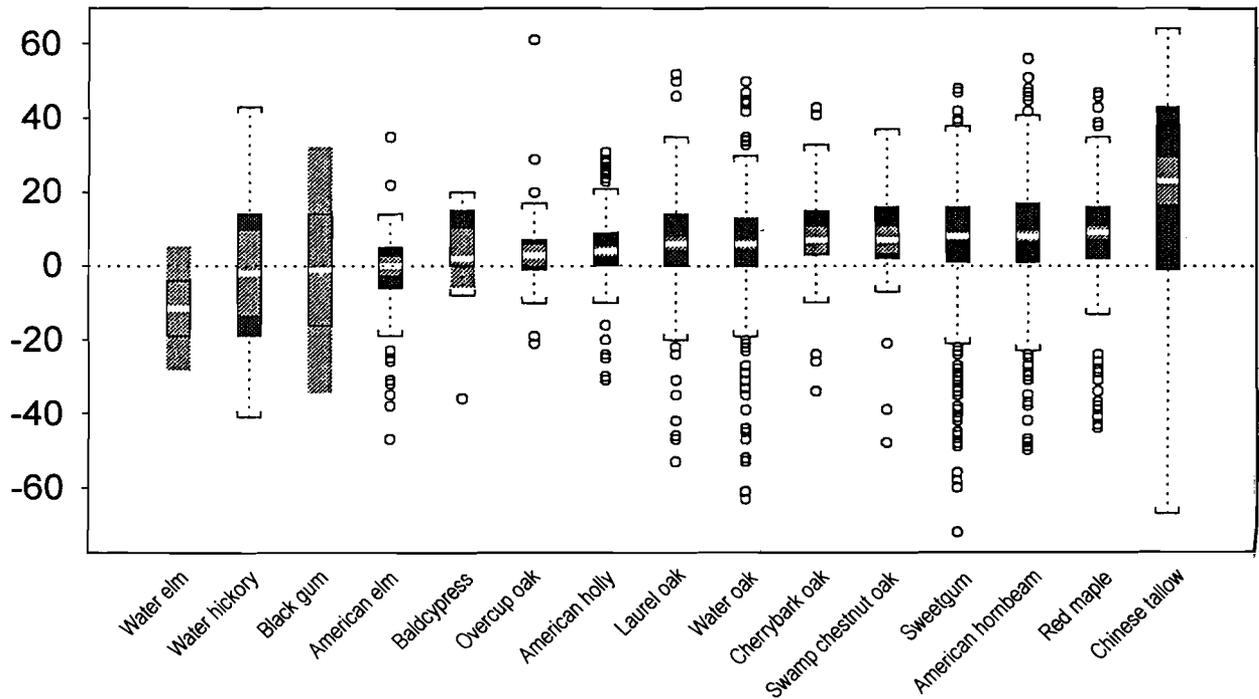


Figure 5-7. Box plots of median height growth of small saplings by species at wet site (from Hall 1993). For each boxplot, the white bar represents the median, the light gray bar represents the 95% confidence interval, the dark gray bar and the black outlined box represent the interquartile range, the brackets or whiskers represent 1.5 times the interquartile range, and the empty circles represent outlying data points.

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

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

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

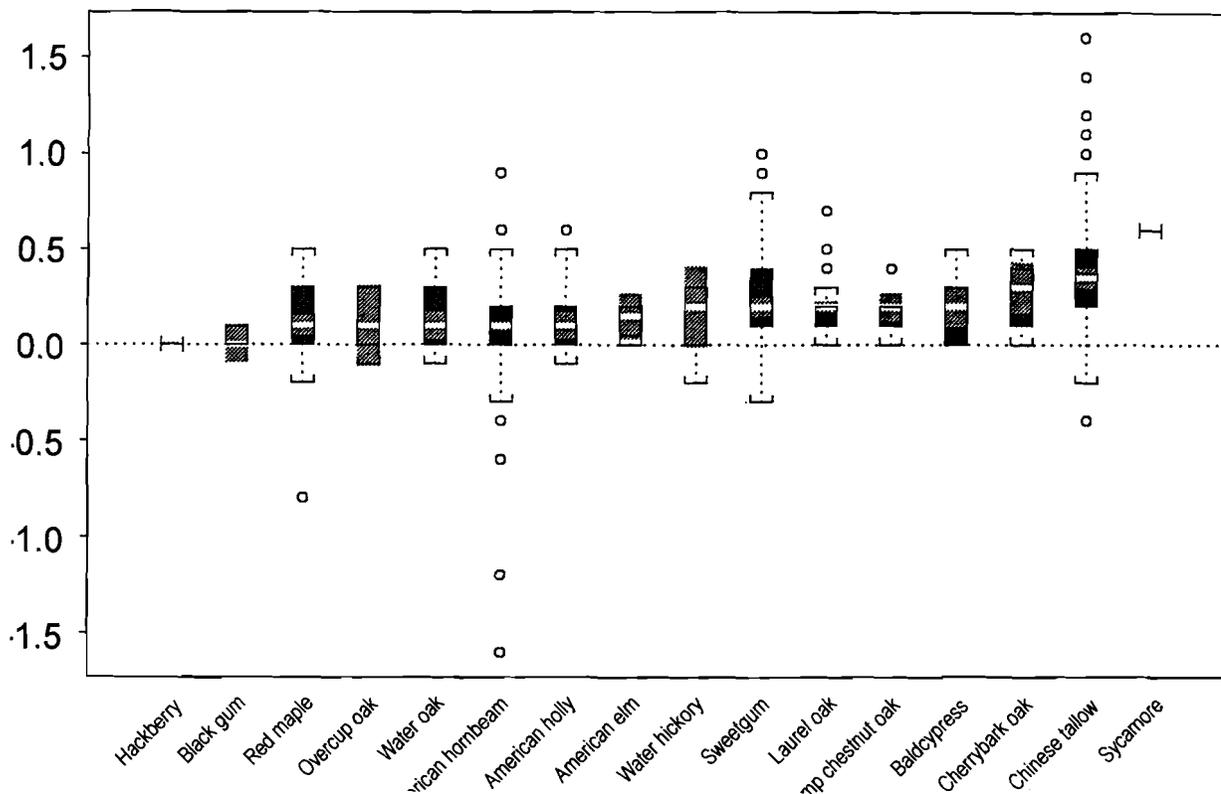


Figure 5-8. Box plots of median dbh growth of large saplings by species at the wet site (From Hall 1993). See Fig. 5-7 for explanation of box plots.

Tree Ring Analysis Along a Climatic Gradient

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

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

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

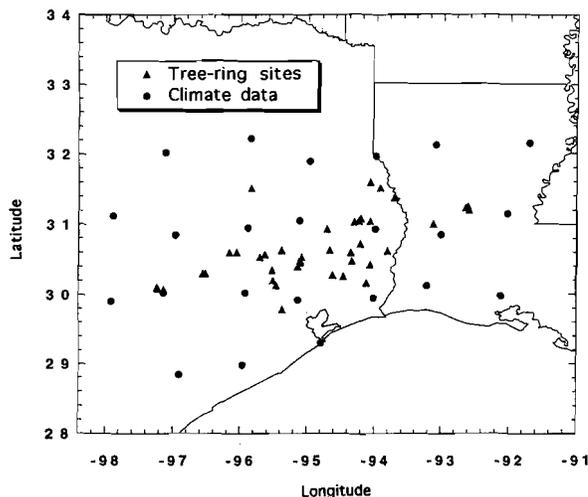


Figure 5-9. Tree-ring site locations in the Big Thicket region.

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

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

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

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

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

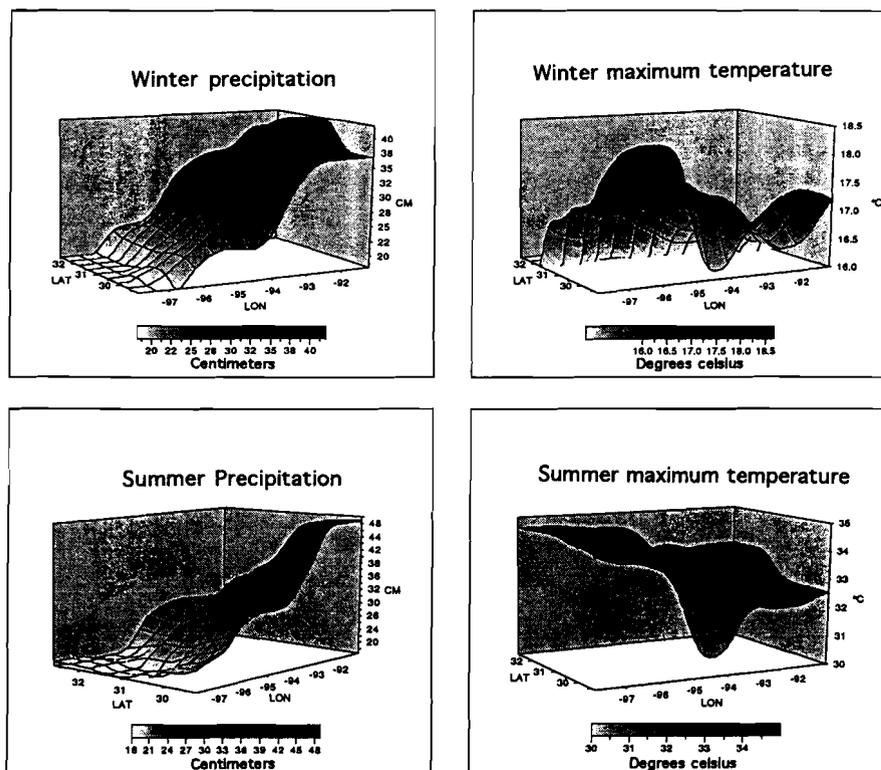


Figure 5-10. Surface maps of precipitation and maximum temperature over the Big Thicket region.

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

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

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

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

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

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

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

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

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

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

For input data, we used tree-ring indices which sequentially removed sources of extraneous variation to focus on year-to-year variability in growth due to climate. Construction of these indices involves two steps (Cook 1985; Fritts and Swetnam 1989). First, long-term, relatively inflexible trend lines are fitted to the individual tree-ring widths and deviations from these fitted lines (residuals) are preserved for analysis. This technique effectively removes gradual

changes in growth due either to intrinsic properties of trees (i.e., all other factors being equal, younger trees grow faster than older trees) or to long-term trends in biotic or abiotic environment (e.g., growth of trees into canopy gaps; see Glitzenstein et al. 1986). These gradual trends, while ecologically interesting, tend to obscure short-term growth responses related to climate.

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

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

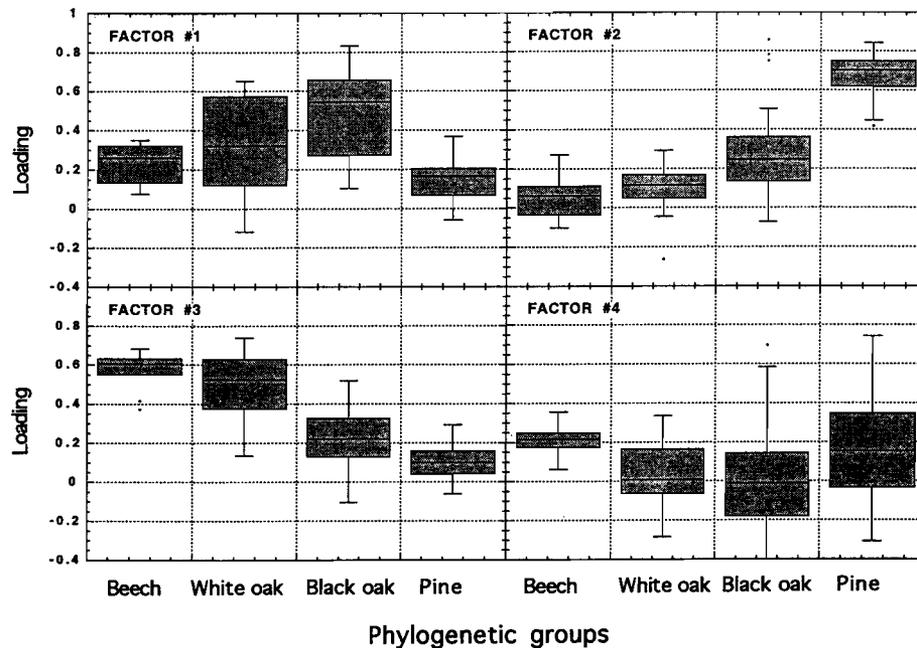


Figure 5-11. Varimax rotated factor loadings for each phylogenetic group on each principal components analysis (PCA) factor. Each of the four sections corresponds to one of the PCA factors. Within each section there is a box plot of the factor loadings for all chronologies (species x sites) within each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

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

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

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

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

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

Conclusion

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

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

At the mesic site, we had an opportunity to directly observe the effects of a hurricane. Even though it caused only a small rise in mortality of canopy trees, this storm had an important impact on forest regeneration processes. Long intervals between canopy opening events gradually reduce understory trees and shrubs, providing opportunities for regeneration of canopy species. Consequently, increasing frequency of large storms may maintain uncharacteristically dense shrub populations, with detrimental consequences for canopy tree regeneration. This suppression of tree regeneration, coupled with higher storm-related mortality could result in a decline in the standing biomass

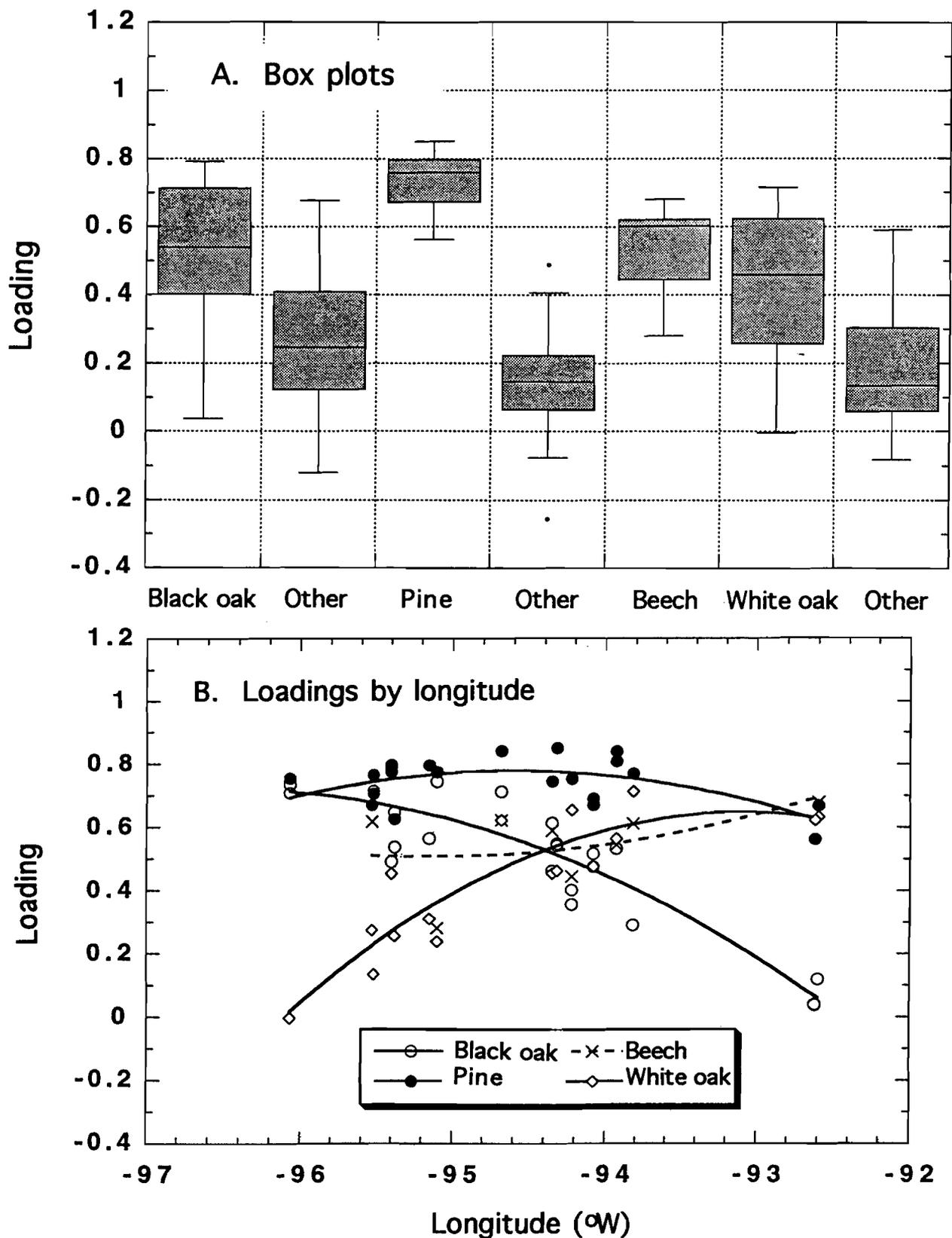


Figure 5-12. Varimax factor loadings for each of the four phylogenetic groups. Black oak loadings are Factor 1 values for the oak subgenus *Erythrobalanus*, pine loadings are Factor 2 values for pine species, beech loadings are Factor 3 values for American beech, and White oak loadings are Factor 3 values for the subgenus *Leucobalanus*.

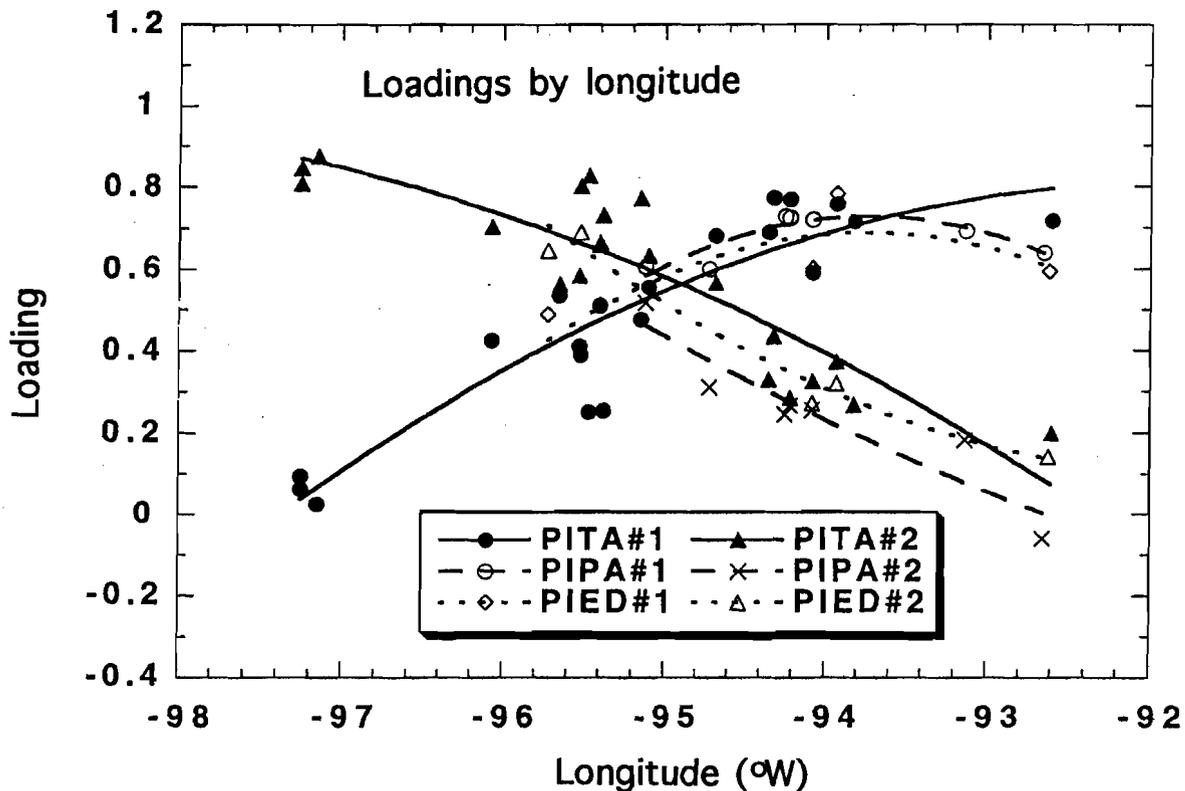


Figure 5-13. Varimax loadings by longitude for pine chronologies.

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

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

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

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

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

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

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

indicate that the ability to survive suppression is at least as important as growth in determining shade tolerance.

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