RICE UNIVERSITY

Fluctuations in abundance and mortality of *Carpinus caroliniana* (American hornbeam) and the invasion of *Sapium sebiferum* (Chinese tallow)

By

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A Thesis Submitted in Partial Fulfillment of the Requirements for the Degree of

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ABSTRACT

Fluctuations in abundance and mortality of Carpinus caroliniana (American hornbeam) and the invasion of Sapium sebiferum (Chinese tallow)

by

Lisa E. Mann

A bottomland hardwood forest stand located in east Texas experienced a hurricane-related flood event in 1989. After this event, Carpinus caroliniana Walt. had a large pulse in mortality, decreasing dramatically in abundance (47%) over a 5-year period. The decline was greater at low elevations suggesting that at least part of the mortality was related to flooding. The flood was the longest summer flood on record. The duration of this growing season flood may have been partly a consequence of upstream dam management.

Linear regression showed that in areas where Carpinus death was greater, several sapling species had increases in basal area growth. The invasive species Sapium sebiferum (L.) Roxb. had the greatest increase. This suggests that the Carpinus death and concomitant increase in light availability resulted in accelerated invasion of this forest by Sapium.
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TABLE OF CONTENTS

LIST OF TABLES v
LIST OF FIGURES vi
LIST OF APPENDICES vii
INTRODUCTION 1

CHAPTER 1. Background
   Bottomland hardwood forests 3
   Impoundment effects 4
   Flooding responses 5
   Shade tolerance 7
   Demographic strategies 8
   Population decline 9
   Invasive species 11
   Chapter aims 15

CHAPTER 2. Fluctuations in abundance and mortality of Carpinus caroliniana 17
   Site description 19
   Methods 21
   Results 25
   I. Literature investigation 25
      Pests or pathogens 25
      Climate 25
      Flood tolerance 26
   II. The flood 27
   III. Population analysis 28
      Population structure 28
      Mortality 30
      Age 31
      Ingrowth 33
   IV. Flooding analysis 33
      Discussion 35

CHAPTER 3. Invasion of Sapium sebiferum 42
   Methods 43
   Results 46
   Discussion 47
   CONCLUSION 51
   REFERENCES 52
   TABLES 72
   FIGURES 82
   APPENDICES 100
# LIST OF TABLES

Table 1. Major tree species found in the Neches Bottom study site .......................... 72  
Table 2. Flood tolerance of major Neches Bottom tree species .................................. 72  
Table 3. Number of stems per hectare of *Carpinus* for selected years by zone .......... 73  
Table 4. Basal area per hectare of *Carpinus* for selected years by zone ................. 73  
Table 5. Number of stems per hectare of *Carpinus* for selected years by zone .......... 73  
Table 6. Number of stems at three sites during the flood period ............................... 74  
Table 7. Growth estimation and age results for *Carpinus* ....................................... 74  
Table 8. Spring and summer flooding pre-dam, 1921-1964 ...................................... 75  
Table 9. Spring and summer flooding post-dam, 1965-2003 ..................................... 76  
Table 10. Spring and summer flooding pre- and post-dam, 1921-1964 ....................... 77  
Table 11. Comparison of the two 1989 floods ....................................................... 77  
Table 12. Comparison of 1989 flood to median days flooded 1922-1965 and 1965-1990 77  
Table 13. Monthly length of mild to extreme droughts 1970-2005 ............................ 78  
Table 14. Monthly length of moderate drought of 1988-1989 .................................. 78  
Table 15. Monthly length of extreme drought of 1999-2000 ................................... 79  
Table 16. Sapling species analyzed in competition analysis .................................... 80  
Table 17. Analysis of variance for growth model ................................................... 80  
Table 18. Slopes for the interaction between species and competition index due to *Carpinus* death ........................................... 81  
Table 19. Slopes for the interaction between species and competition index 1994 ........ 81  
Table 20. Zones and percent of time flooded during the growing season from Hall and Smith (1955) study .................................................. 109  
Table 21. Percent of time flooded until death based on 3 growing season lengths ...... 109  
Table 22. Growth comparison of *Carpinus* trees that survived or died in the following interval .................................................. 117  
Table 23. Drought intervals based on percentage of normal precipitation ............... 141  
Table 24. Impoundments above the study site ....................................................... 152
LIST OF FIGURES

Figure 1. The study site by plot and flooded condition 82
Figure 2. The range of *Carpinus caroliniana* 82
Figure 3. Trends in live tree basal area and abundance 83
Figure 4. Size distribution of the *Carpinus* population 84
Figure 5. Number of trees dying per year 85
Figure 6. The mortality rates of *Carpinus* trees during various time intervals 85
Figure 7. Live *Carpinus* in 1989 still alive in 1989 86
Figure 8. The population structure of *Carpinus* by elevation zone 87
Figure 9. The probability of *Carpinus* death by size and elevation 88
Figure 10. *Carpinus* growth during three sapling size classes 89
Figure 11. *Carpinus* growth during three tree size classes 89
Figure 12. Ingrowth/year/hectare for important species 90
Figure 13. Small sapling dynamics 91
Figure 14. Large sapling dynamics 91
Figure 15. The mean daily streamflow 1922-2003 92
Figure 16. Mean daily streamflow for some large growing season floods 93
Figure 17. Flow comparison and precipitation for the 1989 growing season 93
Figure 18. Mean daily temperature 1985-1989 compared with normal mean monthly temperature 1978-2004 94
Figure 19. Mean daily temperature 1989-1984 compared with normal mean monthly temperature 1978-2004 94
Figure 20. The mortality risk of selected species as a function of light 95
Figure 21. Total 2.0 cm ingrowth 1997-2000 and *Carpinus* basal area loss 1990-1994 96
Figure 22. Ingrowth versus *Carpinus* basal area loss 97
Figure 23. Subject sapling growth 1994-1997 98
Figure 24. Trends in species growth and decreased competition from *Carpinus* death 99
Figure 25. Trends in species growth and competition in 1994 99
Figure 26. Variation over time in average annual tree growth rates 118
Figure 27. Growing season length for several species 119
Figure 28. Comparison of Hall (1993) and Mann and Harcombe (2005) elevation measurements at the study site 129
Figure 29. Live *Carpinus* in 1980 still alive in 1989 144
Figure 30. The fraction of 2-4.5 cm DBH *Carpinus* saplings dying 1981-1989 versus *Carpinus* stems per plot in 1980 144
Figure 31. Dead *Carpinus* by elevation zone and year 146
Figure 32. The probability of *Carpinus* death for all combinations of DBH and elevation 148
Figure 33. The probability of *Carpinus* death 1980-1989 by size and elevation 149
Figure 34. The probability of *Carpinus* death 1990-1994 by size and elevation 150
Figure 35. The probability of *Carpinus* death 1994-2003 by size and elevation 151
Figure 36. The watersheds of east Texas 153
Figure 37. The Neches River watershed and major impoundments 153
**LIST OF APPENDICES**

<table>
<thead>
<tr>
<th>Appendix</th>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>Flood responses and adaptations</td>
<td>100</td>
</tr>
<tr>
<td>B</td>
<td>Flooding and determination of flood tolerance</td>
<td>103</td>
</tr>
<tr>
<td>C</td>
<td>Growth</td>
<td>113</td>
</tr>
<tr>
<td>D</td>
<td>Background on major Neches Bottom species</td>
<td>119</td>
</tr>
<tr>
<td>E</td>
<td><em>Carpinus</em> age estimation</td>
<td>126</td>
</tr>
<tr>
<td>F</td>
<td>Comparing elevation measurements of 1989 and 2005</td>
<td>126</td>
</tr>
<tr>
<td>G</td>
<td>Permanent pathogens of hardwoods in eastern forests</td>
<td>130</td>
</tr>
<tr>
<td>H</td>
<td>Episodic mortality</td>
<td>135</td>
</tr>
<tr>
<td>I</td>
<td>Climate</td>
<td>138</td>
</tr>
<tr>
<td>J</td>
<td>Tropical storm Allison</td>
<td>142</td>
</tr>
<tr>
<td>K</td>
<td>Pre-flood decline</td>
<td>143</td>
</tr>
<tr>
<td>L</td>
<td>Time to <em>Carpinus</em> death</td>
<td>145</td>
</tr>
<tr>
<td>M</td>
<td>Probability of death analysis</td>
<td>146</td>
</tr>
<tr>
<td>N</td>
<td>Impoundments</td>
<td>152</td>
</tr>
<tr>
<td>O</td>
<td>Shade tolerance</td>
<td>154</td>
</tr>
</tbody>
</table>
INTRODUCTION

A long-term study of a bottomland hardwood forest stand in east Texas affords the opportunity to document magnitudes of changes in tree populations and invites investigation of the causes of anomalous variations. Two large changes have been observed in this forest in the last 25 years; a rapid decline in the abundant native, Carpinus caroliniana Walt. (American hornbeam), and a rapid increase in the invasive alien Sapium sebiferum (L.) Roxb. (Chinese tallow). Since Carpinus is abundant and widespread in bottomland hardwood forests throughout the southeastern United States (Monk 1965, Sullivan and Nixon 1971, Nixon et al. 1973, Nixon and Willett 1974, Chambless and Nixon 1975, Nixon and Raines 1976, Nixon et al. 1977, Metzger 1990, Christensen 2003, Greller 2004, Robertson 2006) and Sapium is a particularly noxious invasive (Bruce et al. 1997, Bogler 2000), documentation of the changes is important to our knowledge of the dynamics of these forests. Using long-term data, I examined mortality rates, growth rates, ingrowth rates, abundance, and basal area changes for over a period of approximately twenty years in a bottomland hardwood forest stand. Data from an United States Geological Survey (USGS) gage provided information regarding flood frequency and duration (USGS 2004).

Several possible explanations exist for the decline of a woody plant species in a floodplain, including flooding (Broadfoot and Williston 1973, Kozlowski 1984a, Kozlowski and Pallardy 1997), pests (Campbell and Sloan 1977, Davidson et al. 1999), disease (Horst 1979, Sinclair et al. 1987), and climate change (Iverson and Prasad 1998, Kullman 1996, Iverson and Prasad 2002). I inspected existing literature to identify patterns and investigate causes of other observed population fluctuations. With this
information, I am addressing three questions in particular: 1. Can flooding, pest or pathogen outbreak, climate change or some combination of factors provide an explanation for the decline of *Carpinus*? 2. If flooding is implicated, why should a floodplain dominant be so severely affected by a flood? 3. Did canopy opening resulting from death of *Carpinus* accelerate invasion of *Sapium*, i.e., did disturbance accelerate alien plant invasion in this bottomland hardwood forest?

In Chapter 1, I will provide background information on several relevant topics. I will first present literature on bottomland hardwood forests and then introduce some of the known effects of impoundments on vegetation and water flows. I will proceed to consider flood tolerance, shade tolerance, demographic strategies, and causes for population decline that will be mainly relevant to the decline of *Carpinus* addressed in Chapter 2. Finally, I will address topics that pertain mainly to the increase of *Sapium* presented in Chapter 3. These topics include invasibility, the effects of invasive species, and previous research on *Sapium* in east Texas.
CHAPTER 1. Background

Bottomland hardwood forests

Bottomland hardwood forests occur in the southeastern, central, and eastern United States (Taylor et al. 1990). These habitats are often characterized by long periods of winter flooding that result in soil saturation in the root zone area. Because of the accompanying anoxic conditions, the dominant woody species in these habitats usually possess particular morphological or physical adaptations that allow them to survive and grow (Huffman and Forsythe 1981), including specialized roots (Kozlowski 1979), the ability to reopen stomata under flooded conditions, hypertrophied lenticels, and aerenchyma tissue (Kozlowski and Pallardy 1997).

Small differences in soil texture, structure, or elevation have marked effects on soil chemistry, moisture, aeration, and the frequency and magnitude of flooding in these systems. For example, Bledsoe and Shear (2000) found that differences in elevation of 10 cm resulted in a difference of 20% in the frequency of surface flooding. Plant communities are often stratified according to elevation in relation to area flooded (Hall and Smith 1955, Whitlow and Harris 1979, Battaglia et al. 2002, Denslow et al. 2002).

Bottomland hardwood forests provide several ecosystem services, such as habitats for animal species, water quality maintenance, and regulation of hydrologic cycles (Tickner et al. 2001). Unfortunately, these forests are rapidly diminishing. In southern Illinois, 98% of the original bottomland hardwood forest has been depleted (Tiner 1984). In east Texas, only 47% of the original bottomland hardwood forest area remained in 1980 (Frye 1987). More than 70% of Texas bottomland hardwoods are located in east Texas (Frye 1987). These habitats are negatively impacted by clearing for agriculture,
development of flood control structures, reservoirs, surface mining, urban development, conversion to pine forests, and oil extraction (Tiner 1984, Allen et al. 2001).

**Impoundment effects**

The flow regime in river systems has five main components that are crucial to ecological processes: magnitude, frequency, duration, timing, and rate of change of hydrological conditions (Poff et al. 1997). River impoundment may alter these flow characteristics, resulting in several changes in the river and floodplain ecosystem. Flow stabilization associated with dams alters the magnitude and frequency of high flows (Poff et al. 1997). In some rivers, loss of high magnitude flows after impoundment results in streambed and streambank colonization downstream due to decreased flood scour (Williams and Wolman 1984). One study of 21 dams on alluvial rivers found that most dams decreased flood peaks (Williams and Wolman 1984). One result of decreasing peak flows is extending the duration of high flows (Poff et al. 1997, Rood et al. 2005). Extended duration of flows may permit some flood-tolerant species to displace less tolerant species at low elevations (Hall et al. 1946, Chapman et al. 1982, Poff et al. 1997).

Many river systems experience a winter flood on a nearly annual basis, which has been called the flood pulse (Junk et al. 1989). Changes in the timing of the flood pulse can also affect vegetation composition in floodplains. This may happen when the seasonality of flooding shifts from spring to summer, which often takes place when reservoirs are managed for irrigation water supply (Poff et al. 1997). For example, one dominant tree species in Arizona, *Populus fremontii* (Fremont cottonwood), is unable to recruit new individuals because of a flood pulse that has been delayed by dams until after its period of germination. This species relies on high floodwaters to disperse and
germinates on the moist soil after the water recedes. A delayed flood pulse means that *P. fremontii* only disperses short distances and has reduced germination on dry soil (Fenner et al. 1985). For species with similar reproductive phenologies, the rate at which the water recedes is also important. If the floodwaters recede too quickly before seedfall, recruitment can be halted (Poff et al. 1997). For example, seed fall of *Eucalyptus camaldulensis* (red gum) and *Melaleuca leucadendra* (weeping teatree) on the Ord River in Australia coincides with receding of floodwaters. This allows germination on the moist soil after the water retreats. These species only produce one crop of short-lived seeds per year (Pettit and Froend 2001). Thus, if waters recede too quickly before seedfall, dispersal and recruitment could be limited.

**Flooding responses**

Flood tolerance is the ability of a species to withstand waterlogging during the growing season (Hook 1984a). During flooded conditions, water occupies the pores in the soil and a deficiency of oxygen occurs belowground (Kozlowski and Pallardy 1997). Plant roots may switch from aerobic to anaerobic respiration, resulting in the accumulation of toxic compounds (Kozlowski 1979). Photosynthesis may be reduced, and several other negative responses may occur as well (Kozlowski and Pallardy 1997, Appendix A). Flooding can also cause root decay, chlorosis of leaves, and induce leaf senescence and abscission (Kozlowski 1984a). Mortality from flooding during the growing season may also result (e.g. Hall et al. 1946, Hall and Smith 1955, Harms et al. 1980, Yin et al. 1994).

Species respond to extended periods of flooding differently, i.e., they vary in flood tolerance (Appendix B). Flood intolerant species are unable to reopen stomata that
close in response to soil hypoxia during flooded conditions. In contrast, flood tolerant species can reopen their stomata and nearly regain their original photosynthetic rate (Kozlowski and Pallardy 1997). In addition, species that are morphologically adapted to poor soil aeration are able to absorb oxygen through stomata or lenticels. From the pores or lenticels, the oxygen is moved downward and is diffused out of the roots to the rhizosphere. This oxygen oxidizes reduced soil compounds, like toxic ferrous and manganous ions (Kozlowski and Pallardy 1997). Two other adaptations that allow for increased oxygen transport include formation of hypertrophied lenticels and aerenchyma tissue. The lenticels on the stem surface increase in size and intercellular space, which permits greater gas exchange between the interior tissues and surrounding air. Oxygen is moved downward and diffuses out of the roots, oxidizing reduced compounds. Aerenchyma tissue also permits greater oxygen transfer because of its large intercellular spaces (Kozlowski and Pallardy 1997).

Adventitious roots at or below the water level may allow flood tolerant species the best chance of survival under flooded conditions. This adaptation takes advantage of the slightly higher oxygen and slightly lower toxin concentrations found in the uppermost soil. In addition, adventitious roots increase the amount of surface area available for water and nutrient uptake and oxidize the rhizosphere (Kozlowski 1979).

The effects of flooding vary due to several factors, including soil type, depth and duration of floodwater, season, water temperature, and whether or not the water was flowing (Appendix B, see also Hall et al. 1946, Teskey and Hinckley 1977, Harms et al. 1980, Kozlowski 1984a, Yin et al. 1994).
Shade tolerance

Previous studies in the same east Texas stand under investigation in this work have indicated that shade tolerance plays an important role in determining bottomland hardwood composition (Streng et al. 1989, Hall and Harcombe 1998, Hall and Harcombe 2001, Lin et al. 2004). Shade tolerance is usually described in terms of discrete categories. However, species responses to light variation actually fall along a "multidimensional continuum" (Pacala et al. 1994). The traditional placement of species into categories stems from observations that, in general, some species (shade intolerant) grow faster in high light conditions and slower in low light conditions than other species (shade tolerant) (Boardman 1977, Lorimer 1981, Kobe et al. 1995, Lin et al. 2004). Other studies have found that the low-light trade-off involves survivorship in low light conditions instead of growth. In this case, species classified as shade intolerant have faster growth in high light but higher mortality in low light than shade tolerant species (Pacala et al. 1994, Pacala et al. 1996).

According to light competition models, shade tolerant species should eventually displace these shade intolerant species as dominants in bottomland hardwood forests (Lin et al. 2004). In actuality, shade intolerant species usually remain dominant in these communities over time (Jones et al. 1994, Lin et al. 2004). Several studies have suggested that a combination of low light availability and flooding are the main reason for this dynamic (Jones and Sharitz 1989, Hall and Harcombe 1998, Jones and Sharitz 1998, Lin et al. 2004). Very few species can persist under the combined stresses of low light and flooding. Consequently, success depends strongly on the relative performance in gaps where there is abundant light. Under these conditions, shade-intolerant species
get taller more quickly than the shade-tolerant species, and the shade tolerant species then succumb to continued stresses of low light and frequent flooding.

Consistent with this, in one study of bottomland hardwood forest saplings, some relatively shade tolerant species were found in areas of higher light than expected (Hall and Harcombe 1998). In a following study, these species had higher mortality at low light levels than is typical for shade tolerant species (Lin et al. 2004). The high mortality at low light, which accounts for the shift in local distribution, was attributed to flooding. When flooding mortality was accounted for, shade tolerant species had the expected lower risk of mortality at lower growth than the shade intolerant species (Lin et al. 2004).

Demographic strategies

Another study of this east Texas bottomland hardwood forest found emergence time to be one of the main factors that affected dynamics and composition of the seedling layer (Streng et al. 1989). Species that emerged earlier in the season usually had higher survival rates than species that emerged later (Streng et al. 1989). However, in some years, early season flooding killed the early-emerging species (Streng et al. 1989). Another important factor was seed mass: seedlings of heavier-seeded species were better equipped to survive periods of adversity, such as flooding or drought. Lighter-seeded species, in contrast, were more delicate and prone to decline during adverse periods. Although the late-emerging, heavier-seeded species were better adapted to survive flooding, the early-emerging, light-seeded species had higher fecundity, which allowed them to regenerate more rapidly (Streng et al. 1989).
Population decline

Typically, tree populations are quasi-stable in floodplains; that is, floods do not cause major episodes of mortality (Hupp 2000, Shafroth et al. 2002), although it has been known to occur. For example, after a 51-day growing season flood along the Mississippi River in Missouri, mortality of stems greater than ten cm ranged from one to thirty-three percent depending on river reach (Yin et al. 1994). Most other examples of mortality due to flooding involve continuous flooding (e.g. Harms et al. 1980) or consecutive years of growing season flooding (e.g. Hall and Smith 1955). In the present study, after a 1989 flood event due to Tropical Storm Allison, Carpinus suffered high mortality. The timing suggests that the flood might account for the Carpinus mortality, yet, as a dominant species in a floodplain community, Carpinus should be physiologically adapted to such events. Consequently, other possibilities for the Carpinus death must be considered.

In many forest types, pest outbreaks may cause fluctuations in tree species. For example, Lymantria dispar (gypsy moth) has been known to cause mortality after multiple years of defoliating healthy trees or from a single defoliation of weak trees (Campbell and Sloan 1977). Disease may also result in tree mortality, often affecting large geographic areas over a lengthy period of time (Scheffer 1997). Some pathogen-caused diseases are species-specific, such as Chestnut blight on Castanea dentata (American chestnut) caused by a fungus, Cryphonectria parasitica (Scheffer 1997). Other diseases, such as Phymatotrichum omnivorum (Texas or cotton root rot), may affect several species. P. omnivorum affects over 2000 plants species, including Carpinus, Liquidambar, Taxodium, and Acer in Texas (Horst 1979). The time to death
resulting from disease varies from weeks to years, including mortality due to \textit{P. omnivorum} and Dutch elm disease caused by \textit{Ophiostoma ulmi}.

Another factor that could cause changes in a tree population is climate. Tree species are constrained geographically by numerous factors. These may include humidity, substrate composition, nighttime temperatures, and water table levels (Box et al. 1993). For example, \textit{Bursera simaruba} (gumbo limbo) shows a horseshoe shaped distribution along the Florida peninsula, which seems to be related to higher humidity, nighttime temperatures, or substrate differences in coastal areas (Box et al. 1993). Species on the edge of their range where they are presumably near their physiological tolerance limits are expected to be first and most heavily affected by changing climate (Botkin 1993, Cramer and Leemans 1993).

The importance of climatic conditions to trees means that a shift in climate may influence tree growth and distribution (Box et al. 1993, Iverson and Prasad 1998). Studies of Holocene vegetation in the United States support the notion that plant ranges change with shifts in climate; these studies found that many species ranges shifted northward after warming (Delcourt and Delcourt 1988). Iverson and Prasad (2002) predicted that many modern species ranges would move northward under the various climate change scenarios. They found that the potential future range of several species ranges would result in decreases in populations in certain areas and increases in populations in others, depending on species.

Some increases and decreases of tree populations have been attributed, at least in part, to climate change. These changes in abundance are gradual and many have been found to take place on time scales over several decades (e.g. Hennon and Shaw 1994,
Kullman 1996, Jha et al. 2004) or millennia (e.g. Davis et al. 1998). For example, *Picea abies* (Norway spruce) increased in abundance between 1900 and 1950 due to increased summer temperatures. It declined in the last half of the 20th century owing in large part to cooler winter soil temperatures (Kullman 1996). In another example, *Fagus grandifolia* (American beech) declined over a 15-year study period due to a combination of several potential factors, including increasing temperatures, pathogens, and hurricane damage (Jha et al. 2004).

This brief literature review suggests the death of *Carpinus* could be due to several reasons. Flooding, although not a common cause of mortality, can cause the death of individuals in tree populations over a period of several years. Insect and disease outbreaks are other reasons that tree populations can decrease, and these occur over time scales of weeks to years (Campbell and Sloan 1977, Sinclair et al. 1987, Runkle 1990, Daughtrey and Hibben 1994, Agrios 1997, Scheffer 1997). Finally, climate change can cause declines in tree populations over several decades to millennia (e.g. Hennon and Shaw 1994, Kullman 1996, Jha et al. 2004, Davis et al. 1998).

**Invasive species**

Despite the importance of bottomland hardwood forests, there is still a dearth of data and knowledge regarding the interactions between vegetation and the environment in this system (Gore and Shields 1995, Bledsoe and Shear 2000). Areas needing more study in wetland forests include the role of disturbance in controlling vegetation composition and the interactions between invasive and native plant species (Tickner et al. 2001).

*Sapium sebiferum* (Chinese tallow) is a relatively recent addition to the floodplain forest under study, having arrived in the early 1970s. *Sapium* is an invasive, deciduous
tree in the southeast United States, native to subtropical areas (Bruce et al. 1997). *Sapium* was originally planted in the United States as an oil crop or as an ornamental due to its brightly colored foliage (Bruce et al. 1997). This fast-growing species has changed many native prairies into tallow-dominated communities (Bruce et al. 1995, Bruce et al. 1997). Both before and after the flood event, it was increasing rapidly in abundance, although it may have increased faster after the flood event.

In several arid habitats, invasions have been attributed to a decrease in flooding, e.g. the invasion of *Tamarix ramosissima* (salt cedar) and the concomitant replacement of native *Populus* (cottonwood) and *Salix* (willow) species (Sher et al. 2002) in the southwest United States. Several responses appear to contribute to the success of *Tamarix* in invading these riparian zones, including longer duration of seed production than the natives (Horton et al. 1960, Sher et al. 2002). This allows *Tamarix* to take advantage of late floods, fire, or clearings created by humans after the native species have stopped producing seeds (Sher et al. 2002). Furthermore, *Tamarix* seeds and seedlings are adapted to saline conditions, drought, and fire which occur when over-bank flooding is decreased (Horton et al. 1960, Busch and Smith 1993, 1995, Cleverly et al. 1997, Tickner et al. 2001).

In New Zealand, South Africa, Israel, and Hawaii, various *Acacia* (black wattle) species have invaded riparian areas (Tickner et al. 2001). *A. mearnsii* has become a successful invader by producing large crops of long-lived seeds and shading out other species with its wide crown (ISSG Global Invasive Species Database 2005). A few other species that have invaded floodplain areas include *Impatiens glandulifera* (Himalayan balsam), *Mimosa pigra* (giant sensitive plant), and *Fallopia japonica* (Japanese
knotweed). *I. glandulifera* is a competitive species well adapted to the frequent disturbance by floods (Tickner et al. 2001). *M. pigra* may be quickly spreading due to seed flotation that enables it to disperse to normally dry areas during wet periods as well as production of aerial roots during flooding (Lonsdale 1993, Tickner et al. 2001). *F. japonica* forms dense thickets through fast vegetative reproduction (Tickner et al. 2001). All of these plants invade and sometimes result in monospecific stands.

Several hypotheses have been proposed to explain why some plant invaders are successful. The evolution of increased competitive ability hypothesis (EICA) suggests that chronic low loss from herbivores of the introduced species in the new environment can result in a shift in allocation of resources from defense to growth (Blossey and Nötzold 1995). This growth advantage allows them to compete successfully with natives. A second hypothesis for why some non-native plant species become invasive is the enemy release hypothesis (Mack et al. 2000, Keane and Crawley 2002, Siemann and Rogers 2003a, Joshi and Vrieling 2005). According to this hypothesis, invasive species are escape from their native herbivores or diseases, and so have lower losses to pests and pathogens than do native species. This translates into rapid growth or higher reproduction, allowing invaders to compete successfully against native species (Crawley 1987).

A final hypothesis suggests that disturbances may provide an opportunity for non-native species to invade (Harper 1965, Davis et al. 2000, Mack et al. 2000). For example, intact primary and secondary rainforests in Singapore are threatened by only one species, and that species invades the forests via tree fall gap disturbances. In contrast, the highly disturbed open areas are dominated by invasive species (Corlett 1992).
Several experiments have been conducted on *Sapium* to investigate the reasons for its success in the southeastern United States. One study compared sapling growth and survivorship of *Celtis* versus *Sapium* and found that herbivores damaged *Celtis* significantly more than *Sapium* (Siemann and Rogers 2003a). This supported the enemy release hypothesis that invasive species have a competitive advantage over native species due to a paucity of herbivores. However, when insect herbivores were suppressed, *Sapium* had greater increases in survivorship and growth than *Celtis* (Siemann and Rogers 2003a). This implies that another reason *Sapium* is such a successful invader is because it can grow very rapidly. The capacity for rapid growth was attributed to reallocation of resources from defense to growth, i.e., EICA (Siemann and Rogers 2001, Rogers and Siemann 2003, 2004).

Two studies that support the EICA hypothesis have shown that Texas *Sapium*, despite having lower allocation to defense compared to native Chinese ecotypes, is tolerant of intense herbivory and is able to compensate for lost leaf and root mass (Rogers and Siemann 2003, 2004). This ability of the Texas ecotypes to tolerate herbivory is unlike the native *Sapium* ecotypes in China, which have highly defended leaves and are negatively impacted by herbivory (Rogers and Siemann 2004). Instead of having expensive defenses like the Chinese ecotypes, the Texas ecotypes produce relatively less costly tissues that can be easily and quickly replaced.

Another *Sapium* study also adds support for the EICA hypothesis. *Sapium* genotypes from Asia (its native range), Georgia (introduced in the late 1700s), and Texas/Louisiana (introduced in the early 1900s) were compared in a plantation by Siemann and Rogers (2001). They found that individuals of the invasive genotypes were
larger than the native genotypes. The invasive types had relatively poorly defended
leaves of lower quality than the native types, yet were more likely to produce seed. This
study suggests that post-introduction changes in genetics play an important role in the
success of *Sapium* as an invasive species (Siemann and Rogers 2001).

In conclusion, *Sapium* is a successful invader due to two main attributes. First, it
grows faster because of the absence of herbivores and diseases from its native range in
Asia, which is consistent with the enemy release hypothesis. This gives *Sapium* a
competitive edge over native species that are impacted by native herbivores (Siemann
and Rogers 2003a) and allows *Sapium* to outperform natives in a variety of light
conditions (Siemann and Rogers 2003b). Second, *Sapium* has lesser allocation to defense
and greater allocation to growth (Siemann and Rogers 2001, Rogers and Siemann 2003,
2004). This is consistent with the EICA hypothesis; reallocation of resources to growth
results in *Sapium*’s high growth ability relative to native species (Siemann and Rogers

With regard to the question posed in this thesis of whether or not canopy opening
from *Carpinus* death accelerated *Sapium* invasion, the background provided in the
preceding paragraphs may shed light on the mechanisms for *Sapium*’s response to
disturbance at the study site under investigation.

**Chapter aims**

The purpose of the following chapters is to examine the causes of changes in
abundance and mortality in a bottomland hardwood forest. The decline of *Carpinus* will
be investigated in Chapter 2. If it turns out that flooding is a reasonable explanation,
another goal of this chapter is to consider why a dominant floodplain species would

decline due to flooding.

The increase in abundance of *Sapium* will be explored in Chapter 3. The goal is
to see how the increase in *Sapium* may be related to the decline in abundance of *Carpinus*
and whether it benefited more from the disturbance than other species.
CHAPTER 2. Fluctuations in abundance and mortality of *Carpinus caroliniana*

After a flood event in 1989 due to a tropical storm, *Carpinus caroliniana* suffered a pulse of mortality. This chapter describes the rapid decline of this dominant midstory tree. The main question is: What combination of factors (flooding, pest outbreak, disease, or climate change) provides a reasonable explanation for the decline of *Carpinus*? A second question is: If the flooding was important, then why might a floodplain dominant be so severely affected by a flood?

To investigate these questions, I examined temporal trends in *Carpinus* abundance, population structure, mortality, and recruitment. To differentiate among the various possibilities for the decline of *Carpinus*, different aspects, including when, where, and in what size classes the decline occurred need to be considered.

If pest outbreak or disease was an important cause for *Carpinus* death, then the *Carpinus* mortality might have a similar temporal pattern to other population declines due to insects or disease. In addition, there should be evidence that *Carpinus* is more susceptible than other species at the study site to some type of pest or pathogen. If climate change was a cause of decline in *Carpinus*, then climate models should predict that the range of this species will shrink. In addition, *Carpinus* should show a temporal pattern of decline similar to that of other tree populations negatively affected by climate change. Another possibility is that *Carpinus*, being near the edge of its range, is highly susceptible to stress (Botkin 1993, Cramer and Leemans 1993). If the flood was important, *Carpinus* should have higher mortality levels at lower areas where the duration of flooding was longer than in higher areas. Also, *Carpinus* should have low flood tolerance relative to other species at the study site and the other species should not
show large declines after the flood event. The hypothesis that a flood killed *Carpinus* would not be supported if species with a similar flood tolerance to *Carpinus* did not also experience high mortality.

Ingrowth after the flood may also be informative. If *Carpinus* did not increase after its decline, then this could indicate that climate change was affecting the population.

A large amount of evidence in the literature suggests that trees about to die grow more slowly than trees that are not about to die (see Pedersen 1998 and references therein). Exploratory analyses indicate that this is true in the case of *Carpinus* (Appendix C). However, it is not clear that this allows differentiation between the hypotheses for *Carpinus* death. Therefore, this line of inquiry is not pursued further. In addition to growth rate analysis, growing season information can be found in Appendix C.

If flooding was a factor contributing to *Carpinus* death, there are two plausible hypotheses to explain the flooding effect. First, it could be that the *Carpinus* population had expanded into lower areas during a long period of low flooding following dam construction, and a large portion of the population was highly susceptible to the flood in these low elevations. This expansion hypothesis can be tested by determining tree ages; the age of the *Carpinus* trees killed by the flood should be less than the time since impoundment. The second hypothesis is that the flood was abnormally long, resulting in atypically high mortality. If this were true, it could be confirmed by inspection of long-term flood records.
Site description

The study site is located in the Neches Bottom unit of the Big Thicket National Preserve in southeast Texas (Marks and Harcombe 1981). At the study location, the floodplain is broad (approximately 10.3 km), with a main channel and several interconnecting sloughs that form a network of braided channels. The soils are fine, smectitic, acid, thermic Aeric Fluvaquents that are very deep, somewhat poorly drained, and very slowly permeable (Caird 1996, USDA 2003). The soil is composed of small particles with small pore spaces between them. This results in water strongly adhering to the particles and a high water holding capacity. The soils are typically wet and so recently formed that the horizons are not well defined (Caird 1996). The amount of available water is usually sufficient for tree growth throughout the year. The water table is typically highest during the spring and winter, at a depth around 30-60 cm (Hall and Harcombe 1998).

The climate is humid subtropical with an average rainfall of 1457 mm/yr (NCDC 2004, 40-yr record for Beaumont Research Center). The average annual temperature is 20.1°C and the lowest mean annual temperature exceeds 10°C (NCDC 2004, 40-yr record for Beaumont Research Center). The growing season lasts from March to November, with approximately 240 consecutive frost-free days (Hall and Harcombe 2001).

The major tree species in the overstory of the Neches Bottom floodplain plots include Liquidambar styraciflua (sweetgum), Quercus michauxii (basket oak), Acer rubrum (red maple), and Quercus nigra (water oak, see Table 1, Appendix D). In the subcanopy, Carpinus and Ilex decidua (deciduous holly) are important species.
*Taxodium distichum* (bald cypress) and *Nyssa aquatica* (water tupelo) are commonly found in the sloughs.

The composition and structure of this forest are similar to many bottomland hardwood forests on the floodplains of large rivers throughout the southeastern United States (Putnam et al. 1960, Wharton et al. 1982, Hodges 1995). This forest type has been called many different names, including Floodplain Hardwood Forest (Mohler 1979, Marks and Harcombe 1981), Southern Floodplain Forest (Küchler 1964), Swamp Chestnut Oak (*Q. michauxii*) – Cherrybark Oak (*Q. falcata*) Forest Type (Society of American Foresters 1980, type 91), and Sweetgum-Willow Oak (or water oak) Forest Type (Society of American Foresters 1980, type 92). *Carpinus* is more abundant in this forest than these forest types, but the dominance of *Carpinus* is not unique to only this area of the Neches Bottom. Other studies conducted in east Texas without logging have found similar stands in which *Carpinus* was the dominant tree (Nixon and Raines 1976, Nixon et al. 1977). Other studies in Texas, Florida, and North Carolina also place *Carpinus* among the dominant trees (Monk 1965, Sullivan and Nixon 1971, Nixon et al. 1973, Nixon and Willett 1974, Chambless and Nixon 1975, Greller 2004).

Some selective logging might have occurred at the study site in the early 1900s (Streng et al. 1989), but the only direct evidence is *Taxodium* stumps dating back to the early 20th century in the sloughs. The stand is uneven-aged with some trees originating prior to 1800 (Hall and Harcombe 2001).
Methods

The study site consists of four hectares subdivided into 100 contiguous 20 x 20 m quadrats. Each tree is numbered and mapped. Since 1980, all stems greater than 2.0 cm diameter at breast height (DBH) have been periodically measured for growth and mortality (during the first two surveys in 1980 and 1982, not all stems ≥ 2.0 cm DBH and < 4.5 cm DBH were measured). Trees are here defined as stems ≥4.5 cm DBH.

Mortality surveys were done annually; DBH measurements were made in 1980, 1982, 1985, 1989, 1994, 1997, 2000, and 2003. Tree growth is expressed as increases in DBH.

Sapling growth, recruitment, and mortality have been measured annually in 15 quadrats randomly chosen in 1980. The saplings are individually numbered and mapped within each quadrat. Every year, height was measured on small saplings (≥50 cm and <140 cm). Large saplings (≥140 cm height/ ≥0.1 cm DBH and <4.5 cm DBH) were measured for height and DBH. Sapling growth is the difference between two annual size measurements of either DBH or height.

Abundance of *Carpinus* stems ≥ 2.0 cm DBH were compared at the Neches Bottom study site and two nearby sites; a mesic hardwood pine stand (Wier Woods, see Harcombe et al. 2002) and a well-drained upper slope pine stand (Turkey Creek, see Marks and Harcombe 1981, Lin 2002).

Age of the *Carpinus* trees could not be directly determined accurately due to indeterminate ring patterns (Hall and Harcombe 2001, James Speer personal communication). Despite the indeterminate ring structure, James Speer did conduct two ring counts on one sample from 2005 to obtain a rough estimate of age. The ring widths were not plotted and dated against each other, or against other samples.
Therefore, growth rates of *Carpinus* saplings and trees in this stand were used to estimate age following techniques similar to those used in the tropics for estimating age (Brown 1919, Nicholson 1965, Lieberman and Lieberman 1985, see Appendix E). First, individuals were selected according to the following criteria: (1) survival for a minimum of four surveys for the adult tree classes and several years in the sapling classes and (2) stems should have a net increase in size over time, biasing the estimates toward faster growing trees. It was not known whether or not the stems used in the analysis were from gaps and elevation was not taken into consideration. For each individual, the number of years to reach the next size class was determined. Summing across size classes of minimum and maximum number of years for transition provided an approximation of the range of years for a tree to reach a certain DBH class.

Elevation was used to examine differences in population structure, recruitment, and probability of death. Relative elevations for the plots were obtained by Hall (1993). This was done by subtracting the water depth at each location from the maximum water depth during a period of particularly high water (Hall 1993). The site low was the relative zero value. She measured water depth every 20 m at plot corners on the flat surface and every 2 m in the slough areas (Figure 1), and the average elevation for each plot was calculated. The elevation range for the study site was approximately 140 cm. Hall (1993) delineated four zones based on the elevation and flood condition at the study site (Figure 1). When water reached the 91 cm elevation at the site, the sloughs were filled, which corresponded to a flow rate of 400.3 m$^3$/s at the Evadale gage. When flow rate at Evadale reached 490 m$^3$/s, water at the site reached the 108 cm elevation and the site lows were flooded. When the flow at Evadale reached 569.2 m$^3$/s, water reached the
123 cm elevation at the site and the flats were flooded. When the Evadale flow reached 632.5 m$^3$/s, water at the site reached 135 cm elevation, which flooded the highest surfaces and entire site (Hall 1993). I used these zones in examining variation in DBH distributions and recruitment. All regressions to examine effects of elevation were completed using the average plot elevation. Elevation measurements of the site were also made in May 2005 to compare with Hall's measurements (Appendix F). No major differences were found except that one section of the slough appears to have deepened and a downstream section became shallower, presumably as a result of sediment transport from upper to lower sections.

Historical flow data are available from a USGS gauge located in Evadale, Texas (USGS 2004). Flow data were analyzed for differences pre- and post-dam in peak flow, which is the highest level that is reached by the water surface (Hall 1993). In this study, I did not distinguish between soil waterlogging due to a high water table and inundation due to a flooded state. Soil waterlogging occurs either whether the soil is flooded or when it is saturated with water (Hook 1984a).

Random error is not computed and no statistical test of differences is used in comparing DBH distributions because this is a complete census, not a sample, of a population. Inferential statistics that account for random error are only appropriate for drawing inferences about a larger population.

For analysis of river flows, I used the NPAR1WAY procedure in SAS to perform two-sided, nonparametric Mann-Whitney tests (SAS 2003). For comparison of mortality in different elevation zones, I used a two-sided Chi-square test, as described by Brower et al. (1998). To compare probability of death based on size (DBH) and plot elevation, I
used the Genmod procedure for fitting generalized linear models in SAS and SigmaPlot 8.0 to plot the results (SAS 2003).

To examine several different possibilities suggested for the decline of *Carpinus*, I conducted a literature review using Web of Science and various Internet search engines (search terms such as a combination of: *Carpinus caroliniana*, forest, demographics, bottomland, floodplain, mortality, disturbance, invasion, and competition). I examined flood tolerance literature on the most common species in the study site (Table 2, Appendices A and B). I also used the literature and the Internet\(^1\) to investigate effects of pathogens and diseases (Appendix G) and major eastern deciduous forest pests (Appendix H) on tree populations. Finally, I inspected reports of expected climate change patterns associated with *Carpinus* (Appendix I).

On approximately 10 occasions from May to October 2004 and 8 from May to October 2005, I examined *Carpinus* stands in the Neches Bottom area for pest or pathogen outbreaks. The majority of visits took place in May and June, with two in August, three in September and two in October. I examined individual trees throughout the site and surrounding areas, looking for evidence of herbivory, insects, disease symptoms, or pathogen presence on trunks, leaves, and stems. On the September 2004 and October 2004 trips I collected leaf samples and took pictures of specimens.

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\(^1\) The insights of tree pathologist Joe Shaw were helpful in guiding the literature search.
Results

I. Literature investigation

Pests or pathogens

In my literature search I did not find any specific pests or pathogens to which *Carpinus* is known to be particularly susceptible (Appendices G and H). One of the shortcomings of using the lack of documentation of outbreaks in the literature to examine the hypothesis that pests caused the decline in *Carpinus* is the general paucity of information on outbreaks. This may be especially true for bottomland hardwood forests. Flood periods are probably less likely to be surveyed for outbreak situations, making it less likely that outbreaks are documented during these time periods when insect activity might be increased (E. Siemann personal communication). During the 1989 flood, Hall (1993) did describe an outbreak of *Malacosoma disstria* (forest tent caterpillars) at the Neches Bottom site. However, she found little damage done by the caterpillar herbivory to *Carpinus*. Other documented outbreaks at the study site consist of *Malacosoma disstria* and *Datana* sp. (walnut caterpillars, Siemann and Rogers 2003a). In addition to the literature search, I did not find any evidence of pest or pathogen outbreak from the several field trips to the site 2004-2005.

Climate

The *Carpinus* population at the Neches Bottom site is within the climatic envelope defined by Elgene Box (personal communication, see Appendix I). This means that the conditions at the study site fall within the expected ranges of temperature and precipitation that characterize the geographic range of *Carpinus*. However, the study site is on the southwestern edge of *Carpinus*’s range in the United States (Little 1971,
Metzger 1990, see Figure 2), so it could be more stressed than populations nearer to the center of the range (Botkin 1993, Cramer and Leemans 1993).

Another piece of evidence regarding climate change effects comes from several models of tree distribution changes used by Iverson and Prasad (1998, 2002) that assume a doubling of carbon dioxide from pre-industrial levels by 2100. These models incorporated over 100 environmental, land use, and socioeconomic variables, including species importance values, precipitation, temperature, potential evaporation, soil factors, land use factors, elevation, and forest cover patterns (Iverson and Prasad 1998). While ranges of several species are predicted to shift northward, that of *Carpinus* is not.

**Flood tolerance**

According to the literature, *Carpinus* is among the least flood tolerant of the important bottomland species found in the Neches Bottom floodplain (Appendix B and Table 2, see also Hall and Smith 1955, McKnight et al. 1981, Whitlow and Harris 1979, Hall et al. 1946). In addition, in a flood damage survey conducted after the 1989 storm event at the Neches Bottom, Hall (1993) found that *Carpinus* saplings were more physically damaged than other species. *Ilex decidua* and *Sapium* were damaged less by the flooding than other species (Hall 1993).

A more direct assessment of flood tolerance was made by Hall and Smith (1955), who examined the effects of a reservoir on vegetation. They established a "healthy line," defined by elevations taken from the bases of at least ten of the lowest healthy trees, and a "dead line," consisting of the lowest unhealthy trees found among the dead and dying trees. They ranked species for tolerance to flooding based on the lowest observed healthy tree. In addition, they determined the percent of time that the healthy and dead lines for
each species were flooded during the growing season. Using this information, I estimated the number of consecutive days flooded for the healthy line and the dead line (Appendix B). Assuming a 184-day growing season length (Hall and Smith 1955), *Carpinus* became unhealthy after 42 days of flooding and death occurred after 48 days. Based on the Hall and Smith percentages and the minimum length of the growing season for *Carpinus* found by Winters (1995), *Carpinus* would become unhealthy after 27 days and die after 30 days of flooding. Using Winters’ (1995) estimate of maximum growing season length, *Carpinus* would become unhealthy after 41 days of flooding and die after 46 days. According to these calculations, the flats and highest areas of the site were not flooded long enough to cause *Carpinus* mortality (see Results: II. The flood).

Hall and Smith (1955) also found that the percentage of time flooded during the growing season to become unhealthy and die was lower for *Q. nigra* than *Carpinus*. This is not consistent with the flood hypothesis.

**II. The flood**

The stalling of Tropical Storm Allison over southeast Texas led to heavy rainfall from June 25 through June 30, 1989. According to the National Climatic Data Center (2005), almost 38.1 cm of rain fell over the Evadale area during this storm event. As the storm approached the Neches Bottom area, the winds were 30-35 mph. In the springs following the flood, P.A. Harcombe (personal communication) noticed that many *Carpinus* trees leafed out and then died before full leaf expansion.

Prior to and during the storm, water was released from a large dam above the study site, Sam Rayburn Dam (May 25 through June 27, 1989). It was released at a maximum of 306 m³/s from June 22 through June 26. Following the storm, Rayburn
flows exceeded 325 m$^3$/s from July 16 through August 6, peaking at 546 m$^3$/s on July 18 (U.S. Army Corps of Engineers 2005). This second release resulted in an extended duration of high flows downstream at Steinhagen and Evadale after the storm event (Appendix J).

III. Population analysis

Population structure

_Carpinus_ suffered a major decline in both density and basal area after the 1989 flood (Figure 3). No other species experienced a similar decline. The _Carpinus_ decline was concentrated in 5-20 cm DBH stems (Figure 4a). _Carpinus_ experienced a smaller decrease before 1989 in mostly small stems (Figure 4c). This small decline may not be related to the large decline after 1989, but it could affect the interpretation of population dynamics. After the large decline 1990-1994, _Carpinus_ experienced a rebound in small stems between 1994 and 2003 (Figure 4b). The overall magnitude of the _Carpinus_ mortality pulse during the flood interval was large (Figure 5). Mortality rate was higher in all DBH classes during the flood interval than before or after (Figure 6). Before the flood, the average loss of _Carpinus_ was 51 stems per year, while during the flood interval the average loss was 114 stems per year (Figures 4a,c).

During the flood interval (1990-1994), the number of stems of other species increased by an average of 25 stems per year (range: -0.7 to 82). Before the flood (1980-1989), the number of stems of other species showed little change (Figure 3b). Overall, the number of stems of all other species combined increased by 1.7 (range: -3 to 8) stems per year during this interval and mortality was relatively low and uniform (Figure 5). This may suggest that the canopy was relatively closed during the pre-flood interval; if
so, the declines in smaller stems of *Carpinus* could be explained by suppression. In addition, the fraction of 2.0-4.5 cm DBH *Carpinus* saplings dying per plot in the period of 1981-1989 was greater in plots that had more *Carpinus* stems in 1980 ($R^2=0.202$, p<0.001, Appendix K). Higher mortality of small stems with increasing *Carpinus* density suggests that this may have been the final stages of thinning following gap closure.

The decline in *Carpinus* was greater in the lower elevation zones ($X^2_3= 27.05$, p<0.001) where the flooding lasted longer. Density of *Carpinus* decreased by 38% in the slough, 41% in the depressions, 40% in the flats, and 21% in the highest areas (Table 3). Basal area per hectare of *Carpinus* decreased by 76% in the slough, 57% in the site lows, 52% in the flats, and 22% in the highest areas (Table 4). An example of the changes in one size class is given in Table 5. Density of the 5-8 cm size class *Carpinus* decreased by 46% in the slough, 46% in the site lows, 34% in the flats, and 29% in the highest areas (Table 5). In contrast, for the pre-flood interval (1980-1989), there was no significant difference in survivorship between zones ($X^2_3= 4.999$, p>0.05, Appendix K). See Appendix L for information on year of death for *Carpinus* stems in the different elevation zones during the flood interval.

Changes in DBH distribution during the flood interval occurred in all topographic positions (Figure 8b,e,h,k). Decline was lowest in small stems and greatest in the 5-14 cm range. After the flood (1994-2003), the number of small stems increased in all elevation zones (Figure 8c,f,i,l). Before the flood (1980-1989), small stems declined at higher elevations (Figure 8d,g,j).
If the flood event was the cause of *Carpinus* mortality, it would be expected that the two other species, *Q. michauxii* and *Q. nigra*, at the lower end of the relative flood tolerance gradient at the study site should have declined as well. However, they increased (range: +2 to +11) during the flood interval. If the species are, in fact, nearly equally as flood-intolerant as *Carpinus*, then the lack of a mortality pulse suggests that flooding alone is not sufficient to explain *Carpinus* decline.

The abundance of *Carpinus* stems was compared between the Neches Bottom site and two other nearby sites, Wier Woods, and Turkey Creek (Table 6). During the flood period, stems greater then 2.0 cm DBH declined by 63% at Neches Bottom and 5-9% at Wier Woods. At Turkey Creek, they increased.

**Mortality**

The probability of death in relation to DBH and plot elevation was analyzed with the Genmod procedure in SAS in order to better understand the interaction between size and elevation in affecting mortality (Appendix M). A logistic regression model was used with a binomial distribution. Before the flood, there were significant main effects for elevation ($X^2_1 = 53.31, p<0.0001$) and DBH ($X^2_1 = 46.28, p<0.0001$). The interaction effect elevation X DBH was also significant ($X^2_1 = 49.11, p<0.0001$). There were three notable aspects of the results. First, there was a higher probability of death at higher elevation and small size (Figure 9a), and this is evident in graphs of 1980 and 1989 size distributions by elevation zone (Figure 8a,d,g,j). Second, there was a higher probability of death at lower elevation and large size. However, this is not evident in the size distribution graphs (Figure 8a,d,g,j). This inconsistency may be a result of poor model fit because of sample size at low elevations: only 40 stems (average = 13.5 cm DBH,
4.5 \leq \text{DBH} \leq 24.9 \) died in plots below 100 cm in elevation. In addition, there were relatively few large stems at low elevations. The third notable model result is the difference in the mortality between low and high elevations. This is not consistent with a pattern of expected flood-related mortality in which all stems should have a higher probability of mortality at low elevations.

For the flood interval, the main effect for elevation was not significant \((X^2_1 = 0.37, p=0.541)^2\), the main effect for DBH was significant \((X^2_1 = 28.61, p<0.0001)\), and the interaction effect was significant \((X^2_1 = 20.80, p<0.0001)\). There was a higher probability of death at low elevations for all size stems (Figure 9b). At low elevations, large stems had a higher probability of death than small stems. This is evident in graphs of population structure of \textit{Carpinus} by elevation zone (Figure 8b,e,h,k); it is consistent with the histogram of \textit{Carpinus} abundances in 1989 and 1994 by elevation zone (Figure 7). At all elevations, the probability of death was lower for small stems, which is also evident in the graphs of population structure of \textit{Carpinus} by elevation zone (Figure 8b,e,h,k).

Post-flood, the main effects for elevation \((X^2_1 = 0.23, p=0.631)\) and DBH \((X^2_1 = 1.73, p=0.1880)\) were not significant; neither was the interaction model \((X^2_1 = 0.27, p=0.6038, \text{Figure 9c})\). Apparently, mortality was not strongly related to either tree elevation or size during this time period.

\textbf{Age}

If \textit{Carpinus} had been growing into lower areas during times of low flooding after the dams were built, then most of the trees that died during the flood should have had a

\footnote{Calculations based on elevation zone (Figure 6) found a higher probability of mortality in the lower elevation zones. The Genmod model uses elevation at the plot level, which suggests the disparity may be explained by the greater amount of variability in the Genmod elevation data compared with the zone data.}
growth analysis estimation (Table 7, Figures 10-11), the time for a *Carpinus* tree to reach
20 cm DBH ranges from about 71-123+ years. This greatly exceeds the time window for
post-dam colonization (25-39 years). I also calculated the maximum size that could be
expected in 39 years (post-Steinhagen) and in 25 years (post-Sam Rayburn). It was 12
cm DBH for 39 years and 6 cm for 25 years. Nearly half (43%) of the ≤12 cm DBH
*Carpinus* that died in the slough and site lows were present before Steinhagen dam (≥39
years) and nearly all (94%) of the ≥6 cm stems were present before Sam Rayburn dam
(≥25 years). Values for the flats and highest surfaces were 48% pre-Steinhagen (≥39
years) and 90% pre-Sam Rayburn (≥25 years). Comparing the frequencies of occurrence
of dead stems, I found no significant differences between low and high elevation zones
for pre- versus post-Steinhagen stems ($X^2_1 = 0.546, p>0.05$) and pre- versus post-Sam
Rayburn stems ($X^2_1 = 1.97, p>0.05$). Thus, even though many stems that died in the
slough and site lows became established after the dams, it is unlikely that the death of
*Carpinus* after the flood was a result of population expansion into lower, normally more
flood-prone areas post-dam.

According to two ring counts conducted by James Speer (personal
communication) on one 22.2 cm DBH *Carpinus* sample from 2005, the tree was 67-68
years old. Like the growth analysis results, this would place the origin of this size tree
long before dam construction and suggests that *Carpinus* in lower areas were not a post-
dam, low-flood phenomenon.
**Ingrowth**

For most species, 2.0 cm ingrowth was higher after the flood from 1994 –1997 than in 1980-1989 (Figure 12). Some species experienced large amounts of ingrowth during the post-flood interval in the flats, including *Sapium* (48 stems/ha/yr), *Liquidambar* (64 stems/ha/yr), and *I. decidua* (26 stems/ha/yr). *Q. nigra* had high ingrowth if both the flats (15 stems/ha/yr) and the highest areas (12 stems/ha/yr) are included. Species with high amounts of ingrowth over all areas included *Liquidambar* (96 stems/ha/yr), *Sapium* (93 stems/ha/yr), and *I. decidua* (60 stems/ha/yr). Although *Carpinus* did not benefit greatly post-flood compared to these three species (39 stems/ha/yr), it did experience a substantial rebound (Figure 8c,f,i,l).

The effect of the 1989 flood is evident in the sapling dynamics both in mortality and subsequent increase (Figure 13). The open canopy following the flood seems to have allowed a burst in sapling ingrowth. The species that responded most were *Carpinus* and *Sapium*. It is interesting to note the inverse relationship between *Sapium* and *Liquidambar* sapling populations 1980-1989 and 1980-2003 (Figures 13-14).

**IV. Flooding analysis**

Above the site, there are eight impoundments (Appendix N). After the filling of Lake Rayburn in 1965, one of the closest dams to the study site, notable decreases in flooding frequency and duration occurred. The mean annual peak flow before Sam Rayburn Dam was 1012 m$^3$/s (Figure 15a) and the mean annual peak flow after impoundment was 612 m$^3$/s (Figure 15b). This was a significant difference in peak flow (Mann-Whitney test, z=-2.68, p=0.007). In addition, after 1965, there was a shift in the amount of spring flooding. This can be seen by comparing Figures 15a and 15b as well
as by comparing flooding frequencies displayed in Tables 8-10. The highlighted periods show the spring floods starting between March 15 and June 14 that lasted longer than 10 days and the summer floods starting between June 15 and September 14 that lasted longer than 10 days. Pre-dam, there was approximately one spring flood every 2-3 years. Post-dam, there was about one spring flood every 7-8 years.

During the 1989 flood, water filled the slough for 48 consecutive days, the site lows for 43 days, the flats for 19 days, and the highest surfaces for 17 days (Hall 1993) (Figure 1). The magnitude of the 1989 flood was large when put into terms of flood return periods. According to calculations by Hall (1993), the peak flow associated with the 1989 flood exceeded the expected post-dam 100-year flood. This means that the flow exceeded the expected maximum flow that occurs in 1% of the years based on flow-frequency curves (Bedient and Huber 1992).

The 1989 flood due to Tropical Storm Allison was not long lasting compared with the number of days flooded in the largest floods pre-dam (1922-1964) and post-dam (1965-2003, see Table 12). However, the duration of the 1989 flood is important when put into a seasonal perspective: no summer floods occurred during the pre-dam period, 1921-1964 (Table 8, Figure 15a, Appendix J), and the flood of 1989 was the longer of two summer floods between 1965-2003 (Table 9, Figure 15b). The 1989 flood is compared to other long growing season floods in Figure 16. Part of the reason for this large flood event is the high flows persisting from spring flooding up until the tropical storm event (Figure 17, Table 11).

The percentage of the growing season that was flooded due to the late spring floods and the tropical storm (Table 11) is near the percentages that Hall and Smith
(1955) found to be required for *Carpinus* to be killed or become unhealthy (Appendix B). It is not known whether or not the two floods acted as one long flood on the *Carpinus* population (Table 11). However, according to Toner and Keddy (1997), a second flood that occurs soon after a first flood may just extend the adverse effects of the first due to too short a recovery time between the two events. The soils at the study site are slowly draining and have a high water holding capacity (Caird 1996), so it is possible that the soils remained waterlogged in the slough areas between floods. It seems reasonable that at least in the slough areas, the two floods may have acted in an additive manner.

Daily temperatures both before and during the flood interval were near the normal monthly mean of 1978-2004 (NCDC 2005) (Figures 18 and 19), although nighttime temperatures were above normal levels (Jha et al. 2004). Many mild to moderate droughts occurred 1970-2005, as indicated by the Palmer Drought Severity Index for Texas Region 8 (Table 13). The two worst droughts of this time period are of interest. First, there was a moderate drought from May 1988 to April 1989 (Tables 13 and 14). Second, an extreme drought occurred from February 1999 to October 2000 (NOAA 2006, see Tables 13 and 15). For precipitation information, see Appendix I.

**Discussion**

The decline in *Carpinus* before the flood consisted of mainly small trees between 2 and 8 cm DBH (Figure 4). There was no clear elevation pattern (Appendix K, Figures 8a,d,g,j and 9a). The most plausible explanation is suppression-related mortality. The fraction of 2.0-4.5 cm DBH *Carpinus* saplings dying per plot 1981-1989 was greater in plots that had more *Carpinus* stems in 1980. In addition, Hall (1993) found that sapling
ingrowth during this time period occurred in patches. This suggests that the forest was closed and that small gaps were the main areas of recruitment prior to 1989. Her analysis corresponds with Harcombe’s personal observation that many 2-5 cm *Carpinus* stems died in old gaps during this period, presumably as a result of thinning in gaps and canopy closure.

There is no evidence linking the episode of mortality in the Neches Bottom *Carpinus* population after the 1989 flood to pathogens. My literature search did not reveal any specific pathogens to which *Carpinus caroliniana* is known to be particularly susceptible (Appendix G), and tree pathologist Joe Shaw\(^3\) (personal communication) concurred with my conclusion that pathogens and disease are unlikely culprits in the *Carpinus* decline. However, data were not collected on pathogen or disease presence before or after *Carpinus* decline. Therefore, this possibility cannot be ruled out, although it seems unlikely that a disease was responsible for the decline.

Likewise, I found no evidence linking the decline of *Carpinus* to insects. The effects of defoliation depend on the length of an outbreak, the condition of the tree before pest attack, the time of year, other concurrent stressors (such as flooding or drought), and the severity of defoliation (Reichle et al. 1973, Davidson et al. 1999). If a species causing defoliation similar to that caused by *Lymantria dispar* (gypsy moth) attacked *Carpinus* trees after the flood already had weakened them, it is a possibility that they would have died. However, there are no known pests specific to *Carpinus* in east Texas. In addition, I did not find any specific pests in the literature to which *Carpinus* is known

\(^3\) Shaw received his Ph.D. in plant pathology from University of California-Davis. At the time of our communication, he was working as a scientist at Lexicon Genetics Inc., The Woodlands, TX.
to be particularly susceptible. Furthermore, I did not find any evidence of pest or pathogen outbreak during several trips to the field site. However, insect outbreaks could have occurred and gone undetected prior to *Carpinus* decline, especially since insect outbreaks are likely to occur when floodwaters are high and no observations were made. Therefore, the lack of evidence is not conclusive, but only suggestive, that insects did not cause the decline.

The rebound of *Carpinus* after the flood event would seem to be one bit of evidence against either a persistent pest or a disease. Logic suggests that if a pest or disease had caused the *Carpinus* mortality and remained present at the study site, then the population would not be expected to rebound so quickly because the pest or pathogen should still affect it.

Climate change cannot be ruled out either. One investigation near the study site found that increasing nighttime temperatures over the last 20 years might be contributing to the decline of *F. grandifolia* and this trend could also be affecting *Carpinus* (Jha et al. 2004). However, studies of future climate trends do indicate that the potential suitable range of *Carpinus* is not expected to contract (Iverson and Prasad 1998, 2002). Also, the pulse of mortality and subsequent rebound by the *Carpinus* population is not a pattern typical of tree populations suffering from the negative effects of climate change. These latter populations are thought to decline over long time periods, not displaying a short temporal burst in mortality or strong post-mortality recruitment (e.g. Hennon and Shaw 1994, Kullman 1996, Jha et al. 2004).

Turning to flooding, the evidence was mixed. First, even though *Q. michauxii* and *Q. nigra* are also on the lower end of the flood tolerance gradient of species at the
study site. These species should have declined as well. Also, the length of time the flats were flooded in 1989 was less than the time that Hall and Smith (1955) found to be necessary to kill *Carpinus*. The most plausible way to rationalize these conflicting results is to suggest that site conditions are different (soil composition, site history, and other factors, see Appendix B) between this floodplain in southeast Texas and the Hall and Smith (1955) study site in a Tennessee reservoir, and so it is conceivable that flood tolerances of some species could be different between the sites.

Information that supports flooding was a cause, or at least a partial cause, of the *Carpinus* decline may be found in several observations. First, in the spring following the flood, Paul Harcombe (personal communication) noticed that several trees leafed out, but died before the leaves fully expanded. This may have indicated that these trees had damaged root systems that lacked the ability to uptake the necessary nutrients and water to maintain photosynthesis and the leaves. Similarly, in a study of a flood along the Mississippi River that caused mortality in a variety of species and lasted longer than the 1989 flood, many trees did not leaf out in the spring and died that summer (Yin et al. 1994).

Additional support for flooding as a plausible contributor to the *Carpinus* decline lies in the fact that it is among the least tolerant species at the study site (Table 2, Appendices A and B). Also, there was greater decline at lower elevations where flooding duration would have been longer. Furthermore, the Hall and Smith (1955) study showed that the length of time flooded in the sloughs and site lows were long enough to cause *Carpinus* mortality. Finally, two drier sites near the Neches Bottom that did not have a flood did not show dramatic *Carpinus* death during the flood interval.
Taking into account the positive and negative evidence for the hypothesis that a flood killed *Carpinus*, it seems that flooding did play a role in the decline. However, it seems that something else may have also been involved, as well. One logical candidate derives from the fact that the study site is on the edge of *Carpinus*'s southwestern range. That is, the population may have already been stressed due to being on the edge of its physiological tolerance limits. The moderate drought preceding the flood in 1989 (Tables 13 and 14) might have also contributed to the *Carpinus* mortality. However, two pieces of evidence suggest that the drought alone did not kill the *Carpinus* trees. First, *Q. michauxii* and *Q. nigra* are also sensitive to drought (Cook et al. 2001), but they did not decline after the 1988-1989 drought. Second, *Carpinus* did not decline after an extreme drought between 1999-2000 (Tables 13 and 15, Figure 1). Nevertheless, it seems plausible that the flooding triggered an episode of mortality in a population already under stress of marginal climate conditions, possibly including drought stress, and may have resulted in the *Carpinus* death after 1989.

Species on the edge of their climatic range are presumably near their physiological tolerance limits (Botkin 1993, Cramer and Leemans 1993). One effect of this could be increased susceptibility to abnormal flood conditions. In addition to providing part of the explanation for the *Carpinus* decline, the climate stress argument may also help explain the lack of decline in the equally flood intolerant *Q. nigra*. It is not so subject to chronic stress as *Carpinus* because it is farther from the edge of its range (Little 1971). Its range extends farther west than *Carpinus*'s. The climate stress argument does not help, however, with the other species that is also at the low end of the flood tolerance gradient, *Q. michauxii*; the western edge of its range is similar to
Carpinus's. The explanation for the lack of a decline in Q. michauxii may be that it is actually more flood tolerant than Carpinus, as found in the observational Hall et al. (1946) reservoir study (Table 2). Another piece of evidence for greater flood tolerance of Q. michauxii is that it is found along the frequently flooded bottomlands of the Mississippi River Valley where Carpinus is absent (Little 1971).

Since it does seem that the 1989 flood did play a role in the Carpinus death, it is reasonable to investigate why. The hypothesis that Carpinus expanded into lower elevations more prone to flooding during the post-dam period was not supported by the age analysis. More than half of the Carpinus trees that died during the flood interval were too old to have established during the post-dam time period (Table 7, Figures 10 and 11). The hypothesis that Carpinus declined because of a unique flood event during the growing season seems more likely. The flood of 1989 was long in duration relative to other flood events post-dam (Tables 8-10, Figures 15 and 16), and it was also the longest summer flood on record (Tables 8-10, Figures 15 and 16).

This unique growing season flood was the result of a combination of factors, including late spring flooding, a tropical storm, and upstream impoundment management that may have extended the duration of the flood. Without the dams, the growing season flood would have probably had a much higher peak and shorter duration. The event began with an extended period of moderate to high flows remaining from late spring flooding. This effect was compounded by a tropical storm, which caused additional growing season flooding (Table 11, Figure 17). Finally, sustained release after the storm event pushed the flood long into the summer months. Such an event must have been extremely rare in the pre-dam floodplain (Tables 8-10).
The implication of flooding in the dramatic decline of *Carpinus* begs the question, “How can a flood intolerant species become so abundant in a floodplain?” The answer may lie in demographics. Even a relatively flood-intolerant species like *Carpinus* may achieve importance in floodplains if its flood tolerance is rarely exceeded and it is capable of rapid demographic response. The large increases in the number of small individuals of *Carpinus* 1994-2003 (Table 5 and Figures 4b and 8c,f,i,l) suggest that high fecundity and vagility may be as important as physiological flood tolerance in maintaining this species in river floodplains. Because *Carpinus* is a light-seeded and flood intolerant species, its seedlings and trees do relatively poorly during times of flooding. However, the light seeds can be readily dispersed over long distances during advantageous time periods enabling the population to rebound after flood events. In addition, *Carpinus* seedlings and saplings are shade-tolerant and are thus able to remain in the understory to a certain extent. When any canopy opening occurs, some individuals are already present and able to quickly respond to the increased light with faster growth. To summarize, the high abundance of a relatively flood-intolerant species in a floodplain is perhaps best explained by two main factors. First, it is shade-tolerant, so it can remain in the understory, and take advantage of light gaps when they arise. Second, it produces many light seeds that allow rapid colonization of gaps during flood-free intervals.
CHAPTER 3. Invasion of *Sapium sebiferum*

After the decline of the dominant midstory species *Carpinus caroliniana, Sapium sebiferum* experienced a rapid increase in abundance. This chapter focuses on the increase of this invasive species. *Sapium* was already increasing rapidly before the *Carpinus* death (Figure 14). The main question in this study was whether the canopy opening resulting from *Carpinus* death accelerated the invasion of *Sapium*. In other words, did disturbance accelerate invasion?

To investigate these issues, variability in species ingrowth over time was examined. Also, sapling growth between 1994-1997 was examined to determine whether or not it was higher where competition had been reduced due to death of *Carpinus* between 1990-1994. To do this, a competition index was used to estimate the reduction in competition experienced by individual saplings due to the death of *Carpinus*. Since it was important to know whether the growth response of saplings was due to the death of *Carpinus* or due to the death of species besides *Carpinus*, a competition index was also computed for trees of species other than *Carpinus* that died between 1990-1994. Finally, to account for the effect of live trees, a competition index was computed for live stems in 1994, and all three components were included in a regression.

Species responses to light provided a useful framework for interpreting the effects of *Carpinus* death, the death of other species, and surrounding tree abundance on sapling species growth. In general, shade intolerant species grow faster in high light conditions and slower in low light conditions than shade tolerant species (Boardman 1977, Lorimer 1981, Kobe et al. 1995, Lin et al. 2004). Other studies have found that the low light response of importance is survivorship, not growth (Pacala et al. 1994, Pacala et al.
1996). For example, three of the species in this forest with fastest growth in high light conditions, *Sapium, Liquidambar,* and *Q. nigra,* were found previously to have had the highest mortality risk at low light (Lin et al. 2004) (Figure 20).

In this study, performance in relation to light was assumed to be a good indicator of the effects of *Carpinus* death, other species death, and tree abundance on sapling growth. It was also assumed that individual growth could be a surrogate for population change; saplings that experienced higher growth were presumed to reach the canopy faster and recruit earlier than slower growing individuals, leading to population growth. It was hypothesized that increased light due to *Carpinus* death would affect individual sapling growth differently depending on species. The expectation was that, if *Sapium* individuals had a stronger growth response to reduced *Carpinus* competition than other species, then the *Sapium* population would have experienced a more rapid increase than other species. In other words, invasion would be accelerated because of the greater positive response to higher light.

**Methods**

Refer to the methods described in Chapter 2 for information on the site and survey techniques. The long-term data set described in Chapter 2 was used to calculate abundance, ingrowth by elevation zone, and various ingrowth/basal area relationships. There was minimal ingrowth for *Q. michauxii* and *Taxodium,* so these analyses are not presented.

In a previous study of sapling growth at the study site, the growth responses of some species to high light conditions were investigated (Lin et al. 2004). I used the top
quartile growth rates from that study to rank the species in order of decreasing maximal growth rates (Table 16). Species that were not included in that analysis were inserted into the rank order by examining the shade tolerance literature (Appendix O). This ranking provided the expected increased growth response to increasing light levels (i.e., higher competition index values for dead Carpinus or other species) and the expected decreased growth response to decreasing light levels (i.e., higher competition index values for saplings located close to large, live trees).

Hegyi’s index was chosen because it is a commonly-used density-dependent method to analyze competition, which considers both distance and size of competitors (Cole and Lorimer 1997, Nyström and Kexi 1997, Mailly et al. 2003). Competition was measured using a modified Hegyi’s index, which makes no assumptions about the factors important to competition (Hegyi 1974):

\[
\text{Competition Index} = \frac{1}{\sum_{c=1}^{n} \left( \frac{\text{Competitor DBH}}{\text{Subject DBH}} * \frac{1}{\text{Distance}_{sc}} \right)}
\]

Where subject DBH is the diameter at breast height of the subject sapling; Competitor DBH is the diameter at breast height of a competitor tree; Distance_{sc} is the distance between the subject sapling and competitor. Closer and larger competitors are given a greater weight.

For each subject sapling, three index values were calculated; the first used all live competitor stems in 1994 (Cl_{1994}), the second all the Carpinus stems that died 1990-1994 (Cl_{dCarp1990-1994}), and the third included the dead stems of species other than Carpinus from 1990-1994 (Cl_{dOther1990-1994}). All stems ≥ 2.0 cm DBH were used in calculating the competition indices. Subject saplings were only included from plots surrounded by other plots so that the competition indices could be accurately calculated. Therefore, subject saplings were used only in the 66 inner plots and the border plots were excluded. Only
species with greater than nine subject saplings were included in the analysis. There were two classes of subject sapling stems, 1) those that were between 2.0-4.5 cm DBH in 1989 and 2) those that were not in the sample in 1989 (<2.0 cm DBH), but between 2.0-4.5 cm DBH in 1994. A radius of 3.5 x mean crown radius of canopy trees was specified in Hegyi (1974). Calculations were initially made both with and without a search radius around each subject sapling (e.g. 20 m); the term did not make an appreciable difference in the results. Therefore, there was no set search radius, as there seemed to be no logical mathematical or biological reason for setting one.

Growth of the subject saplings was measured as the change in basal area (BA), since this is a better indicator of actual increase in plant biomass than change in DBH. As an example, a 2.0 cm and 3.0 cm DBH stem may both increase by 0.3 cm in diameter, but the smaller stem increased in BA by only 1.01 cm² and the larger stem increased by 1.48 cm². Sapling growth was measured from 1994 to 1997 to investigate the response of saplings following the pulse of Carpinus mortality 1990 to 1994. Species and the three competition indices were included in the model as main effects. In addition to these main effects, the interactions of species X each competition index were included in the model. The following regression model was used:

\[ \text{GROWTH}_{1994-1997} = b1*\text{species} + b2 * \text{CI}_{1994} + b3 * \text{CI}_{\text{Carp1990-1994}} + b4 * \text{CI}_{\text{Other1990-1994}} + b5*\text{species} * \text{CI}_{1994} + b6*\text{species} * \text{CI}_{\text{Carp1990-1994}} + b7*\text{species} * \text{CI}_{\text{Other1990-1994}} \]

Where growth was measured as the 1997 basal area minus the 1994 basal area. CI<sub>1994</sub> equaled the amount of competition in 1994 due to the live stems greater than 2.0 cm DBH surrounding each large sapling stem. CI<sub>\text{Carp1990-1994}</sub> was the amount of reduced competition due to the death of Carpinus between 1990-1994. CI<sub>\text{Other1990-1994}</sub> was the amount of competition lost due to the death of trees other than Carpinus between 1990-1994. Coefficients are indicated by b#. 
The competition indices were calculated by Evan Siemann using PASCAL. To test for effects of components of competition on sapling growth, I used analysis of variance via the SAS General Linear Model procedure (SAS 2003).

**Results**

There was a burst in sapling ingrowth in 1980 (Figures 13 and 14) followed by a decrease in 1990 after the flood, and then another increase in 1993. Most ingrowth after 1989 was concentrated in the flats (Figure 12). *Carpinus* ingrowth was highest in 1997 and 2003. *Sapium* had a sharp increase in ingrowth in 1997-2000. High *Liquidambar* ingrowth occurred in 1994-1997 and in 1997-2000. *A. rubrum* ingrowth remained fairly steady. *Q. nigra* ingrowth has been increasing since 1994 in all but the lowest elevation zone. *I. decidua* had an increase in ingrowth in 1994-1997 and has since fluctuated.

Total 2.0 cm ingrowth during 1997-2000 was highest in plots where there was high *Carpinus* BA loss (Figure 21). When individual species were analyzed, only *Sapium* showed a significant effect of *Carpinus* BA loss on ingrowth (Figure 22). The relationship between the ingrowth of the other major species for 1997-2000 versus *Carpinus* basal area loss is weak, especially as compared to the *Sapium* relationship (Figure 22).

The regression model described in the methods permitted a more fine scale analysis of the effects of the competitive environment on sapling growth in the interval immediately following the *Carpinus* decline. The overall model was significant ($F_{39,1250} = 49.35; \ p<0.0001$). The main effect, species, was also significant ($F_{9,39} = 82.64$;
p<0.0001, see Table 17). The average growth of *Sapium* between 1994-1997 was significantly greater (p<0.05) than all other species, except for *Q. laurifolia* (laurel oak, see Table 16, Figure 23). None of the other main effects were significant. The interaction between species and competition index of dead *Carpinus* was significant (F\(_{9,39}\) = 15.62; p<0.0001, see Table 17, Figure 24). *Sapium* had the strongest growth response to *Carpinus* death (Table 18), and *Liquidambar* and *Q. nigra* had the next greatest responses. The interaction between species and CI\(_{1994}\) was also significant (F\(_{9,39}\) = 11.39; p<0.0001, see Table 17, Figure 25). *Sapium* had the most negative response to competition (Table 19). *Liquidambar* and *Q. nigra* had the second and third greatest growth responses to competition. The interaction between species and CI\(_{dOther1990-1994}\) was not significant (F\(_{9,39}\) = 0.89; p=0.54, see Table 17).

**Discussion**

*Sapium, Liquidambar,* and *Q. nigra* had the largest decreases in growth in response to competition with live trees (Figure 25, Table 19). This is consistent with expectation based on shade tolerance (Table 16) and supports the assumption that light is important. *Sapium* was the most negatively affected, and it grew more slowly at very low light levels than the native species. This latter finding is in contrast with previous studies in which *Sapium* had faster growth rates than native species under both shaded and light conditions (McLeod 1989, Jones and Hall 1993, Rogers and Siemann 2003). The discrepancy may be due to differences in the ranges of light, with lower light levels included in the present study.
Another unexpected result is that *A. rubrum* had a lower growth decrease than expected. The slope of its response was 0.001, which indicates it was not growing much differently in response to low or high light levels. This is an anomaly that warrants further study, and it is discussed in the context of growth versus *Carpinus* death.

*Sapium* was rapidly increasing before *Carpinus* death (Figure 14) and it is not clear whether the rate of increase after the flood was greater than the rate of increase before the flood (i.e., that invasion was accelerated). However, growth analysis provides a clearer answer.

*Sapium* had the greatest increase in growth with increasing *Carpinus* death (Figure 24, Table 18). It benefited five times more than *Liquidambar* from the *Carpinus* decline and ten times more than *Q. nigra*. The finding that *Liquidambar* and *Q. nigra* were second and third suggests that under conditions without *Sapium* present, *Liquidambar* and *Q. nigra* would normally be the first species to respond and fill in the gaps if they were present at the time of gap formation. At zero *Carpinus* loss, *Sapium* was growing faster than the native species by a 2.6:1 to 15:1 ratio in growth rate. At high *Carpinus* death, this factor increased substantially to a range of ratios of 3.6:1 to 210:1. This indicates that *Carpinus* death accelerated *Sapium* invasion by increasing the margin between its growth rate at low *Carpinus* loss and high *Carpinus* loss.

The response of *A. rubrum* was, again, anomalous in that its growth was actually lower where *Carpinus* death was higher. This contrasts with the results of Lin et al. (2004); they found that *A. rubrum* had a high growth response to light, i.e. *A. rubrum* is shade intolerant, like *Sapium, Liquidambar*, and *Q. nigra*. If this were the case, then the lack of response at high light would have to be attributed to strong competition from
other saplings that is not adequately captured by Hegyi’s index, which gives heavy weight to large individuals. *Carpinus* also had a declining growth rate in response to increasing *Carpinus* death, presumably because it too suffered from competition with other saplings.

Previous work has shown that the Texas *Sapium* has shifted its allocation of resources from defense to growth in the absence of its native herbivores (Siemann and Rogers 2001, Rogers and Siemann 2003, Rogers and Siemann 2004). In addition, it has a paucity of pests and diseases in its introduced range (Siemann and Rogers 2003a). Both of these advantages have been shown to contribute to the fast growth of *Sapium* relative to native species (Siemann and Rogers 2001, Rogers and Siemann 2003, Siemann and Rogers 2003a, Rogers and Siemann 2004). The fast growth of *Sapium* relative to other species in the Neches Bottom may be a result of these adaptations (Figure 23).

The ability to grow fast in high light areas means that disturbance can accelerate the invasion of bottomland hardwood forests by aggressive aliens, similar to other systems (Corlett 1992, Davis et al. 2000, Tickner et al. 2001, Mack et al. 2002). The death of *Carpinus* resulted in many canopy openings. *Sapium* responded to this increase in light with a greater increase in individual growth rates than that of native species. Individuals with the greatest increases in growth will reach the canopy faster than other individuals, i.e. individual growth responses imply a population response. Since most of the saplings with increased growth were *Sapium*, this species will benefit by getting to the canopy faster than other species and having increased recruitment, and so *Sapium* will increase in relative abundance faster than it would have in the absence of disturbance. That is, *Carpinus* death accelerated *Sapium* invasion.
Invasive plant species are known to have resulted in decreased diversity in a variety of systems (Gordon 1998, Tickner et al. 2001, Rogers and Siemann 2003, Yurkonis et al. 2005). Displacement and reduced colonization rates of native species are two ways in which diversity is decreased by invaders (Yurkonis et al. 2005). From my analyses, it appears that, historically, the light-intolerant species *Liquidambar* and *Q. nigra* should have been the most aggressive in responding to disturbance and filling in light gaps in this forest. However, *Sapium* responded to the high resource availability with faster growth than *Liquidambar, Q. nigra,* or any other native species. Therefore, much of the *Sapium* gain may come at the expense of these native species.

In September 2005, Hurricane Rita passed through this Neches Bottom study site. Much of the canopy at the site was destroyed. The fast response and rapid growth rates of *Sapium* compared to native species suggests that *Sapium* could become even more important in this forest stand in a relatively short period of time.
CONCLUSION

In this study, a chain of events resulted in the decrease of a native species and the accelerated increase of an invasive species. The combination of a tropical storm and flood-flow regulation by upstream dams may have resulted in a long growing season flood that probably contributed to the death of a major midstory species, *Carpinus*. It may well have been the trigger that led to a pulse of mortality in a population already stressed by climatic conditions (especially a recent drought) and climatic change (nighttime temperature warming trend).

The decline of *Carpinus* resulted in canopy openings and likely caused increases in light availability. The growth response at the sapling level was strongest in three shade-intolerant species, the invasive *Sapium* and the natives *Liquidambar* and *Q. nigra*. *Sapium* responded much more strongly than *Liquidambar* and *Q. nigra*. The increasing growth response of *Sapium* to greater amounts of *Carpinus* death implies that invasion in this bottomland hardwood forest was accelerated by disturbance.
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Tables

Table 1. Major tree species found in the Neches Bottom study site.

<table>
<thead>
<tr>
<th>Latin name</th>
<th>Common name</th>
<th>Basal area %</th>
<th>Abundance %</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Liquidambar styraciflua</em></td>
<td>Sweetgum</td>
<td>23</td>
<td>9.3</td>
</tr>
<tr>
<td><em>Carpinus caroliniana</em></td>
<td>American hornbeam</td>
<td>15</td>
<td>41</td>
</tr>
<tr>
<td><em>Quercus michauxii</em></td>
<td>Basket oak</td>
<td>10</td>
<td>1.1</td>
</tr>
<tr>
<td><em>Quercus nigra</em></td>
<td>Water oak</td>
<td>8.7</td>
<td>1.4</td>
</tr>
<tr>
<td><em>Acer rubrum</em></td>
<td>Red maple</td>
<td>9.1</td>
<td>9</td>
</tr>
<tr>
<td><em>Taxodium distichum</em></td>
<td>Bald cypress</td>
<td>5.4</td>
<td>2.3</td>
</tr>
<tr>
<td><em>Ilex decidua</em></td>
<td>Deciduous holly</td>
<td>1.1</td>
<td>11.5</td>
</tr>
<tr>
<td><em>Sapitum sebiferum</em></td>
<td>Chinese tallow</td>
<td>0.53</td>
<td>3.6</td>
</tr>
</tbody>
</table>

Table 2. Flood tolerance of major Neches Bottom species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Flood tolerance</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Carpinus</em></td>
<td>Weakly tol [1], Intermediate tol [2], Intolerant [3,4]</td>
</tr>
<tr>
<td><em>Q. michauxii</em></td>
<td>Weakly tol [1], Intolerant [2], Moderately tol [4]</td>
</tr>
<tr>
<td><em>Q. nigra</em></td>
<td>Moderately - Weakly tol [1], Moderately tol [3,4], Tol [2]</td>
</tr>
<tr>
<td><em>Liquidambar</em></td>
<td>Moderately tol [1], Tol - Very tol [2], Tol [3,4]</td>
</tr>
<tr>
<td><em>A. rubrum</em></td>
<td>Moderately tol [1], Tol [2,3,4]</td>
</tr>
<tr>
<td><em>I. decidua</em></td>
<td>Moderately tol [4], Very tol [3]</td>
</tr>
<tr>
<td><em>Sapitum</em></td>
<td>Very tol [5,6,7]</td>
</tr>
<tr>
<td><em>Taxodium</em></td>
<td>Tol [1,4], Very tol [2,3,7]</td>
</tr>
</tbody>
</table>

1. Review by McKnight et al. (1981).
4. Observational study by Hall et al. (1946).
5. Greenhouse experiment by Butterfield et al. (2004).
**Table 3.** Number of stems per hectare of *Carpinus* for selected years in four elevation zones.

<table>
<thead>
<tr>
<th>Year</th>
<th>Banks</th>
<th>Lows</th>
<th>Flats</th>
<th>Highs</th>
</tr>
</thead>
<tbody>
<tr>
<td>1980</td>
<td>189</td>
<td>405</td>
<td>843</td>
<td>816</td>
</tr>
<tr>
<td>1989</td>
<td>167</td>
<td>347</td>
<td>653</td>
<td>584</td>
</tr>
<tr>
<td>1994</td>
<td>103</td>
<td>205</td>
<td>390</td>
<td>463</td>
</tr>
<tr>
<td>2003</td>
<td>187</td>
<td>212</td>
<td>465</td>
<td>455</td>
</tr>
</tbody>
</table>

**Table 4.** Basal area per hectare of *Carpinus* for selected years in four elevation zones.

<table>
<thead>
<tr>
<th>Year</th>
<th>Basal area / hectare</th>
<th>Banks</th>
<th>Lows</th>
<th>Flats</th>
<th>Highs</th>
</tr>
</thead>
<tbody>
<tr>
<td>1980</td>
<td></td>
<td>0.39</td>
<td>0.74</td>
<td>2.24</td>
<td>2.25</td>
</tr>
<tr>
<td>1989</td>
<td></td>
<td>0.31</td>
<td>0.71</td>
<td>2.01</td>
<td>2.10</td>
</tr>
<tr>
<td>1994</td>
<td></td>
<td>0.08</td>
<td>0.30</td>
<td>0.97</td>
<td>1.64</td>
</tr>
<tr>
<td>2003</td>
<td></td>
<td>0.10</td>
<td>0.30</td>
<td>0.85</td>
<td>1.18</td>
</tr>
</tbody>
</table>

**Table 5.** Number of stems per hectare of 5-8 cm *Carpinus* for selected years in four elevation zones.

<table>
<thead>
<tr>
<th>Year</th>
<th>Density</th>
<th>Banks</th>
<th>Lows</th>
<th>Flats</th>
<th>Highs</th>
</tr>
</thead>
<tbody>
<tr>
<td>1980</td>
<td></td>
<td>32</td>
<td>109</td>
<td>184</td>
<td>175</td>
</tr>
<tr>
<td>1989</td>
<td></td>
<td>37</td>
<td>90</td>
<td>119</td>
<td>98</td>
</tr>
<tr>
<td>1994</td>
<td></td>
<td>20</td>
<td>49</td>
<td>79</td>
<td>70</td>
</tr>
<tr>
<td>2003</td>
<td></td>
<td>34</td>
<td>46</td>
<td>68</td>
<td>59</td>
</tr>
</tbody>
</table>
Table 6. Number of stems >2.0 cm DBH and percent change at three sites during the flood period.

<table>
<thead>
<tr>
<th>Site</th>
<th>Year</th>
<th>Abundance</th>
<th>Percent change</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neches Bottom</td>
<td>1989</td>
<td>1861</td>
<td>-63%</td>
</tr>
<tr>
<td></td>
<td>1994</td>
<td>1176</td>
<td></td>
</tr>
<tr>
<td>Wier Woods</td>
<td>1989</td>
<td>57</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1992</td>
<td>52</td>
<td>-5.3 to 8.8%</td>
</tr>
<tr>
<td></td>
<td>1995</td>
<td>54</td>
<td></td>
</tr>
<tr>
<td>Turkey Creek</td>
<td>1988</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1993</td>
<td>3</td>
<td>+0 to 233%</td>
</tr>
<tr>
<td></td>
<td>1996</td>
<td>7</td>
<td></td>
</tr>
</tbody>
</table>

Table 7. Growth analysis and age results for Carpinus.

<table>
<thead>
<tr>
<th>Growth form</th>
<th>Size class</th>
<th>Years spent in class</th>
<th>Age (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small sapling</td>
<td>0-50 cm height</td>
<td>3-5*</td>
<td>3-5</td>
</tr>
<tr>
<td>Small sapling</td>
<td>50-140 cm height</td>
<td>3-15</td>
<td>6-20</td>
</tr>
<tr>
<td>Large sapling</td>
<td>0.1-2.0 cm DBH</td>
<td>6-10</td>
<td>12-30</td>
</tr>
<tr>
<td>Large sapling</td>
<td>2.0-4.5 cm DBH</td>
<td>7-23</td>
<td>19-53</td>
</tr>
<tr>
<td>Tree</td>
<td>4.5-10 cm DBH</td>
<td>15-24</td>
<td>34-77</td>
</tr>
<tr>
<td>Tree</td>
<td>10-20 cm DBH</td>
<td>37-46</td>
<td>71-123</td>
</tr>
<tr>
<td>Tree</td>
<td>20-30 cm DBH</td>
<td>45-59</td>
<td>116-182</td>
</tr>
</tbody>
</table>

*No data available for this size class. Estimate based on personal observation by Harcombe.
### Table 8: The number of days the entire study area had flooded (greater than 63.2 cm) during the pre-cean period (1961-1964) and from December 1971 to October 1973.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1961-1964</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1971-1973</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(Note: High flows are highlighted.)
<table>
<thead>
<tr>
<th>Month</th>
<th>Jan</th>
<th>Feb</th>
<th>Mar</th>
<th>Apr</th>
<th>May</th>
<th>Jun</th>
<th>Jul</th>
<th>Aug</th>
<th>Sep</th>
<th>Oct</th>
<th>Nov</th>
<th>Dec</th>
</tr>
</thead>
<tbody>
<tr>
<td>Days</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>5</td>
<td>7</td>
<td>5</td>
<td>7</td>
<td>5</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Rain</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>5</td>
<td>7</td>
<td>5</td>
<td>7</td>
<td>5</td>
<td>3</td>
<td>1</td>
</tr>
</tbody>
</table>

*Explanation:* The number of days the water study was flooded (greater than 63.5 cm) during the post-dam period, 1965-2003.
Table 10. Spring and summer flooding of the entire study site (beginning by March 15-September 14) pre- and post-dam. The starting date and number of days the study site was flooded are included (USGS 2004).

<table>
<thead>
<tr>
<th>Pre-dam 1921-1964</th>
<th>Post-dam 1965-2003</th>
</tr>
</thead>
<tbody>
<tr>
<td>4/2/1922</td>
<td>5/7/1969</td>
</tr>
<tr>
<td>3/1/1924</td>
<td>6/1/1991</td>
</tr>
<tr>
<td>3/15/1927</td>
<td>3/10/2001</td>
</tr>
<tr>
<td>5/19/1929</td>
<td>6/15/2001</td>
</tr>
<tr>
<td>5/1/1929</td>
<td>16</td>
</tr>
<tr>
<td>5/12/1935</td>
<td>20</td>
</tr>
<tr>
<td>4/13/1938</td>
<td>13</td>
</tr>
<tr>
<td>5/5/1944</td>
<td>27</td>
</tr>
<tr>
<td>6/12/1944</td>
<td>12</td>
</tr>
<tr>
<td>4/5/1945</td>
<td>22</td>
</tr>
<tr>
<td>3/18/1947</td>
<td>11</td>
</tr>
<tr>
<td>3/13/1950</td>
<td>13</td>
</tr>
<tr>
<td>6/3/1950</td>
<td>17</td>
</tr>
<tr>
<td>3/26/1953</td>
<td>6</td>
</tr>
<tr>
<td>5/3/1953</td>
<td>29</td>
</tr>
<tr>
<td>5/2/1957</td>
<td>21</td>
</tr>
</tbody>
</table>

Table 11. The number of days between the first and second growing season floods of 1989 and the total number of days flooding during the growing season of 1989 (1989a was initiated by late spring flooding and lasted 5/19-6/20; 1989b was initiated by Tropical Storm Allison and lasted 6/23-8/9).

<table>
<thead>
<tr>
<th></th>
<th>1989a</th>
<th>Days between flooding</th>
<th>1989b</th>
<th>1989 total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sloughs</td>
<td>33</td>
<td>2</td>
<td>48</td>
<td>81</td>
</tr>
<tr>
<td>Site lows</td>
<td>19</td>
<td>13</td>
<td>43</td>
<td>62</td>
</tr>
<tr>
<td>Flats</td>
<td>5</td>
<td>33</td>
<td>19</td>
<td>24</td>
</tr>
<tr>
<td>Highest areas</td>
<td>3</td>
<td>34</td>
<td>17</td>
<td>20</td>
</tr>
</tbody>
</table>

Table 12. For years with floods above slough level, the longest number of consecutive days flooded during the biggest flood pre-dam (1922-1965), which occurred during the winter of 1940, and the biggest flood post-dam (1965-2003), which occurred during the winter and spring of 1992, compared with the 1989 flood (1989a was initiated by late spring flooding and lasted 5/19-6/20; 1989b was initiated by Tropical Storm Allison and lasted 6/23-8/9).

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Sloughs</td>
<td>79</td>
<td>128</td>
<td>33</td>
<td>48</td>
</tr>
<tr>
<td>Site lows</td>
<td>63</td>
<td>122</td>
<td>19</td>
<td>43</td>
</tr>
<tr>
<td>Flats</td>
<td>58</td>
<td>46</td>
<td>5</td>
<td>19</td>
</tr>
<tr>
<td>Highest areas</td>
<td>47</td>
<td>38</td>
<td>3</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>Severe</td>
<td>Moderate</td>
<td>Mild</td>
<td>Dry</td>
</tr>
<tr>
<td>-------</td>
<td>--------</td>
<td>----------</td>
<td>------</td>
<td>-----</td>
</tr>
</tbody>
</table>

Table 1.4: Monthly length of moderate drought of 1988-1998 (NOAA 2006).

<table>
<thead>
<tr>
<th>6</th>
<th>5</th>
<th>4</th>
<th>3</th>
<th>2</th>
<th>1</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>6</td>
</tr>
<tr>
<td>1</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>6</td>
<td>9</td>
</tr>
<tr>
<td>4</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

Table 1.5: Monthly length of mild to extreme droughts 1970-2005 (NOAA 2006).

- Extreme = 4.0 or less
- Severe = 3.0 to 3.9
- Moderate = 2.0 to 2.9
- Mild = 1.0 to 1.9
- Dry spell = 0.5 to 0.9

Palmer Drought Severity Index:
<table>
<thead>
<tr>
<th>Date</th>
<th>Initial</th>
<th>End date</th>
<th>Initial</th>
<th>End date</th>
<th>Initial</th>
<th>End date</th>
<th>Initial</th>
<th>End date</th>
<th>Initial</th>
<th>End date</th>
<th>Initial</th>
<th>End date</th>
<th>Initial</th>
<th>End date</th>
<th>Initial</th>
<th>End date</th>
</tr>
</thead>
</table>

Table 16. Sapling species analyzed in competition analysis in order from fastest expected growth to least expected growth and greatest expected growth decrease to least expected growth decrease with exposure to increasing light and competition, respectively.

<table>
<thead>
<tr>
<th>Species</th>
<th>Expected response order</th>
<th>Shade tolerance</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Sapium</em></td>
<td>1</td>
<td>Intolerant</td>
</tr>
<tr>
<td><em>Liquidamber</em></td>
<td>2</td>
<td>Intolerant</td>
</tr>
<tr>
<td><em>Q. nigra</em></td>
<td>3</td>
<td>Intolerant</td>
</tr>
<tr>
<td><em>A. rubrum</em></td>
<td>4</td>
<td>Tolerant</td>
</tr>
<tr>
<td><strong>Q. pagoda</strong></td>
<td>5</td>
<td>Intolerant [1,2,3]</td>
</tr>
<tr>
<td><strong>Q. laurifolia</strong></td>
<td>6</td>
<td>Intermed-tolerant [1,4]</td>
</tr>
<tr>
<td><em>Fraxinus caroliniana</em></td>
<td>7</td>
<td>Tolerant-intermed [1,5]</td>
</tr>
<tr>
<td><em>I. decidua</em></td>
<td>8</td>
<td>Tolerant</td>
</tr>
<tr>
<td><em>I. opaca</em>*</td>
<td>8</td>
<td>Tolerant [4]</td>
</tr>
<tr>
<td><em>Carpinus</em></td>
<td>10</td>
<td>Very tolerant</td>
</tr>
</tbody>
</table>

*Expected growth ranking and shade tolerance from Lin et al. (2004) based on top quartile growth rates.  **Expected growth ranking based on shade tolerance literature.  *I. decidua* and *I. opaca* received the same expected order because there was no basis for expecting one to grow faster than the other.

1. McKnight et al. 1981  
2. Jones and McLeod 1989  
3. Lotti 1965  
4. Burns and Honkala 1990  
5. Sargent 1961

Table 17. Analysis of variance for sapling growth model.

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>F value</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>9</td>
<td>82.64</td>
<td>p&lt;0.0001</td>
</tr>
<tr>
<td>CI94</td>
<td>1</td>
<td>2.35</td>
<td>p=0.13</td>
</tr>
<tr>
<td>Clc carp</td>
<td>1</td>
<td>0.51</td>
<td>p=0.47</td>
</tr>
<tr>
<td>Clc other</td>
<td>1</td>
<td>0.00</td>
<td>p=0.98</td>
</tr>
<tr>
<td>CI94 *species</td>
<td>9</td>
<td>11.39</td>
<td>p&lt;0.0001</td>
</tr>
<tr>
<td>Clc carp *species</td>
<td>9</td>
<td>15.62</td>
<td>p&lt;0.0001</td>
</tr>
<tr>
<td>Clc other *species</td>
<td>9</td>
<td>0.89</td>
<td>p=0.54</td>
</tr>
</tbody>
</table>

Where growth was measured as the 1997 basal area minus the 1994 basal area.  CI$_{1994}$ equaled the amount of competition in 1994 due to the live stems greater than 2.0 cm DBH surrounding each large sapling stem.  CI$_{(\text{Carp1990-1994})}$ was the amount of reduced competition due to the death of *Carpinus* between 1990-1994.  CI$_{(\text{Other1990-1994})}$ was the amount of competition lost due to the death of trees other than *Carpinus* between 1990-1994.
Table 18. Slopes and relative magnitude to Sapium slope for the interaction between species and competition index due to the death of Carpinus. Only species with significant parameter estimates are shown.

<table>
<thead>
<tr>
<th>Species</th>
<th>Slope</th>
<th>Magnitude compared to Sapium</th>
<th>Expected growth increase from Table 13</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sapium</td>
<td>2.21</td>
<td>1.00</td>
<td>1</td>
</tr>
<tr>
<td>Liquidambar</td>
<td>0.44</td>
<td>0.20</td>
<td>2</td>
</tr>
<tr>
<td>Q. nigra</td>
<td>0.23</td>
<td>0.10</td>
<td>3</td>
</tr>
<tr>
<td>I. opaca</td>
<td>0.08</td>
<td>0.04</td>
<td>8</td>
</tr>
<tr>
<td>I. decidua</td>
<td>0.06</td>
<td>0.03</td>
<td>8</td>
</tr>
<tr>
<td>Carpinus</td>
<td>-0.02</td>
<td>-0.01</td>
<td>10</td>
</tr>
<tr>
<td>A. rubrum</td>
<td>-0.35</td>
<td>-0.16</td>
<td>4</td>
</tr>
</tbody>
</table>

Table 19. Slopes and relative magnitude to Sapium slope for the interaction between species and competition index for 1994. Only species with significant parameter estimates are shown.

<table>
<thead>
<tr>
<th>Species</th>
<th>Slope</th>
<th>Magnitude compared to Sapium</th>
<th>Expected growth decrease from Table 13</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sapium</td>
<td>-0.48</td>
<td>1.00</td>
<td>1</td>
</tr>
<tr>
<td>Liquidambar</td>
<td>-0.1</td>
<td>0.21</td>
<td>2</td>
</tr>
<tr>
<td>Q. nigra</td>
<td>-0.07</td>
<td>0.15</td>
<td>3</td>
</tr>
<tr>
<td>I. decidua</td>
<td>-0.01</td>
<td>0.03</td>
<td>8</td>
</tr>
<tr>
<td>Carpinus</td>
<td>-0.02</td>
<td>0.04</td>
<td>10</td>
</tr>
<tr>
<td>F. caroliniana</td>
<td>-0.02</td>
<td>0.04</td>
<td>7</td>
</tr>
<tr>
<td>A. rubrum</td>
<td>0.001</td>
<td>0.00</td>
<td>4</td>
</tr>
<tr>
<td>I. opaca</td>
<td>0.057</td>
<td>-0.12</td>
<td>8</td>
</tr>
</tbody>
</table>
FIGURES

<table>
<thead>
<tr>
<th>Class</th>
<th>Flooded Condition</th>
<th>Area (ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>50-91 cm</td>
<td>Slough</td>
<td>0.76</td>
</tr>
<tr>
<td>91-188 cm</td>
<td>Site lows</td>
<td>1.12</td>
</tr>
<tr>
<td>123-135 cm</td>
<td>Flats</td>
<td>1.56</td>
</tr>
<tr>
<td></td>
<td>Highest surfaces</td>
<td>0.56</td>
</tr>
</tbody>
</table>

One square = one 20x20 m plot

Figure 1. The four-hectare site consists of 100 contiguous 20x20 m plots. Each plot was placed in one of four zones based on elevation and flood condition. These zones were used to examine DBH distributions and recruitment in different elevation zones (Hall 1993). The bold, black lines indicate the slough that runs through the site.

Figure 2. The range of *Carpinus caroliniana*. From Metzger (1990).
Figure 3a-b. Trends in live tree basal area (a) and density (b) for the eight most common species in the period for 1980-2003.
**Figure 4a-c.** Size distribution of the *Carpinus* population during the flood (a), post-flood (b), and pre-flood (c) intervals.
Number of trees dying each year

![Graph showing the number of trees dying each year for Carpinus versus all other species from 1981-2003.]

**Figure 5.** Number of trees dying per year for *Carpinus* versus all other species 1981-2003.

Annual *Carpinus* mortality by 3 cm size class

![Graph showing the annual mortality rate for *Carpinus* trees by 3 cm size class from 1983-2003.]

**Figure 6.** The mortality rates for *Carpinus* trees during various time intervals. *Average of all stems >26 cm DBH*
Figure 7. The abundance of the 1989 *Carpinus* population, 4.5 cm DBH and greater, is compared with its abundance in 1994. Percent surviving is indicated above the bars for each zone.
Figure 8a-l. The population structure of *Carpinus* is displayed by elevation zone (horizontal panels) for selected years (vertical panels). Note: The scale on the Y-axes, which represent the number of stems per elevation zone, differ for display purposes.
Figure 9a-c. The probability of death of *Carpinus* trees by DBH (cm) and elevation (cm) for pre-flood, flood, and post-flood intervals. The black circles are individual stems on which the model is based; the colored sheet is the result of smoothing the data with a tricube weight function of polynomial degree 1. This function unrealistically increases the probability of death over 1.0. The legend is shaded according to the probability of death.
Figure 114c: 'Cathaysia' growth for three tree size classes, ranging from 4.5 cm to 30+ cm DBH.
**Figure 12.** Ingrowth/yr/ha for the common species.
Figure 13. Small sapling ($\geq 50$ cm and $<140$ cm height) numbers for the common species over time.

Figure 14. Large sapling ($\geq 0.1$ cm DBH and $<4.5$ cm DBH) numbers for the common species over time.
Figure 15a. The mean daily streamflow (m$^3$/s) of the Neches River at Evadale, Texas for the pre-dam period 1922-1964 (USGS 2004). The study site is fully flooded when the flow reaches the upper horizontal line. The bankfull condition for the slough that runs through the study site is indicated by the lower horizontal line (Hall 1993).

Figure 15b. The mean daily streamflow (m$^3$/s) of the Neches River at Evadale, Texas for the post-dam period 1965-2003 (USGS 2004).
**Figure 16.** The mean daily streamflow (m³/s) for the 8 main growing season flood years after 1965 and part of 2004 (USGS 2004). The study site is fully flooded when the flow reaches the upper horizontal line. The bankfull condition for the slough that runs through the study site is indicated by the lower horizontal line (Hall 1993).

**Figure 17.** Precipitation and mean daily streamflows during the 1989 growing season (National Climatic Data Center 2005, USGS 2004, U.S. Army Corps of Engineers 2005).
Figure 18. The mean daily temperature values during 1985-1989 are compared to the normal mean monthly temperatures (indicated by black squares). Data from Beaumont Research Station, TX located 33 km south of the Evadale study site (National Climatic Data Center 2005).

Figure 19. The mean daily temperature values during 1989-1994 are compared to the normal mean monthly temperatures (indicated by black squares). Data from Beaumont Research Station, TX located 33 km south of the Evadale study site (National Climatic Data Center 2005).
Figure 20. The mortality risk of selected species as a function of light. Modified from Lin et al. (2004).
**Figure 21.** Displays the ingrowth of all species versus *Carpinus* basal area loss at the plot level. All plots are contained in 21a; plots with no *Carpinus* ba loss (m²/ha) are removed in 21b. The exponential trend lines are black; the linear trend lines are red.
Figure 22. Displays the ingrowth for several species versus *Carpinus* basal area loss at the plot level.
Subject sapling growth 1994-1997
least squares mean

Figure 23. The adjusted means growth response of species for which subject saplings were included in the competition model. The same letter indicates values are not significantly different from each other. Different letters between species indicates a significant difference (p<0.05). The number of saplings (n) included in the analysis for each species is indicated above the letters.
Figure 24. Relationship between growth and competition index of dead Carpinus for species with significant parameter estimates.

Figure 25. Relationship between growth and competition index of 1994 for species with significant parameter estimates.
APPENDICES

APPENDIX A

Flood responses and adaptations

Under normal conditions, the aboveground atmosphere is able to replenish the soil oxygen consumed during root and heterotrophic respiration via diffusion. Water occupies the soil pores under flood conditions and impedes gas exchange between the soil and air. This results in an almost immediate deficiency of soil oxygen. Within a few hours, roots and microorganisms consume the remaining oxygen in the soil (Kozlowski and Pallardy 1997).

The upper levels of drained soils are typically between 10-21% oxygen. Roots begin to show signs of injury when the soil concentration of oxygen drops below 10%. When the soil oxygen concentration is reduced to 3%, root growth is halted. Most land plant roots are restricted to the layers above the water table level, because directly above the water table, the oxygen concentration is 1% (Kozlowski 1979).

Flooding reduces the amount of water absorption by plants; it increases the resistance to water flow in roots and induces stomatal closure (Kozlowski and Pallardy 1997). Stomatal closure decreases the amount of carbon dioxide absorption by leaves, resulting in a decrease in photosynthesis (Kozlowski 1979, Kozlowski and Pallardy 1997). Over time, there may also be negative effects on photosynthetic capacity. This may occur when there are changes in the amount of carboxylation enzymes, decreases in leaf chlorophyll content, and reductions in leaf surface area. Leaf surface area may be reduced by injury, abscission, or inhibition of leaf formation and expansion (Kozlowski and Pallardy 1997). Root respiration under flooded conditions may partially or fully
change from aerobic to anaerobic. This results in the accumulation of toxic compounds, including nitrites, and reduced forms of iron and manganese, hydrogen sulfide, ethylene, ethanol, and organic acids. Energy from respiration is decreased, which impedes the energy-requiring process of mineral uptake (Kozlowski 1979). Thus, the absorption of the macronutrients nitrogen, phosphorous, and potassium decreases (Kozlowski and Pallardy 1997). Poor soil aeration and reduced ion uptake inhibit nitrogen fixing soil organisms, such as mycorrhizae (Kozlowski 1979, Kozlowski and Pallardy 1997). Flooding can also cause root decay, chlorosis of leaves, and induce leaf senescence and abscission (Kozlowski 1984a).

Later responses to flooding include changes in hormone levels. For example, adventitious root formation and imbalanced growth that leads to curvature may be due to high auxin levels. The growth regulating gibberellin hormones are reduced in response to flooding. Decreased production of cytokinins in roots is associated with chlorosis of leaves (Kozlowski 1979). Ethylene concentrations under flood conditions increase because the hormone cannot escape from the inundated roots. The low solubility of ethylene results in its accretion in the roots and its following movement up the shoots. Ethylene is associated with numerous plant responses, including leaf abscission, growth of buds, stems, and roots, hypertrophy of tissues, flowering, and ripening of fruits (Kozlowski and Pallardy 1997).

Extended periods of flooding result in varying responses among species depending on their flood tolerance. Flood intolerant species are unable to reopen stomata that close in response to soil hypoxia (Kozlowski and Pallardy 1997). The mechanism by which plants close their stomata in response to flooding seems to be hormonal and
may involve the transmission of abscisic acid from the roots to the leaves (Kozlowski 2002b). In contrast to flood intolerant species, some flood tolerant species can reopen their stomata and regain nearly their original photosynthetic rate (Kozlowski and Pallardy 1997). In addition, some species that are morphologically adapted to poor soil aeration are able to absorb oxygen through stomatal pores on leaves or through lenticels (pores of woody plants that allow for gas exchange) on twigs, stems, and roots. From the pores or lenticels, the oxygen is moved downward and is diffused out of the roots to the rhizosphere. This oxygen oxidizes reduced soil compounds, like toxic ferrous and manganous ions (Kozlowski and Pallardy 1997). Two other adaptations that allow for increased oxygen transport include formation of hypertrophied (enlarged) lenticels and aerenchyma tissue (oxygen is easily transported through the large intercellular spaces) on the parts of the plant that are underwater (Kozlowski and Pallardy 1997). Maintaining carbohydrate reserves and the ability to utilize them to sustain ATP levels at low oxygen concentrations may be another component of tolerance to anoxic conditions. The maintenance of cell membranes before and after anoxia may also be important. Flood intolerant species often incur membrane lipid damage during or after anoxia due to the accumulation of toxic chemicals (Kozlowski 2002a). Some flood tolerant species accumulate organic acids when oxygen concentrations are low. The production of organic acids is an alternative to the toxic accumulation of ethanol, a byproduct of anaerobic respiration (Teskey and Hinckley 1977).

Adventitious roots at or below the water level are one adaptation that allows some flood tolerant species increased chances of survival under flooded conditions. This adaptation takes advantage of the slightly higher oxygen and slightly lower toxin
concentrations found in the uppermost soil. In addition, adventitious roots increase the amount of surface area available for water and nutrient uptake and oxidize the rhizosphere (Kozlowski 1979). Some flood tolerant species lose large portions of their original root systems and form soil water roots from the remaining portions. Another type of root that forms in flood tolerant species is more succulent and opaque in appearance compared to the original roots (Hook 1984b).

APPENDIX B

Flooding and determination of flood tolerance

Bottomland hardwood forests are characterized by cyclical floods that occur during the winter and spring months when the vegetation is dormant (Kozlowski 1984b). Typically, if dormant season flooding recedes before the beginning of the growing season, the floodwaters will not have negative effects on tree growth (Broadfoot 1967, Kozlowski 1984a). On the other hand, flooding that extends for four weeks or more during the growing season usually has detrimental effects on tree growth (Kozlowski 1984a). This difference is attributed to the low oxygen requirements during the dormant season when plants have no or small amounts of growth compared to the growing season plants are growing and the root systems require much larger amounts of oxygen, quickly using up the oxygen in the floodwater (Teskey and Hinckley 1977). Thus, as defined by Hook (1984a), a species’ flood tolerance refers to its ability during the growing season to tolerate soil saturation or waterlogging. One observational study conducted in a reservoir found that flooding Fagus grandifolia (beech) for 14 days continuously during the growing season killed large stems. In contrast, when F. grandifolia was flooded for 18 days during the winter months no adverse effects were apparent (Hall and Smith 1955).
One study of *Liriodendron tulipifera* (tuliptree) seedlings flooded on a plantation found that all died after 53 days of partial submersion during the growing season (Kennedy and Krinard 1974). In contrast, another study found no effect of partial submersion during the dormant season (Teskey and Hinckley 1977).

The mortality of trees due to growing season flooding varies, partly depending on the tree species, the duration and depth of flooding, and the age of the tree. A study examining four years of continuous flooding in the Mississippi River Valley found that some tree species died after the first year of flooding, while other species died after the second or third year (Broadfoot and Williston 1973, Kozlowski 1984a). Harms et al. (1980) found that a Florida swamp forest showed increased mortality with greater floodwater depth. Greater water depth resulted in a larger proportion of root system death and a decrease in the starch loads in living roots (Harms et al. 1980). Another study along the Mississippi River in Missouri showed increasing mortality with greater depth and duration (Yin et al. 1994). Part of the reason that depth is important in woody plant water tolerance may be that deeper water blocks more lenticels rendering them unable to contribute to gas exchange (Teskey and Hinckley 1977).

Flood tolerance of seedlings is usually much less than that of adult trees (Kozlowski 1984a). This is due in part to the older trees usually having their crowns above the water and not being as vulnerable to being washed away, pushed over by flowing water, or buried in mud (Kozlowski 1984a).

The mortality of trees due to growing season flooding sometimes also varies with size. Hall et al. (1946) assert that observations in the southeast United States indicate that larger trees are more vulnerable to flooding than smaller trees. In contrast, one study
after a large flood that lasted approximately 51 days during the growing season along the Mississippi River in Missouri found greater mortality among smaller trees (Yin et al. 1994). Harms et al. 1980 found that two tree species in a Florida swamp forest had greater mortality among smaller trees, but the mortality in two other tree species did not vary with size.

The condition of the floodwaters can also be important to tree survival. Precipitation can temporarily raise oxygen levels to pre-flood conditions. Stagnant water contains less oxygen than moving water, so trees in moving water are typically healthier and have better growth rates than trees in stagnant water. Finally, temperature is also a factor because cool water can hold more oxygen than warm water (Teskey and Hinckley 1977).

The time it takes for a tree to die due to flooding varies. Yin et al. (1994) found that some trees died during the flood and others during the winter after one long growing season flood. However, large numbers of trees did not leaf out the following spring, so death was concentrated in the following summer, one year after the flood (Yin et al. 1994). Unfortunately, this study by Yin et al. (1994) did not follow death for more than one year after the flood. An observational study in a reservoir by Hall and Smith (1955) found that the time to death due to non-continuous growing season flooding varied between and within species, ranging from one to many years. Green (1947) showed that it took between one and five years for trees to die under permanent flooding.

Flood tolerance has been examined using many different methods. Some studies employ observational methods, including examining the effects of flooding on vegetation around reservoirs (e.g. Hall et al. 1946, Hall and Smith 1955, Bedinger 1971) and
observing the zonation of vegetation in a floodplain (e.g. Hall 1993). Often, observational studies designate zones on the basis of soil saturation and flooding regimes in order to delineate community-level patterns (Conner et al. 1990). One problem with observational studies that use zones to estimate relative flood tolerance is that location is not necessarily a flawless indicator of flood tolerance (Hall et al. 1946, Loucks and Keen 1973). In other words, some upland species may be more flood tolerant than some lowland species. Another problem with applying the results of observational studies to other sites is that soils, site history, and other factors may differ substantially (Hook 1984b). Despite this shortcoming, information about the relative flood tolerance of species from these studies can be useful (Chapman et al. 1980). Other studies use experiments conducted outdoors (e.g. Jones and Sharitz 1990, Conner 1994) and/or in greenhouses (e.g. Butterfield et al. 2004). Most of the experiments that examine flood tolerance of vegetation study seedlings or saplings rather than trees. The results of such work on seedling and saplings should be considered with caution, since they are not expected to be as flood tolerant as trees (Kozlowski 1984a). Therefore, the results found in this body of literature may not give a completely accurate depiction of a species’ relative flood tolerance.

Examination of the literature on flood tolerance is one way to determine the susceptibility of Carpinus to flooding, especially with relation to the other common Neches Bottom species. An observational study by Hall and Smith (1955) is one main study cited in the major reviews of flood tolerance by Teskey and Hinckley (1977), Whitlow and Harris (1979), and McKnight et al. (1981). Hall and Smith (1955) studied the vegetation effects of a Kentucky reservoir over the course of several growing seasons.
First, using aerial reconnaissance, they looked for evidence of stratification by elevation with respect to species survival. After confirming the differential survival of species, they delineated five zones, defined by the percent of time flooded. In the zone that experienced the longest period of flooding, no trees were found alive. The zone on the opposite end of the gradient had only a few dead trees, while the intermediate zones showed moderate mortality levels. Transects were made at various locations and elevation readings were taken at the bases of some trees. For each species, two main elevations were established. This was done by establishing a “healthy line,” defined by elevations taken from the bases of at least ten of the lowest healthy trees, and a “dead line,” consisting of the lowest unhealthy trees found among the dead and dying trees. They ranked the species for tolerance to flooding based on the lowest observed healthy tree. In addition, they determined the percent of time that the healthy and dead lines for each species were flooded during the growing season (Table 20). The relevant Neches Bottom species that they found in their study are, ranked from least to most tolerant, as follows: *Q. nigra*, *Carpinus*, *Q. michauxii*, *Liquidambar*, *I. decidua*, and *A. rubrum*.

Multiplying the percentage of time flooded during the growing season by the 184-day growing season used in that study gives the number of days flooded during the growing season for the healthy line and dead line (Table 21). The percentage of time flooded during the growing season can also be multiplied by the growing season length found by Winters (1995) on species in the Neches Bottom study site. She calculated growing season length for three seasons; the minimum length and maximum length are used for calculating the number of days for the healthy line and dead line.
The number of days *Carpinus* was flooded at the study site during the 1989 flood caused by the tropical storm was within the estimated number of days to cause death at the two lower elevation levels (Tables 10 and 21). *Q. nigra* required a lower number of days flooded if the calculations were based on the generic growing season length used by Hall and Smith (1955), but it required a higher number of days to be flooded using the range of growing season lengths found by Winters (1995) at the study site. This analysis of the number of flooding days required to kill *Carpinus* cannot be directly extended to the Neches Bottom study because there are substantial site differences, but it does suggest that the duration of the 1989 flood(s) was long enough to cause mortality at least in the lowest areas. A lower number of days than found in the Hall and Smith (1955) study may actually be necessary to cause *Carpinus* death at the Texas study site. Logic suggests that since southeast Texas is hotter than Tennessee, heat load during the flood would be higher in Texas. The higher respiration rates of roots could accelerate anoxia and fewer days would be required to kill trees.
Table 20. Modified from Hall and Smith (1955)

<table>
<thead>
<tr>
<th>Zone</th>
<th>Contours between elevations</th>
<th>Percent of time flooded during growing season (Apr. 1 – Oct. 1)</th>
<th>Effects of flooding</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>343-346 ft</td>
<td>54-99</td>
<td>All woody species dead.</td>
</tr>
<tr>
<td>II</td>
<td>346-348 ft</td>
<td>41-54</td>
<td>Most species suffered high mortality but living specimens of several, including Liquidambar present.</td>
</tr>
<tr>
<td>III</td>
<td>348-355 ft</td>
<td>16-41</td>
<td>The number of species surviving increases up to band formed by healthy stands of Carpinus (at 355 ft).</td>
</tr>
<tr>
<td>IV</td>
<td>355-359 ft</td>
<td>1-16</td>
<td>The number of species surviving increases with elevation until upland forests are reached at 359 ft. After a growing season flood in 1951, some beech died in 1952.</td>
</tr>
<tr>
<td>V</td>
<td>359-360 ft</td>
<td>0-1</td>
<td>Nearly total survival, with only a few species dead in the lower part of the zone...</td>
</tr>
</tbody>
</table>

Table 21. The percent of time flooded during all growing seasons in Hall and Smith (1955) equated with the number of days flooded according to the growing season length used by Hall and Smith (1955) and the minimum and maximum growing season lengths found by Winters (1995). “Healthy” indicates the maximum number of days flooded for a tree to be healthy. “Dead” indicates the number of flooded days after which no live trees were found.

<table>
<thead>
<tr>
<th>Species</th>
<th>Percent of time flooded (Hall &amp; Smith 1955)</th>
<th>Number of days based on Hall &amp; Smith (1955) 184-day growing season</th>
<th>Number of days based on Winters (1995) growing season (GS)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Healthy Dead</td>
<td>Healthy Dead</td>
<td>Min GS length</td>
</tr>
<tr>
<td>Q. nigra</td>
<td>16% 24%</td>
<td>29 44</td>
<td>26 39 38</td>
</tr>
<tr>
<td>Carpinus</td>
<td>23% 26%</td>
<td>42 48</td>
<td>27 30 41</td>
</tr>
<tr>
<td>Q. michauxii</td>
<td>29% 34%</td>
<td>53 63</td>
<td>47 55 69</td>
</tr>
<tr>
<td>Liquidambar</td>
<td>34% 43%</td>
<td>63 79</td>
<td>47 59 69</td>
</tr>
<tr>
<td>I. decidua</td>
<td>35% 37%</td>
<td>64 68</td>
<td>-- -- --</td>
</tr>
<tr>
<td>A. rubrum</td>
<td>36% 41%</td>
<td>66 75</td>
<td>50 57 77</td>
</tr>
</tbody>
</table>

In an observational study of the White River Basin in Arkansas, Bedinger (1971) found that Carpinus and A. rubrum occupied the highest portion of a zone flooded annually with an average duration of 29-40% of the time, although they were more common in the zone flooded 10-21% of the time. Liquidambar was found in sites flooded 10-21% of the time. In a study of successional changes in New York marshes,
Dane (1959) found that *Carpinus* inhabited moist land and was less tolerant than most of the other species. These other species included *Salix* spp. (willow), *Fraxinus* spp. (ash), *A. saccharinum* (silver maple), *Ulmus americana* (American elm), and *Vaccinium corymbosum* (highbush blueberry) flooded by up to 20 inches of water. Only *Fagus grandifolia* (beech) and *Carya ovata* (shagbark hickory) were found to have the same tolerance as *Carpinus*.

In an observational study of Tennessee Valley reservoirs, Hall et al. (1946) placed species in one of three groups: intolerant, moderately tolerant, or tolerant. Intolerant species did not survive continuous growing season flooding one foot deep for one growing season, with many species dying due to one month or less of flooding. Moderately tolerant species survived one growing season of flooding but usually died during the second growing season if they were continuously flooded by water equal to or greater than one foot in depth. Tolerant species were able to survive continuous inundation for two or more growing seasons by water equal to or greater than one foot deep. The species were also ordered within groups according to their tolerance. Their results yielded an order from least to most tolerant, as follows: *Intolerant Carpinus; Moderately tolerant O. nigra, I. decidua; Tolerant Liquidambar, A. rubrum, and Taxodium*.

In another observational study, Larson et al. (1981) ranked species from most to least tolerant based on 238 belt transects in the southeast United States, including Texas. Zones based on soil saturation and inundation were used to indicate relative tolerance levels of species. The relevant Neches Bottom species, ranked from least to most
tolerant, were: *Q. michauxii, Q. nigra, Carpinus, I. decidua, Liquidambar, A. rubrum,* and *Taxodium.*

Hall (1993), conducted canonical correspondence analysis on Neches Bottom sapling data and found that the measured elevation explained 32.8% of the variance in random plots and 17.5% in patch plots. She ranked the species from least to most tolerant with the mean relative elevations (m) for random and patch plots included in parentheses as follows: *Q. michauxii* (1.17, 1.19), *Liquidambar* (1.11, 1.08), *Carpinus* (1.01, 1.07), *A. rubrum* (1.04, 0.99), *Sapium* (0.98, 1.05), and *Taxodium* (0.82, 0.55). Based on these findings, she asserted the common assumption that elevation was a surrogate for flood tolerance. She also conducted a flood damage survey after the 1989 flood. She found that *Carpinus* was more damaged than other species, *I. decidua* and *Sapium* were damaged less by the flooding than other species.

Wharton et al. (1982) classified floodplain vegetation by presence in zones based upon their studies and field observations in Florida, North Carolina, South Carolina, and Georgia. They defined Zone II by soils as being saturated 100% of the time, including the growing season. Zone III was defined by soils saturated 40% of the time, including a major portion of the growing season, the winter, and spring. Zone IV was defined by soils saturated 22% of the time, including 1-2 months in the growing season and the entire spring and winter. Zone V was characterized by soils saturated during the growing season from 2-12.5% of the time. Their results, ranking the species from least to most tolerant, by zone were: *Zone V Q. nigra; Zone IV Liquidambar, I. decidua,* and *Carpinus; Zone III A. rubrum; Zone II Taxodium.*
In a detailed review, Hook (1984a) examined the literature on bottomland species flooding tolerances. His research included the reviews by Teskey and Hinckley (1977), Whitlow and Harris (1979), McKnight et al. (1981), and Wharton et al. (1982), as well as additional observational and experimental studies. Unlike most flood review studies, he looked at multiple studies for each species and placed each in a particular flood tolerance group. He defined weakly tolerant species as “...capable of living from seedling through maturity in soils that are temporarily waterlogged for durations of 1-4 weeks and usually accounting for 10% of the growing season.” Moderately tolerant species were defined as “...capable of living from seedling to maturity in soils waterlogged about 50% of the time. Waterlogging typically occurs in portions of the winter, spring, and early summer.” He defined the most tolerant species as “...capable of living from seedling to maturity in soils that are waterlogged almost continually year after year except for short durations during droughts. The soils are typically anaerobic in character but are less so where the water is moving.” He placed the following relevant species into tolerance groups: Weakly tolerant *Q. michauxii* and *Carpinus*; Moderately tolerant *Liquidambar, I. decidua*, and *A. rubrum*; Most tolerant *Taxodium*.

In a 16-week greenhouse experiment, Butterfield et al. (2004) found that *Sapium* was flood tolerant. This experiment examined seedling responses to water stress. It outperformed four other tree species native to the southeastern United States, including *Liquidambar* (Butterfield et al. 2004). An outdoor experiment conducted by Jones and Sharitz (1990) involved germinating Texas *Sapium* and South Carolina *Nyssa aquatica* (water tupelo) seeds and eventually transferring the resulting seedlings to outdoor plots. *Sapium* exhibited less mortality than *N. aquatica* in flood tolerance treatments (Jones and
Sharitz 1990). Conner (1994) conducted an outdoor experiment and compared the flood tolerance of *Sapium* and *Taxodium*. This study found that both species were very flood tolerant, but *Sapium* had greater reduction in shoot and root biomass under flood conditions than *Taxodium* (Conner 1994). *Sapium* developed succulent soil roots in response to flooding (Conner 1994), indicating that it responds to flooding with at least one morphological adaptation.

This review amply demonstrates that tree species differ relatively consistently in their ability to grow and survive under flooded conditions during the growing season. This variation in flood tolerance strongly influences the composition and distribution of vegetation in bottomland hardwood forests. *Carpinus* is among the least flood tolerant species present in the Neches Bottom, but in one study each, *Q. michauxii* (Hall 1993) and *Q. nigra* (Hall and Smith 1955) were ranked less tolerant.

**APPENDIX C**

**Growth**

An increasing amount of evidence in the literature suggests that trees about to die grow more slowly than trees that are not about to die (see Pedersen 1998 and references therein). If *Carpinus* had been afflicted with a pest or disease that caused the pulse of mortality, then it is a possibility that growth rate analysis could shed light on the issue. However, there is conflicting evidence in the literature as to whether pests or pathogen outbreaks always result in decreased growth rates. In some studies, stems that died from pests or disease experienced decreased growth rates before death (e.g. Waloff and Richards 1977, Morrow and LaMarche Jr. 1978, Jarosz and Davelos 1995), but there is also some evidence to the contrary (e.g. Koricheva and Larsson 1998).
Even though growth analysis cannot distinguish among causes of the mortality pulse, I conducted growth rate analyses of *Carpinus* stems. I compared growth of trees that died or survived by interval and compared growth rates of trees that died or survived within intervals. I also examined growth rates of several important species other than *Carpinus* by interval.

Growth rate analyses used a full two-factor analysis of variance using the SAS General Linear Model procedure (SAS 2003). The Tukey-Kramer method of multiple comparisons for unbalanced designs was used with the least squares means to examine significant interaction effects (SAS 2003). I used the NPAR1WAY procedure in SAS to perform the two-sided, nonparametric Mann-Whitney test for two-samples (SAS 2003).

Growth rate was analyzed to determine whether trees that died had lower growth rates than trees that survived. Growth rates of *Carpinus* stems were examined for the intervals 1980-1982, 1982-1985, 1985-1989, 1989-1994, 1994-1997, 1997-2000 (Table 22). The sample was divided into two classes, individuals that died and individuals that survived the following interval. Growth rates were modeled with a full two-factor Analysis of Variance using the General Linear Model in SAS. The overall model was significant ($F_{11,716} = 51.74; p<0.0001$). Survival status ($F_{1,11} = 160.58; p<0.0001$) and interval ($F_{5,11} = 26.22; p<0.0001$) significantly affected growth rate. The interaction between survival status and interval was also significant ($F_{5,11} = 14.06; p<0.0001$).

For each interval, I tested the differences in growth rates between the individuals that died and those that survived. For all intervals, the mean growth rate of the individuals that died in the following interval was less than the individuals that survived (Mann-Whitney test, see z values in Table 22, $p<0.0001$, where z is a standard normal
deviate). In conclusion, growth of individuals that died was less than stems that survived the following interval. However, it is not clear that this enables differentiation between the hypotheses for *Carpinus* death. Growth analysis does not distinguish among proximate causes of death (flood, pests, or pathogens), but it is consistent with the hypothesis that stress due to normal climate variation outside of the climate envelope or due to warming was involved.

Growth of all important species at the study site was also examined for temporal variation. There was temporal variation in growth within species (Figure 26). Growth was modeled with a full two-factor Analysis of Variance using the General Linear Model in SAS (F_{55,14653} =195.22; p<0.0001). Growth differed significantly with species (F_{7,55} =554.19; p<0.0001) and interval (F_{6,55} =31.11; p<0.0001). The interaction species X interval was also significant (F_{42,55} =19.07; p<0.0001). The interaction was examined using the Tukey-Kramer method on least-squares means with the General Linear Model in SAS. Although many comparisons were significant, no clear pattern of growth differences emerged by species and interval; presumably because growth was affected by multiple factors including flooding, interannual weather variability, or climate change. For example, in a study of tree growth at the study site, Winters (1995) found that the effects of climate and weather on growth vary by species. Keeland and Sharitz (1995) studied *Nyssa sylvatica* var. *biflora*, *Nyssa aquatica*, and *Taxodium distichum* and found that flooding differentially affected their seasonal growth rates. One study found that tree growth was correlated with the minimum temperature at the beginning of the growing season (Kozlowski et al. 1962). Another study examined growth in *Pinus* and showed
that much of the interannual variation in tree growth is caused by a combination of precipitation, time, temperature, and ozone (McLaughlin and Downing 1995).

The length of the growing season has been found previously to vary between species (Eggle 1955, Day 1985). Some studies have found that dominant trees have faster growth and start their growing season earlier than suppressed trees (Kozlowski and Peterson 1962, Winget and Kozlowski 1965). Day (1985) found that growth rate was dependent upon species and hydrology in a study of 8 species over 4 sites with varying hydrological regimes. *Taxodium, A. rubrum,* and *N. sylvatica* had the highest growth rates on the inundated study site while *Q. laurifolia, Q. alba,* and *Liquidambar* had the highest growth rates on the rarely flooded site. In the Neches study site, the growing season length for tree species ranges widely. The start and end date for 1989 is not known. Winters (1995) documented the start and end dates for six species at the Neches Bottom based on three years of data. The average start and end dates are shown along with post-dam flows at the Evadale gage in Figure 27. *Carpinus* has the shortest growing season of these trees.

There was a large amount of temporal variability in growth rates within species (Figure 26). There was neither an apparent relationship between growing season length (Figure 27) and growth rate (Figure 26), nor between growing season length (Figure 27) and flood tolerance (Table 2). Therefore, these lines of inquiry are not pursued further.
Table 22. Growth comparison of *Carpinus* trees that survived or died in following interval. *Z* values from Mann-Whitney test results.

<table>
<thead>
<tr>
<th>Growth interval</th>
<th>Died or Survived interval</th>
<th>Mean growth, Died</th>
<th>Mean growth, Survived</th>
<th>Within interval difference, Died versus survived</th>
</tr>
</thead>
<tbody>
<tr>
<td>1980-1982</td>
<td>1983-1985</td>
<td>0.057</td>
<td>0.11</td>
<td>0.05 (z = -5.92, p&lt;0.0001)</td>
</tr>
<tr>
<td>1982-1985</td>
<td>1986-1989</td>
<td>-0.0083</td>
<td>0.078</td>
<td>0.09 (z = -11.6, p&lt;0.0001)</td>
</tr>
<tr>
<td>1985-1989</td>
<td>1990-1994</td>
<td>0.10</td>
<td>0.11</td>
<td>0.10 (z = -2.70, p&lt;0.0001)</td>
</tr>
<tr>
<td>1989-1994</td>
<td>1995-1997</td>
<td>0.068</td>
<td>0.16</td>
<td>0.09 (z = -4.97, p&lt;0.0001)</td>
</tr>
<tr>
<td>1994-1997</td>
<td>1998-2000</td>
<td>0.049</td>
<td>0.18</td>
<td>0.13 (z = -6.89, p&lt;0.0001)</td>
</tr>
<tr>
<td>1997-2000</td>
<td>2001-2003</td>
<td>0.054</td>
<td>0.13</td>
<td>0.08 (z = -6.83, p&lt;0.0001)</td>
</tr>
</tbody>
</table>
Figure 26. Variation over time in average annual tree growth rates for several species (species names are given in the panels). Bars show total range in growth.
**Figure 27.** The vertical lines define the growing season for six species (Winters 1995). Post-dam flows 1965-2003 are shown in grey (USGS 2004). The flow for 1989 is depicted in red.

### APPENDIX D

**Background on major Neches Bottom species**

1. *Acer rubrum*

   *Acer rubrum* L. (red maple) is a member of the Aceraceae. This species ranges as far north as Newfoundland, east to eastern Minnesota and eastern Texas, and south to Florida (Walters and Yawney 1990). *A. rubrum* survives on a large range of habitat types, including dry ridges and swamps. It thrives on fairly well-drained soils located at low or moderate elevations (Walters and Yawney 1990). This species is more common in the northern parts of its range (Walters and Yawney 1990).
A. rubrum has very light seeds and is a relatively good disperser (Streng et al. 1989). The maximum lifespan for A. rubrum is 150 years. Mature trees reach 46 to 60 cm in diameter and 18 to 27 m in height on average (Walters and Yawney 1990). It sprouts vigorously, especially after cutting or fire. A. rubrum is shade tolerant (McKnight et al. 1981, Walters and Yawney 1990,) and moderate to tolerant of floods (Hall et al. 1946, Teskey and Hinckley 1977, Whitlow and Harris 1979, McKnight et al. 1981, Walters and Yawney 1990).

II. Carpinus caroliniana

Carpinus caroliniana Walt. (American hornbeam, ironwood) belongs to the Betulaceae. It grows throughout the eastern United States and extends into southern parts of Quebec and Ontario. However, it is absent along the Mississippi River Valley, the southern portion of Florida, and the most southern portions of the Gulf Coastal Plain. It is also absent from certain parts of the northeast (Metzger 1990). Carpinus thrives in areas with plentiful soil moisture and drainage suitable to minimize soil saturation and anoxia during the growing season (Beals and Cope 1964, Metzger 1990). Carpinus is less plentiful in mesic and xeric areas and is most abundant in the ecotone between wet and mesic sites (Metzger 1990). However, it is able to flourish on wetter sites as well, as long as the soil does not become too saturated during the growing season (Chambless and Nixon 1975, Metzger 1990). It is most abundant in the southern portion of its range (Metzger 1990).

In addition to site characteristics, it is also important to examine the history of an area when studying Carpinus. According to Delcourt and Delcourt (1977), Metzger (1990), and Hodges (1995), preferential logging of certain species in the past may
promote growth of and result in a dense canopy of *Carpinus*. In a study of second or third growth wet hardwood flats in North Carolina and Virginia, Rheinhardt and Rheinhardt (2000) suggest that canopy sized (greater than 15 cm dbh) *Carpinus* in some stands were vestiges of past logging. They found that *Carpinus* was likely to be a dominant species in greater than 60% of the stands in which it occurred (Rheinhardt and Rheinhardt 2000).

Although there is evidence of logging in the Neches Bottom site circa 1905 (Streng et al. 1989), the dominance of *Carpinus* is not unique to only this area of the Neches Bottom. Other studies conducted in east Texas have found similar stands in which *Carpinus* was the dominant tree without logging (Nixon and Raines 1976, Nixon et al. 1977). Other studies in Texas, Florida and North Carolina also place *Carpinus* among the dominant trees (Monk 1965, Sullivan and Nixon 1971, Nixon et al. 1973, Nixon and Willett 1974, Chambless and Nixon 1975, Greller 2004).

*Carpinus* has relatively light seeds that are fairly well dispersed (Streng et al. 1989). It is an aggressive species that typically responds quickly to forest disturbances, leading to an increase in importance (Putnam et al. 1960, Metzger 1990). Batista and Platt (2003) found that *Carpinus* incurred very little damage from a hurricane, perhaps because it is windfirm (Metzger 1990), and responded to the event with some release of understory trees and saplings and increased recruitment (Batista and Platt 2003).

One of the largest specimens on record reached 20 m in height and 70 cm in DBH, although the typical size for large trees is around 11 m in height and 25 cm DBH (Metzger 1990). *Carpinus* is shade tolerant (Metzger 1990, McKnight et al. 1981) and is classified as flood intolerant to intermediately flood tolerant (Hall et al. 1946, Teskey and
Hinckley 1977, Whitlow and Harris 1979, McKnight et al. 1981). One study (Lin et al. 2004) that examined growth and survivorship of floodplain species in the Neches Bottom study site found that growth responses to light aligned with the expectation that shade intolerant species grew faster than shade tolerant species. The mortality risks for shade tolerant species *Carpinus* and *A. rubrum* were unexpectedly high due to the extra sapling mortality caused by flooding (Lin et al. 2004).

III. *Ilex decidua*

*Ilex decidua* Walt. (deciduous holly) belongs to the Aquifoliaceae. It ranges from Maryland south along the Atlantic Coastal Plain to Florida, west to eastern Texas, and north along the Mississippi Valley to southern Illinois. *I. decidua* is commonly found in moist sites alongside streams and swamps (Little 1996).

This species has relatively light seeds and is a good disperser (Streng et al. 1989). Under favorable conditions, it may grow to around 6 m in height and 15 cm DBH (Little 1996). It is classified as being shade tolerant (Gilman and Watson 1993) and moderately to very tolerant of flooding (Teskey and Hinckley 1977, Whitlow and Harris 1979).

IV. *Liquidambar styraciflua*

*Liquidambar styraciflua* L. (sweetgum) belongs to the Hamamelidaceae. In the United States, it ranges from southern Connecticut south to central Florida, throughout the southeast, west to eastern Texas, and as far north as southern Illinois (Kormanik 1990). *Liquidambar* thrives in several different habitats, including clay and loamy bottomlands and uplands (Kormanik 1990).

*Liquidambar* has relatively light seeds and is a good disperser (Streng et al. 1989). It begins to reproduce when it reaches between 20 and 30 years old and ceases
reproduction sometime after reaching 150 years old. Vegetative reproduction may be important in this species. Some studies have shown that it can regenerate from root sprouts as a result of suppressed bud release (Kormanik 1990). *Malacosoma disstria* (Forest tent caterpillar) is known to defoliate *Liquidambar* (Kormanik 1990, Hall 1993). *Liquidambar* is classified as shade intolerant (McKnight et al. 1981, Kormanik 1990) and moderately to very tolerant of flooding (Hall et al. 1946, Teskey and Hinckley 1977, Whitlow and Harris 1979, McKnight et al. 1981). Under flooded conditions, it forms succulent soil roots (Hook 1984b).

V. *Quercus michauxii*

*Quercus michauxii* Nutt. (basket oak, swamp chestnut oak) belongs to the Fagaceae. It inhabits wet loamy bottomland areas, streamside regions, and the perimeters of swamps. The native range for *Q. michauxii* extends from New Jersey and eastern Pennsylvania along the Atlantic coast to the northern tip of Florida and west to eastern Texas. Humid, temperate climates are optimal for *Q. michauxii* growth. This species flourishes on well-drained areas with silty clay soils and loamy terraces as well as rocky stream bottoms. In addition, it is widespread on loamy first-bottom ridges (Edwards 1990).

Mature *Q. michauxii* trees may have DBH values between 61-91 cm and reach over 30 m in height (Edwards 1990). A heavy-seeded species, *Q. michauxii* is a relatively poor disperser (Streng et al. 1989). *Q. michauxii* is intolerant (Edwards 1990) to moderately intolerant (McKnight et al. 1981) of shade and requires light gaps for growth (Edwards 1990). This species has been classified as weakly tolerant (McKnight et al. 1981), intolerant (Teskey and Hinckley 1977), and moderately tolerant of flooding..
(Hall et al. 1946). It has been suggested that this species may have an allelopathic effect on understory vegetation when it is mature (Edwards 1990, Rathinasabapathi et al. 2005).

VI. *Quercus nigra*

*Quercus nigra* L. (water oak) belongs to the Fagaceae. It is commonly found along streams or rivers in the southeast and survives in moist floodplain forests as well as drier uplands. This species ranges from eastern Virginia, south to mid-Florida, and west to east Texas (Vozzo 1990). *Q. nigra* produces acorns after it is 20 years old. These large seeds are typically dispersed over short distances (Vozzo 1990). In one study, *Q. nigra* tended to have higher seedling survivorship than several other species (Streng et al. 1989).

A medium sized tree, *Q. nigra* can reach up to 38 m in height (Vozzo 1990). It is classified as shade intolerant (McKnight et al. 1981, Vozzo 1990) and classifications of flood tolerance range from weakly tolerant to tolerant (Hall et al. 1946, Teskey and Hinckley 1977, Whitlow and Harris 1979, McKnight et al. 1981).

VII. *Sapium sebiferum*

*Sapium sebiferum* (L.) Roxb. (Chinese tallow) belongs to the Euphorbiaceae. It is an invasive species originally from China. In the continental United States, it now ranges from North Carolina, south to northern Florida, and west to eastern Texas (Little 1996). It has recently been found in California as well (California Invasive Plant Council 2005). It has also been introduced in Hawaii (Siemann and Rogers 2003c). It is commonly found at low elevations (Little 1996).

*Sapium* was introduced to the United States in 1772 and has more recently become a major problem as an invasive in the southeast (Bruce et al. 1997). This fast-
growing species often forms monocultures. It can reach 9 m in height and 15 cm DBH under favorable conditions (Little 1996). *Sapuum* grows well under several light conditions (Jones and McLeod 1989, Hall 1993, Rogers and Siemann 2003) and is classified as very tolerant of flooding (Jones and Sharitz 1990, Conner 1994, Butterfield et al. 2004). Two adaptations *Sapuum* has to survive flooding for long periods of time are hypertrophied lenticels and succulent soil roots (Conner 1994).

VIII. *Taxodium distichum*

*Taxodium distichum* (L.) Rich. (bald cypress) is a member of the Taxodiaceae. The range for *Taxodium* extends from southern Delaware south along the Atlantic Coastal Plain to southern Florida and west along the Gulf Coastal Plain to eastern Texas and north along the Mississippi Valley to southern Illinois (Wilhite and Toliver 1990). This species flourishes in low elevations on poorly drained sites characterized by frequent flooding.

*Taxodium* has large seeds that are dispersed mainly by animals and water (Wilhite and Toliver 1990). Height growth in *Taxodium* ceases after 200 years. This large conifer reaches 22 to 37 m in height. Some trees develop lateral roots from which “knees” protrude (Wilhite and Toliver 1990). It is classified as having an intermediate shade tolerance (McKnight et al. 1981, Wilhite and Toliver 1990,) and being tolerant to very tolerant of flooding (Hall et al. 1946, Teskey and Hinckley 1977, Whitlow and Harris 1979, McKnight et al. 1981). This species forms succulent soil roots under flooded conditions (Donovan et al. 1988). It is also known to form adventitious roots in response to flooding (Hook 1984b).
Appendix E

*Carpinus* age estimation

Brown (1919) calculated the average amount of time spent in each size class
based on average rate of growth and estimated the rate of growth of tree species over
their lifetime. Similarly, Nicholson (1965) calculated the average growth rate per size
class per year. From that he calculated average time in each size class and summed over
classes to obtain an estimate of age. Since some trees die before reaching the next size
class, Nicholson (1965) also calculated tree ages that only included the fastest growing
trees equal in number to the abundance of individuals in the next larger class.
Additionally, he calculated ages corrected for fast growing trees that have dramatic
changes in growth rate depending on environmental conditions, and thus no real size
class dependent growth rate. In these cases, Nicholson (1965) used the maximum growth
rate per size class that estimated the minimum age of these species. Lieberman and
Lieberman (1985) created growth curves using the average annual growth per size class.
Their simulation growth curves incorporated the variance in the data and provided growth
trajectories that displayed ranges of ages for the tree species depending on DBH. They
found that deterministic techniques, like those of Brown (1919) and Nicholson (1965),
provide reasonable estimates of age as long as the size classes are appropriate for the
species and the "best" data (e.g. Nicholson 1965) are used.

APPENDIX F

Comparing elevation measurements of 1989 and 2005

Relative elevation was measured in 2005 for comparison to the relative elevation
in 1989 (Hall 1993). This was in order to establish whether or not changes in elevation
occurred at the study site between 1989 and 2005. The 1989 elevation data (Hall 1993) were compared to 2005 elevation data. Hall (1993) measured water depth every 20 m at plot corners on the flat surface and every two meters in the slough areas. Relative elevation, measured in cm, was obtained by subtracting the water depth at each location from the maximum water depth (Hall 1993). Elevation data for 2005 were collected on two trips in May for approximately 470 locations using a slip-leg tripod and measuring rod. Subtracting the 2005 data from the smoothed Hall (1993) data gave a range of elevation differences. The average of these differences was used to compare the 1993 (Hall) and 2005 measurements. This was done in order to standardize the data since two different methods were used to obtain relative elevation data. The 1993 (Hall) data minus the sum of the 2005 data and the average difference of the two datasets is displayed in Figure 28. The biggest change over the 17-year period is that one main part of the slough appears to have decreased in elevation since 1993, displayed by the positive values on the graph (Figure 28). Another area within the slough is filling in with sediment, resulting in higher relative elevations at those areas in 2005 (negative values, Figure 28).

I do not expect these two changes to have major effects on the current flooding impact at the Neches Bottom site. The area surrounding the location where the slough has filled in with sediment may experience increased flooding since there is less area for water at that location to remain in the slough. On the other hand, the area surrounding the location where the slough has deepened may experience less flooding because there is a greater amount of area for water to remain in the slough.
For reference purposes, green squares and pink diamonds indicate the 2004 locations of the tripod measuring stations and individual measurements, respectively, in Figure 28. The location of slough tree species *Taxodium distichum* (bald cypress) and *Nyssa aquatica* (water tupelo) are displayed by blue triangles and red circles, respectively. Only large trees greater than 20 cm DBH in 1994 are included.
Figure 28. The difference in elevation* between Hall (1993) data and 2005 data.

*Elevation difference: Hall (1993) data minus [Mann and Harcombe 2005 data + 135.73 cm], where 135.73 cm equals the average absolute difference of smoothed Hall data minus Mann and Harcombe data.
APPENDIX G

Permanent pathogens of hardwoods in eastern forests

Diseases are one factor that may cause species population decline. According to Horst (1979), three pathogens of Carpinus have been found in Texas, although it is possible that not all pathogens that can affect Carpinus have been documented. Microsphaera alni and Phyllosticta corylea cause powdery mildew on Carpinus, as well as on several other species. The United States Forest Service lists powdery mildew as a disease of minor importance. Powdery mildew may result in distorted leaves that fall prematurely (USFS 2004). Since this disease does not result in tree mortality, it is not a likely candidate for the decline in Carpinus at the study site. However, powdery mildew has been known to cause mortality in poor conditions (E. Siemann personal communication).

Phymatotrichum omnivorum, also known as Texas or cotton root rot, is the third pathogen known to affect Carpinus in Texas (Horst 1979). Phymatotrichum attacks over 2000 plant species, including Liquidambar, Taxodium, Sapinum, and members of the genus Acer in Texas (Horst 1979, Sinclair et al. 1987). This soil-borne fungus thrives in alkaline soils and is active most at temperatures ranging between 15-35°C (Sinclair et al. 1987). The disease occurs in isolated pockets that tend to expand over time, but is not readily spread from one place to another (Sinclair et al. 1987, Goldberg 1999). Evidence of the disease begins with a slight yellowing of the leaves and progresses quickly; leaves soon turn bronze and wilt (Goldberg 1999). Permanent wilting occurs in a minimum of 2 weeks (Goldberg 1999). The leaves of trees killed by the disease stay firmly attached, and fungal strands are present on infected roots (Goldberg 1999). In some cases, a
reddish lesion forms around the crown of dead trees (Goldberg 1999). Weakened trees may die within weeks after the start of the disease, while others may live for years with the disease (Sinclair et al. 1987). Trees living with the disease may display stunted growth, yellowing, and dieback in the year or more preceding death (Sinclair et al. 1987).

It is unlikely that Texas root rot caused the decline of *Carpinus* in the Neches Bottom. In the spring of 1993 during the *Carpinus* die-off, David Appel, Professor of Plant Pathology, Texas A&M University, visited the site and found no evidence of pathogens or symptoms of disease (P. Harcombe personal communication). If the *Carpinus* population had been infected with Texas root rot, lesions should have been spotted on at least some of the dead and dying trees. This was not the case. Another factor pointing away from root rot as the culprit is that this disease affects so many species other than *Carpinus*. If the disease were present, other species should also be experiencing declines as well. According to Horst (1979), vegetation is typically killed in a ring-like pattern, reaching for a few yards to over an acre in size. This is not the case in the Neches Bottom. In addition, the fungus requires alkaline soils low in organic matter (Goldberg 1999). Although the soils in the Neches Bottom are low in organic matter (Caird 1996), they are also acidic, with a pH between 4.5 and 5.0 (Hall 1993).

In order to further the investigation of pathogens as a source of *Carpinus* mortality, selected diseases known to cause large episodes of mortality in eastern forests have been reviewed through a literature search. This review evaluates the typical patterns associated with pathogen-related decline in order that a comparison may be made with the pattern of mortality exhibited by the *Carpinus* in the Neches Bottom study site.
I. Beech bark disease

Beech bark disease begins when *Cryptococcus fagisuga*, a scale, attacks and alters the bark of *Fagus grandifolia*. Next, a fungus, *Nectria coccinea* var. *faginata* or *N. galligena*, invades and kills the tree (Latty et al. 2003).

In Europe, trees were dying from the disease before 1849. In 1911, an introduction occurred in Nova Scotia (Houston 1994). By 1932, the disease had spread throughout mature stands in the Maritime Provinces and isolated cases were found in Maine and eastern Massachusetts. Since then, the disease has spread to the north into Quebec, throughout New England, New York, New Jersey, Pennsylvania and West Virginia (Houston and O’Brien 1983).

There is a pattern to the spread of the disease. Initially, sites typically characterized by large, old trees sustain sparse, growing beech scale populations. Once the scale populations become large, the *Nectria* pathogens invade the infested trees, often resulting in greater than 50% mortality in trees exceeding 10 inches in diameter (Houston 1994). The limited dispersal of the disease results in heavy mortality in clumped areas of trees. In addition, large trees are more susceptible than small trees. The previous two attributes result in mortality tending to reduce clumping in a stand and result in a more random distribution of canopy trees (Runkle 1990). Diseased trees can survive for years after the infection. Trees not infected benefit from gaps resulting from mortality of canopy trees (Runkle 1990).

Beech bark disease is more severe in trees with higher bark nitrogen concentration (Latty et al. 2003). Old growth forests are more likely to be infected than second growth forests, because older trees are more likely to have higher bark nitrogen concentrations
than younger trees (Latty et al. 2003). Resistant trees have been found to have lower concentrations of nitrogen in their bark. Trees with higher concentrations are a higher quality food source for the beech scale insects and heavy infestation rates permit greater infection by *Nectria* (Latty et al. 2003).

II. Chestnut blight

In the late 1800s, the range of *Castanea dentata* extended from Alabama into New Hampshire, Vermont, and Maine. To the west, it expanded into southern Ontario, Ohio, southern Indiana, and Tennessee. Despite a shrinking range in Alabama due to a root fungus (*Phytophthora cinnamomi*) from 1825-1875 and in certain areas of the North Carolina Piedmont due to unknown factors, *C. dentata* flourished elsewhere. In several forests, *C. dentata* was a dominant species (Russell 1987). Chestnut blight was first discovered in New York in 1904. The fungus *Cryptonectria parasitica*, native to either Japan or China, was the culprit (Scheffer 1997). The disease spread 25-30 miles per year, invading 10 states by 1910 (Brewer 1995). By the 1950s every natural stand of *C. dentata* was destroyed, killing approximately 3.5 million trees in 50 years (Brewer 1995, Scheffer 1997). Over a 19-year period in one North Carolina stand, *C. dentata* decreased by 98% in basal area and 91% in abundance (Nelson 1955). It had originally comprised 41% of the stand basal area; after reduction by the blight it comprised less than 1% (Nelson 1955). Even before the blight, *C. dentata* reproduced predominately via sprouting. This method of reproduction has resulted in cycles of infection-death-sprouting-infection that take approximately 10 years in sun conditions and up to 40 years under shade conditions (Anagnostakis 2000). Thus, *C. dentata* still persists today, but in much smaller numbers than pre-blight.
III. Dutch elm disease

The fungus *Ophiostoma ulmi* causes Dutch elm disease. First found in Ohio in 1930, it did not spread from this site. New York was the place of first establishment of the virulent form in 1933. (At a later time, a successful invasion occurred in Quebec as well.) A vector, the European bark beetle (*Scolytus multistriatus*), was already present in New York since before 1900. This may have contributed to the establishment of the disease there (Scheffer 1997). Dutch elm disease affects all elm species, but *Ulmus americana* is the most susceptible. The disease is capable of killing branches and trees within a few weeks or years from the start of infection. The disease first appears on branches then spreads to other parts of the tree (Agrios 1997).

IV. Dogwood anthracnose

Dogwood anthracnose is a disease caused by a fungus of unknown origin, *Discula destructiva* (Jenkins and White 2002). This disease was first found in the United States in 1976. It occurs on several species of dogwood, but the major hosts are *Cornus florida* and *C. nuttallii*. The disease spreads rapidly; first found in Vancouver in 1976 on *C. nuttallii*, it spread to Oregon, British Columbia, and northern Idaho by 1983. After identification in New York, Connecticut, Pennsylvania, and New Jersey in 1983, the disease spread to six more states by 1987 (Daughtrey and Hibben 1994). Dogwood anthracnose causes high mortality; it increased mortality in Catoctin Mountain Park, Maryland from 33% in 1984 to 79% in 1988. In the Great Smoky Mountain National Park, the number of plots with a severe epidemic increased by 638% in the period of 1988-1991 (Daughtrey and Hibben 1994).
In conclusion, the episode of mortality in the Neches Bottom *Carpinus* population does not seem to have a disease related pattern, but this cannot be determined directly without evidence of pathogen or disease presence or absence before or after the decline. Many of these major tree diseases affect several species, but one more so than others. There have been no other species in the Neches Bottom also suffering from increased mortality levels. In addition, although several of the tree diseases reviewed also result in extensive mortality across large distances. However, there are no known reports of increased mortality of *Carpinus* trees elsewhere in the southeast Texas area. This could be due to a lack of similar *Carpinus* mortality elsewhere, or due to a lack of reported information.

**APPENDIX H**

**Episodic mortality**

Insect pests can cause declines in tree populations, especially during outbreaks. Since the Neches Bottom forest was not monitored on a weekly basis prior to or following the 1989 flood, it is possible that an insect outbreak occurred on the *Carpinus* population. Such an attack might have caused the trees to weaken and become more susceptible to flooding or die. Known insect outbreaks in the Neches Bottom study area include *M. disstria*, forest tent caterpillars, and *Datana* species, walnut caterpillars (Hall 1993, Siemann and Rogers 2003a). To further evaluate insects as a reason for *Carpinus* mortality, I reviewed the literature on two pests known to have outbreaks in eastern forests. This review examines the typical patterns associated with pest related decline in order that a comparison may be made with the pattern of mortality exhibited by the *Carpinus* in the Neches Bottom study site.
I. Gypsy moth

The gypsy moth, *Lymantria dispar*, is a European native that has infested parts of North America. Introduced to the United States in 1869, outbreaks of these moths have caused extensive mortality of trees via defoliation. Defoliation by gypsy moth caterpillars also results in decreases in tree growth, flowering, and fruiting (Davidson et al. 1999).

The densities of gypsy moth populations cycle, characterized by long periods of low density, followed by sudden, rapid increases to high densities that may be sustained for a long time until the population crashes. A tree’s response to defoliation depends on the species, as well as the intensity, duration, and frequency of defoliation, along with the tree’s physiological condition at the time of defoliation. A tree’s response to defoliation can also depend on the presence of harmful secondary-action organisms, like some species of fungi (Davidson et al. 1999).

Suppressed and intermediate trees are often killed after one defoliation (Campbell and Sloan 1977). One study found that the oak trees with better crown conditions incurred less mortality (7% after one defoliation; 22% after two defoliations) than oaks with poor crowns (36% after one defoliation; 55% after two defoliations) (Campbell and Sloan 1977).

II. Forest tent caterpillar

The forest tent caterpillar, *Malacosoma disstria*, is a native pest of the United States and Canada (Dajoz 2000). A study of a Louisiana swamp (Conner and Day Jr. 1976) reported forest tent caterpillars as being the dominant insect grazer. The most heavily grazed species was *Nyssa aquatica*, while *Liquidambar, Salix nigra* (black
willow), *Carya illinoensis* (pecan), and “oak” (this site contained *Q. nigra* and *Q. nutallii* [Nuttall oak]), were less affected (Conner and Day Jr. 1976). Hodson (1941) reported defoliation of *Quercus* species, *Carya* species, and *Nyssa sylvatica* (black tupelo) in Virginia in 1930. In a study of an outbreak in Minnesota the caterpillars avoided *A. rubrum*, but preferred *Populus tremuloides* (aspen). Other species readily consumed included *A. saccharum* (hard maple), *Tilia americana* (basswood), *Q. borealis* (red oak), *Q. macrocarpa* (bur oak), *Betula papyrifera* (paper birch), and *Ulmus americana* (American elm) (Hodson 1941).

*M. disstria* have a cyclic pattern of major outbreaks, occurring every 7 to 11 years (Hodson 1941). In the Neches Bottom study site, these outbreaks occur annually (E. Siemann personal communication). Conner and Day Jr. (1976) claimed that insect grazing may be a reason that *Taxodium distichum* was the historical dominant in the swamp, giving it a competitive advantage over *N. aquatica*. They further asserted that the increased severity of tent caterpillar attacks in this forest was due to an increase in *N. aquatica* resulting from selective logging of *Taxodium*. However, the authors noted that the timing of the tent caterpillar outbreak is important to tree survival. Outbreaks in the early spring may result in negligible tree damage since early production is supported by carbohydrate reserves (Reichle et al. 1973), while later outbreaks may be more damaging since production is supported by the tree’s photosynthetic biomass (Conner and Day Jr. 1976).

During the 1989 flood, Hall (1993) described an outbreak of *M. disstria* at the Neches Bottom site, taking place between the end of the flood in August and October 1. She estimated damage on the major sapling species, separating the damage from
caterpillars and flooding. Browed or missing leaves were classified as flood damage, while caterpillar damage was identified by the presence of caterpillars, webs, and remaining parts of the mid-rib or rachis. Individual saplings were placed into one of six classes based on the level of defoliation. Undamaged individuals were classed as zero while individuals that lost all leaves, were totally destroyed, or missing were placed in class five. The increments between classes 1-4 represented 20% of leaf area lost or destroyed (Hall 1993). She found little damage done by forest tent caterpillar herbivory on Carpinus. Liquidambar incurred more caterpillar damage than other species and several species were avoided, including Sapium.

The effects of defoliation depend on the length of an outbreak, the condition of the tree before pest attack, the time of year, other concurrent stressors (such as flooding or drought), and the severity of defoliation (Reichle et al. 1973, Davidson et al. 1999). If a species causing defoliation similar to that caused by the Lymantria dispar attacked Carpinus trees after the flood already weakened them, it is a possibility that they would have died. However, there are no known pests specific to Carpinus caroliniana in east Texas. It may be unlikely that such a scenario occurred.

APPENDIX I

Climate

As the Earth warms due to the increase in global atmospheric greenhouse gases, there is a possibility that forests will undergo major changes, such as shifts in species composition (Box et al. 1993, Iverson and Prasad 1998). The western boundary of Carpinus caroliniana’s range is in east Texas (Furlow 1987). Carpinus grows throughout the southern United States, but is missing south of Missouri around the
Mississippi bottomland, the southernmost portion of the Gulf Coastal Plain, and the southern two-thirds of Florida (Metzger 1990).

The average rainfall for the study site area is 1457 mm/yr (NCDC 2004, 40-year record for Beaumont Research Center). The average annual temperature is 20.1°C (NCDC 2004, 40-year record for Beaumont Research Center). Tree growth in the southeast Texas is affected by temperature, precipitation, soil moisture, and water deficit (Winters 1995). Of the major Neches Bottom tree species, *Carpinus* has the shortest growing season, starting last and ending first (Winters 1995, Figure 27). Winters (1995) found that the growth of trees at the Neches Bottom site was limited by excess soil moisture and temperature. She inferred that higher temperatures might induce an earlier start to the growing season. Hall and Harcombe (2001) also found that climate affects species at the study site. Using the Palmer Drought Severity Index to represent soil moisture content, they found that recruitment was higher in wetter years than drier years (Hall and Harcombe 2001). Since it has been found that climate does affect the Neches Bottom vegetation, examination of the literature for predictions regarding the response of *Carpinus* to climate change is warranted.

In order to examine the optimal conditions for various vegetation species, Box et al. (1993) defined a ‘climatic-envelope’ as the geographic range in which a species naturally grows and reproduces. The envelope is defined by several variables, including the mean temperature of the warmest and coldest months, average precipitation for the driest and warmest months, and the coldest temperature ever measured. Recent calibrations for eastern North America define the optimal range for *Carpinus* as having mean temperatures in the warmest months between 18 and 30°C, average precipitation
during the driest month with a minimum of 20 mm, average precipitation during the warmest month with a minimum of 30 mm, and an absolute minimum temperature of between -10 and -40°C (E. Box personal communication).

The values for the study area fall within these limits. The mean temperature in August is 28 °C, and the mean temperature in January is 11 °C (NCDC 2004, 40-year record for Beaumont Research Station). The average precipitation is 80 mm during the driest month and 105 mm during the warmest month (NCDC 2004, 40-year record for Beaumont Research Station). The absolute minimum temperature is -13 °C (Texas A&M University 2004, 34-year record for Beaumont Research Station).

The temperatures preceding and following the 1989 flood were near the normal monthly mean of 1978-2004 (Figures 18 and 19). According to the Palmer Drought Severity Index (PDSI), there was a drought preceding the flood in 1989 (NOAA 2006, Tables 13 and 14). Precipitation near the study site ranged from 16-50% of the 30-year normal monthly mean (1971-2000) from July to December 1989 (Table 23). Precipitation patterns near the study site did not follow closely with the estimated PDSI in the study site area (Tables 12, 13, and 23). This may be due to the PDSI calculation being a combination of temperature, precipitation, and Available Water Content of the soil. The lack of correspondence between PDSI and precipitation could also be due to the unspecified time scale used by PDSI, which can be misleading. In addition, PDSI is sensitive to the available water content of a soil type, so generalized regional results may not be applicable in all areas within the region. It has been suggested that PDSI does not work well in places where rainfall or runoff is variable (Hayes 2006).
Iverson and Prasad (1998) examined various models based on climate and geography to estimate the potential impact of climate change on species ranges. According to these models, *Carpinus* is not expected to be negatively affected in the study site area (Prasad and Iverson 1999).

Some criticism of models that examine climate and forest change note the common assumption that tree species occur only in areas where they are able to survive, and they are not able to survive outside of the climatic conditions of their present range. The models used by Iverson and Prasad (1998) address this problem by incorporating a wide range of variables and they try to only estimate potential shifts in range due to climate change. Their models assume that there are no barriers to migration (Iverson and Prasad 1998).

In conclusion, although many plant species’ ranges may shift due to changes in climate, *Carpinus* is not expected to be strongly affected by these changes. To the contrary, the range for *Carpinus* is actually expected to expand given the current climatic trends (Iverson and Prasad 1998, Iverson and Prasad 2002).

**Table 23.** Drought interval (3+ months of <75% of the normal amount of precipitation 1971-2003) and percentage of the normal precipitation between 1970-1996 for Beaumont Research Center (NOAA).

<table>
<thead>
<tr>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>April-August 1985</td>
<td>28-73</td>
</tr>
<tr>
<td>April-June 1988</td>
<td>16-50</td>
</tr>
<tr>
<td>July-December 1989</td>
<td>32-65</td>
</tr>
<tr>
<td>August-November 1991</td>
<td>44-70</td>
</tr>
<tr>
<td>July-October 1992</td>
<td>41-69</td>
</tr>
</tbody>
</table>
APPENDIX J

Tropical Storm Allison

The stalling of Tropical Storm Allison over southeast Texas led to heavy rainfall from June 25 through June 30, 1989. According to the National Climatic Data Center (2005), close to 38.1 cm of rain fell over the Evadale area during this storm event. As the storm approached the Neches Bottom area, the winds were 30-35 mph.

Water was released from Lake Rayburn from May 25 through June 27, 1989. It was released at a maximum of 306 m³/s from June 22 through June 26. Following the storm, Rayburn released flows exceeding 325 m³/s from July 16 through August 6, peaking at 546 m³/s on July 18 (U.S. Army Corps of Engineers 2005). This second release resulted in an extended duration of high flows downstream at Steinhagen Reservoir and Evadale after the storm event.

Although the Steinhagen Reservoir continually released water from its gates throughout the year prior to Allison, the amount released during and following the storm event was elevated. This excess water was released from Steinhagen June 28 through July 10, but the flow exceeded the necessary level to flood the study site sloughs from June 21 through August 6. On July 3, the maximum gated flow reached 1320 m³/s (USGS 2004, see Figure 17).

Steinhagen Reservoir is not used for flood control due to a small amount of storage; water flows over the crest of the dam during periods of heavy rains or upstream releases (Floyd Boyett, Army Corps of Engineers Park Ranger, Town Bluff Dam/B.A. Steinhagen Reservoir personal communication). Steinhagen is used to impound and re-regulate power releases from Sam Rayburn Dam, to generate hydroelectric power, and to
supply water for human uses (U.S. Army Corps of Engineers 2006). According to Paul
Rodman, Chief of Reservoir Control at Sam Rayburn Dam, the Army Corps of Engineers
avoids exceeding flows of 566 m$^3$/s (20,000 ft$^3$/s) at B.A. Steinhagen Reservoir and of
425 m$^3$/s (15,000 ft$^3$/s) at Sam Rayburn Dam in order to prevent flooding populated areas
downstream. Sam Rayburn Dam is used for various human uses, hydroelectric power
generation, and flood control (Angelina and Neches River Authority 2006). In addition,
water is released from Sam Rayburn Dam when the Lower Neches Valley Authority
requests salt water intrusion control in Beaumont (F. Boyett personal communication).

**APPENDIX K**

**Pre-flood decline**

The pre-flood decline did not differ between elevation zones ($X^2= 4.999, p>0.05,$
Figure 29). The fraction of 2.0-4.5 cm DBH *Carpinus* saplings dying per plot in 1981-
1989 was greater in plots that had more *Carpinus* stems in 1980 ($R^2=0.202, p<0.001$, see
Figure 30). Other comparisons of *Carpinus* sapling and tree interspecific and
intraspecific competition at the plot level had weak correlations ($R^2 <0.05$) and are not
included.
**Figure 29.** The abundance of the 1980 *Carpinus* population, 4.5 cm DBH and greater, is compared with the abundance in 1994. Percent surviving is indicated above the bars for each zone.

**Figure 30.** The fraction of 2.0-4.5 cm DBH *Carpinus* saplings dying in 1981-1989 versus *Carpinus* stems per plot in 1980. Plots without 2-4.5 cm *Carpinus* saplings are not included.
APPENDIX L

Time to *Carpinus* death

For dead *Carpinus* stems, it appears that death was not uniformly distributed in time between 1989 to 1994 for the three lowest elevations (Figure 31). The majority of stems that died in the slough area after the flood died in 1990 ($X^2 = 49.4, p > 0.01$). The majority of stems that died in the site lows died in 1991 ($X^2 = 86.4, p > 0.01$). Most of the stems that died in the flats died in 1991 and 1992 ($X^2 = 134.7, p > 0.01$). The distribution of mortality in the highest areas also varied significantly among years, but most of the death occurred during three years, 1990-1992 ($X^2 = 24.1, p > 0.01$).

There may be an explanation why the highest areas did not follow suit. It is possible that the risk of mortality due to the flood was lower in this zone, and the deaths in this zone were also influenced by factors other than the flood. The lower risk of mortality in the highest elevation zone relative to the other zones during the flood interval supports this explanation (Figure 9b). If flooding did not increase the mortality in the highest areas, then mortality during the flood interval should not have been increased very much relative to previous intervals. This can be examined by comparing the annual mortality levels before and after the flood. In the periods before the 1990-1994 interval, the average mortality rate in the highest areas was 0.032. In the 1990-1994 interval, the mortality rate was 0.054. This shows that the mortality during the flood interval in the highest elevations zones was not particularly elevated relative to the previous interval. Therefore, the highest areas would not be expected to follow the same patterns that are displayed in the lower elevation zones where mortality was increased due to the flood.
Figure 31. The death by year and elevation zone of Carpinus stems that died during the flood interval (1990-1994).

APPENDIX M

Probability of death analysis

In order to better interpret the graph of points and smoothed curves based on the Genmod model using the size and elevation of trees that lived or died in each interval, I created a dataset with DBH (cm) datapoints ranging from 4.5-35 cm in 0.1 cm increments. Each DBH value was combined with every possible plot elevation. I applied the logistic regression equation from the Genmod analysis to these data and obtained a “fuller” representation of the model (Figure 32). This “fuller” representation of the model enabled me to choose the best-matching smoothing function in SigmaPlot. I found the best smoothing function to be the Loess function, a tricube weight function of a polynomial degree of 1. The “fuller” graphs did not exceed a probability of death equal to 1.0 (Figure 32), unlike the graphs using the actual data with the Loess smoothing function (Figure 9). The fuller graphs do not show where the actual stems were located.
Actual stem location is helpful in interpreting the models’ results, therefore the graphs of Figure 9 are still preferable to the graphs of Figure 32.

I also used the Genmod procedure in SAS to calculate logistic regression models based on only DBH (cm) or elevation (cm). This allowed me to see the relationship between the probability of death and only a single variable. I compared the results of these models to the interaction model. For the pre-flood interval, I found that with increasing elevation the probability of death significantly increased ($X^2_1 = 4.54$, $p<0.05$, Figure 33a). These results partially supported the interaction model; the small stems in the interaction model had an increasing probability of death with increasing elevation (Figure 9a). The model based on only DBH (cm) was not significant ($X^2_1 = 1.60$, $p=0.2056$) in the pre-flood interval (Figure 33b).

For the flood interval, I found that the probability of death significantly decreased with increasing elevation ($X^2_1 = 52.27$, $p<0.0001$, Figure 34a). The interaction model shows the similar trend of decreasing probability of death at higher elevations as the elevation-only model. The DBH only model showed an increasing probability of death with larger DBH (cm) ($X^2_1 = 48.61$, $p<0.0001$, Figure 34b). The interaction model showed a similar trend, except at the highest elevations.

The probability of death significantly increased with elevation post-flood ($X^2_1 = 6.10$, $p<0.02$, Figure 35a). The probability of death also significantly increased with DBH (cm) ($X^2_1 = 69.26$, $p<0.0001$, Figure 35b). Although the interaction model shows increasing probability of death at larger DBH (cm), the model was not significant.
Figure 32a-c. The probability of death for all combinations of DBH (cm) and elevation (cm). Panels show the (a) pre-flood interval, (b) flood interval, and (c) post-flood interval.
Figure 33a-b. The probability of death in the pre-flood interval by (a) elevation or (b) DBH.
Figure 34a-b. The probability of death in the flood interval by (a) elevation or (b) DBH.
Figure 35a-b. The probability of death in the post-flood interval by (a) elevation or (b) DBH.
APPENDIX N

Impoundments

The Neches River flows for 670 km, beginning 97 km southeast of Dallas, TX and emptying into Sabine Lake near Port Arthur, TX (Lower Neches Valley Authority 2005, Figures 36-37). It has a drainage area of 26,234 km² (The Texas State Historical Association 2002). The Angelina River is 394 km long and has a drainage area above the confluence of 9,257 km². The Angelina enters the Neches River at km 203 (Lower Neches Valley Authority 2005). There are several impoundments on the Neches River (Table 24).

Table 24. Impoundments on the Neches and Angelina Rivers above the study site (The Texas State Historical Association 2002).

<table>
<thead>
<tr>
<th>Impoundment</th>
<th>Distance from site (km)</th>
<th>Surface acres</th>
<th>Year completed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lake Steinhagen</td>
<td>40</td>
<td>13,700</td>
<td>1951</td>
</tr>
<tr>
<td>Lake Rayburn</td>
<td>71</td>
<td>114,500</td>
<td>1965</td>
</tr>
<tr>
<td>Lake Kurth</td>
<td>127</td>
<td>770</td>
<td>1961</td>
</tr>
<tr>
<td>Lake Striker</td>
<td>187</td>
<td>2,400</td>
<td>1957</td>
</tr>
<tr>
<td>Lake Jacksonville</td>
<td>201</td>
<td>1,320</td>
<td>1959</td>
</tr>
<tr>
<td>Lake Athens</td>
<td>205</td>
<td>1,520</td>
<td>1962</td>
</tr>
<tr>
<td>Lake Palestine</td>
<td>220</td>
<td>25,560</td>
<td>1962</td>
</tr>
<tr>
<td>Lake Tyler</td>
<td>239</td>
<td>2,450</td>
<td>1949</td>
</tr>
</tbody>
</table>
Figure 36. The watersheds of east Texas (modified from U.S. Army Corps of Engineers 2005).

Figure 37. The Neches watershed, including the two major impoundments above the study site, Sam Rayburn and Steinhagen, depicted in yellow. (modified from U.S. Army Corps of Engineers 2005).
APPENDIX O

Shade tolerance

Literature classifications of shade tolerance were used to estimate expected
growth responses of sapling species not examined in Lin et al. (2004). Jones and
McLeod (1989) found that Q. pagoda displayed a shade tolerant pattern, only growing
moderately faster in high light than low light. This study compared Q. pagoda growth to
Sapium and Platanus occidentalis (American sycamore). Measures of net
photosynthesis, stomatal conductance, and photon flux density were examined (Jones and
McLeod 1989). Lotti (1965) classified Q. pagoda as shade intolerant based on the
observation that it is usually a dominant or codominant species, not surviving under
shaded conditions. In a review by McKnight et al. (1981), Q. pagoda (also called Q
falcata var. pagodifolia) is classified as moderately intolerant to intolerant of shade. Q
laurifolia was classified as shade tolerant by Burns and Honkala (1990). The authors
base this designation on general observations that it often establishes and emerges
through dense vegetation (Burns and Honkala 1990). F. caroliniana was classified as
having an intermediate tolerance to shade in a review by McKnight et al. (1981). Sargent
(1961) classifies F. caroliniana as being shade tolerant. I. opaca was classified as being
tolerant to shade based on the observation that it is able to survive in the understory of
most forests (Burns and Honkala 1990).