VEGETATION DYNAMICS AND RESPONSE TO DISTURBANCE, IN FLOODPLAIN FOREST ECOSYSTEMS WITH A FOCUS ON LIANAS

Dissertation

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By

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Southeastern floodplain forests are species-rich ecosystems that respond to dynamic interactions between disturbance and hydrologic regimes. Large-scale natural disturbances such as hurricanes influence forest composition and structure not only by damaging and killing overstory trees, but also by altering environmental conditions on the forest floor. In this dissertation, I examined how the composition and structure of floodplain forest ecosystems are regulated by these disturbances, with a particular emphasis on understanding how large woody vines interact with natural disturbances in floodplain forest ecosystems. Lianas are a long-neglected aspect of floodplain forests that influence tree mortality, recruitment, and growth rates and may be responding to environmental changes. Long-term studies of forest dynamics in the Congaree National Park and the Savannah River floodplains in South Carolina, U.S.A., provide ideal settings to study the interactions of hydrologic and disturbance regimes in species-rich forests with a significant large woody vine component. Understanding how forests respond to natural disturbance will help scientists and resource managers develop and design restoration and management strategies and techniques that emulate the outcomes of natural disturbances.

During the twelve years following Hurricane Hugo in 1989 devastated portions of the old-growth floodplain forest of the Congaree National Park, liana communities have
responded to the changes in forest structure. Liana community densities were determined across hydrologic and disturbance gradients in eight 1-ha plots that were established during the winter and spring 1989-90, and re-sampled in 1994, 1998, and 2002. In heavily damaged bottomland hardwood forests, liana densities initially decreased when the host trees were severely damaged but exceeded pre-hurricane densities after twelve years. Stem densities of *Toxicodendron radicans*, the most common liana, initially decreased by 55 % in the most heavily damaged bottomland hardwood forests. In both low- and high-damaged hardwood forests, vine communities experienced increasing recruitment rates and decreasing mortality rates after twelve years. When compared with trees and shrubs, lianas have higher stem mortality rates (5-6% yr⁻¹ over 12 yr) regardless of size in the Congaree floodplain forest. Liana diameter growth rates continue to reflect size- and species-specific differences, as well as colonization patterns and post-hurricane host damage.

Long-term trends in the density and distribution of lianas may indicate shifts in the composition of plant functional types in these forests. Liana communities in non-fragmented tropical forests in Panama and across the Neotropics have increased in size and density over the last two decades of the 20th century. Long-term studies of liana communities in two temperate floodplain forests in South Carolina suggests a similar pattern where lianas have increased in density over the last two decades of the 20th century. In second-growth forests of the Savannah River system, data from five 1-ha
plots, established in 1979 and monitored for twenty-two years, indicate a steady increase in liana size, density, and proportion of stems. Likewise, in old-growth floodplain forests of the Congaree National Park, liana density has increased over twelve years in six 1-ha plots after hurricane disturbance in 1989. This increase in liana density and size suggest that lianas are prominent features of the old-growth forests and should be included in models of temperate bottomland forest dynamics of the southeastern United States.

Forest management approaches that mimic natural disturbance are thought to be more resilient and more likely to sustain biological diversity. Forest management approaches that emulate natural disturbances may reduce the loss of biological diversity by maintaining composition and structure. Studies of forest development in bottomland hardwood forests have primarily focused on existing conditions in Mississippi River floodplain, ignoring compositional differences with the Atlantic coastal plain forests. Too few studies have used the remaining examples of old-growth floodplain forests as benchmarks with which to compare the composition, structure, and dynamics. We evaluated forest development in 20 to 22-year-old clearcut and selectively cut forests and compared composition with sixteen years of post-hurricane forest development in areas of low and high damage in the old-growth floodplain forests of the Congaree National Park. Species composition was not significantly different in these species-rich systems but differences in canopy and subcanopy composition appear to remain long after management activities.
Radial increment data from lianas can provide insight into long-term trends in diameter growth, response to disturbance, and longevity. Increases in liana density, proportions of stems, and size in temperate and tropical forests may indicate shifts in functional composition of forests through time. The Congaree National Park provides the ideal location to apply dendroecological techniques in a temperate floodplain forest where lianas reach a sufficient size (~4 cm in diameter) for core extraction. One hundred radial cores were collected from two species with distinct annual rings: *Toxicodendron radicans* and *Campsis radicans*. Samples were collected across the range of environments and disturbance histories, from relatively undisturbed old-growth floodplain forests to areas clearcut in the 1970s. Ring width data suggest that liana species respond differently to the extent of canopy disturbance. *Campsis* consistently grew faster than *Toxicodendron*, with one exception being the period of five years following Hurricane Hugo in areas that suffered severe damage. *Toxicodendron* diameter growth rates increased through time starting in the 1970s in areas than were not heavily damaged. Distinct patterns of release and suppression emerge that reflect colonization pattern and the extent of disturbance.

In the last chapter of this study I provide a revised definition for “red river” old-growth floodplain forest ecosystems. “Red rivers”, which originate in the Piedmont or Blue Ridge Mountains and flow onto the Atlantic and Gulf Coastal Plains in the southeastern United States carry large volumes of red clay sediments.
As flow rates decrease when rivers reach the Coastal Plain, sediments are deposited in broad floodplains that support highly productive forests with unique characteristics. Historically, definitions of old-growth red river floodplain forests have focused on the few known remnants and models of floodplain forest development. Existing definitions are either so broad so as to include almost any mature floodplain forest or so narrow as to conclude that they no longer exist. Further refinements are needed that incorporate disturbance regime and patterns of floodplain forest stand dynamics. For example, these floodplain forests are species-rich and are often impacted by hurricanes and other high-wind events. Species composition and disturbance regimes shift from west to east across the southeastern US, with distance from the coast, and with depth of sediments deposited over the last 200 years. In one of the best examples of old-growth floodplain forests on the Atlantic Coastal Plain, the predominance of shade-intolerant tree species that has endured more than 100 years reflect this disturbance regime.
Dedicated to my sparkling daughter Abigail
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CHAPTER 1

INTRODUCTION

Our understanding of large-river floodplain stand dynamics has slowly progressed over the last 50 years (Shelford 1954; Hosner and Minckler 1963; Hodges 1997). Early models of floodplain forest development that predicted composition based solely on position in the landscape (e.g., Clark and Benforado 1981; Wharton et al. 1982; Kellison et al. 1999; Mitsch and Gosselink 2000) have progressed to dynamic models that identify the mechanisms of species change (e.g., Hodges 1997; Battaglia et al. 2004; Battaglia and Sharitz 2006; Francis 2006). As new and more detailed information on the mechanisms that regulate species composition and structure emerge, models will need to be revised. For example, dynamic models that go beyond sediment deposition rate (Hodges 1997) and include life-history characteristics (Battaglia et al. 2004; Battaglia and Sharitz 2006; Niinemets and Valladares 2006), hydrologic regime, disturbance regime, and how these factors interact will be more likely to adapt to changes in global climate than single-factor models of forest development. One area that has evolved rapidly in the last two decades is our understanding of the importance of large woody vines or lianas to forest dynamic processes (Putz and Mooney 1991; Schnitzer and Bonger 2002). As the original floodplain forest ecosystems have all but disappeared from the landscape (Hodges 1997; Shear et al. 1997; Hamilton et al. 2005),
long-term studies of the few that remain are vital not only for efforts to design management systems that emulate natural disturbance processes but also in the restoration of disturbed floodplains.

One factor that clearly effects the development of floodplain forest ecosystems are large-scale disturbances. Large-scale natural disturbances such as hurricanes influence forest composition and structure not only by damaging or killing overstory and understory trees and vines, but also by altering environmental conditions that may effect the growth and regeneration of remaining species. Understanding how species-rich floodplain forests respond to natural and anthropogenic disturbance requires elucidating how forest change through time. Historically, long-term studies and development models of floodplain forest ecosystems have been limited in duration and scope, and most have ignored the large woody vine component (Wharton et al. 1979; Jones et al. 1994; Bell 1997; Hodges 1997; Kellison et al. 1998; Mitsch and Gosselink 2000; Conner et al. 2002: Harcombe et al. 2002). Patterns observed in old-growth and second-growth forests over the scale of decades may provide insights into forest development patterns and response to disturbance.

1.1 Role of lianas

The role lianas, or large woody vines, play in forested ecosystems is coming under increased scrutiny (Philips et al. 2002; Schnitzer and Bongers 2002; Perez-Salicrup et al.
Lianas have been suggested as a mechanism for the maintenance of species richness in tropical forests (Schnitzer and Bongers 2002). Recent studies speculate that increases in liana size and density over the last two decades in the Amazon, Panama, and North America are in response to a variety of possible factors including changes in disturbance and climatic regimes, as well as increases in the concentrations of atmospheric CO$_2$. For instance, in Puerto Rican forests, Rice et al. (2004) documented higher densities of lianas in areas less frequently disturbed by hurricanes and they showed that abundance varies not only with disturbance frequency but also with biogeography, seasonality, and host-tree features. Additionally, several studies have shown that changes in the functional composition may be occurring in temperate and tropical forests (Philips et al. 2002; Wright et al. 2004; Allen et al. 2007) as elevated levels of CO$_2$ have been shown to stimulate liana growth more than tree growth (Condon et al. 1992; Granados and Korner 2002; Mohan et al. 2006; Zotz et al. 2006). This trend may negatively influence global carbon sequestration rates as lianas tend to produce photosynthetic tissues over support tissues.

In the United States, lianas are most abundant and species rich in the Southeast, a region with warm temperatures, long growing seasons, and high precipitation (Teramura et al. 1991). In some temperate floodplain forests, lianas are conspicuous features of the wetland vegetation, however, research on the structure and dynamics of natural liana populations in temperate forests is limited (Penfound 1974; Monsi and Ogawa 1977;
Friedland and Smith 1982; Carter and Teramura 1988; Gartner 1991; Collins and Wein 1993; Putz 1995; Schnitzler 1995; Talley et al. 1996; Allen et al. 1997; Allen et al. 2005; Schnitzler and Heuzé 2006; Allen et al. 2007). Because lianas are shorter-lived than trees, changes in the structure and composition of liana communities in floodplain forests take place over a more rapid time frame than for trees. Consequently, they may provide a better indicator of the influence of the short-term growth response of woody plants following hurricanes and anthropogenic stresses. However, questions remain about the role of natural disturbance in liana community dynamics, particularly in temperate forests.

Disturbances to the forest canopy are known to influence liana populations by altering the light environment, increasing establishment opportunities, and providing trellises for climbing (Siccama and Weir 1976; Davidson and Forman 1982; Putz 1983; Allen et al. 2005; DeWalt et al. 2006). However, damage to a liana’s host tree may have negative consequences for the liana as host tree damage is related to liana mortality rates (Allen et al. 1997). Regardless of the effect, the competition between lianas and tree seedlings at the ground layer plays a vital role in forest dynamics, including how forests respond to changes in the environment. These patterns may reflect the different ways liana species colonize their hosts, the mechanisms used to ascend their host, and species-specific growth and longevity. Under a closed canopy, liana growth is limited by low resource availability and lack of suitable natural trellises (Putz 1980, 1995). The size and species of
host trees may interact with liana climbing mechanisms to influence the composition of the liana community. For instance, the abundance and distribution of lianas in tropical forests have been linked to the availability of trellises furnished by fallen trees in gaps (Hegarty and Caballé 1991).

At the community-scale, the invasion of lianas may be related to the size and frequency of canopy gaps and the type and persistence of disturbances. While disturbance may play an important role in liana population dynamics, lianas may also influence the nature and extent of forest damage associated with canopy disturbance. For example, hurricane damage to trees in the old-growth floodplain forest ecosystems of the Congaree National Park was associated with the number of lianas colonizing them and tree size (Allen et al. 1997).

1.2 Objectives of this dissertation

Long-term studies of vegetation dynamics provide insight into the influence of life-history characteristics on species demographic patterns and ecosystem function (Rees et al. 2001). Studies that follow forests through time contribute to our understanding the processes that structure communities, integrating plant life-histories, disturbance regimes, competition, and successional processes. The purpose of the current research was to address specific gaps in our understanding in large river floodplain forest ecosystem development and the role of lianas in the development process. Most
models of large river floodplain forest ecosystem development in the southeastern United States are based on studies conducted within the Mississippi River watershed. It is unclear if the factors that regulate floodplain ecosystem development in the Gulf Coastal Plain operate in the same manner in floodplain ecosystems of the Atlantic Coastal Plain or how models of forest ecosystem development need to be adapted to reflect these differences.

Using long-term datasets from second-growth and old-growth floodplain forests of the Atlantic Coastal Plain, this dissertation addresses the following questions: 1) How have liana communities in an old-growth floodplain forest changed twelve years after a major hurricane? 2) Are lianas increasing in importance in two Atlantic Coastal Plain floodplain forest ecosystems? 3) Are there differences in forest development following natural and anthropogenic disturbance, and if so, can these differences be used to help guide forest management or restoration that emulates natural processes? 4) How long do lianas live and how do growth rates reflect disturbance history? and 5) Should the definition of old-growth change to fit improved understanding of forest development in Atlantic Coastal Plain floodplain forest ecosystems?

1.3 Long-term datasets utilized in this dissertation

This dissertation examines data from two long-term studies of floodplain forests in South Carolina. Both sites are located just below the fall line on the upper Atlantic Coastal
Plain along floodplains of two major river systems -- the Savannah River and the Congaree River (Fig.1.1).

The first study area, the Savannah River and its tributary, Upper Three Runs Creek, is located south of Augusta, Georgia, on the Savannah River Site (SRS; Fig. 1.1). I utilized seven 1-ha permanent sample plots established by B.J. Good in 1979 distributed across the following areas of the SRS: five of the seven 1-ha permanent plots established in bottomland hardwood and stream bank forests, one plot located in the floodplain of the Savannah River, and four plots along Upper Three Runs Creek. As part of the Savannah River Site, access has been restricted since 1950 and no forest management activities have taken place during that time period within the study sites. The floodplain forests were harvested in the late 1800s (Good and Whipple 1982) and there was little evidence of management activities when the Savannah River Site was established in the early 1950s (E. Odum, Pers. Com.). The overstory of the mesic floodplain forests are dominated by oaks (*Quercus* spp.), sweetgum (*Liquidambar styraciflua* L.), black gum (*Nyssa sylvatica* Marsh.), and red maple (*Acer rubrum* L.). The forests on the driest site, located along the river bank and bluff adjacent to Upper Three Runs Creek, are dominated by oaks (*Quercus* spp.), pines (*Pinus* spp.), and hickories (*Carya* spp.) (Jones et al. 1994). In 1979, when the long-term plots were established, stems ≥ 4.5 cm dbh (measured 10 centimeters below a permanent tag 1.4 m above the ground) were measured, mapped, permanently tagged, and identified to species. Plots were re-sampled in 1989, 1995, and 2001.
The second study area, the 9,953-ha Congaree National Park (CNP) includes a portion of the Congaree River floodplain in central South Carolina (Fig 1.1). The Congaree River watershed receives an average of 122 cm of precipitation annually (Rudell 1984) and flooding occurs frequently in the winter and early spring but is possible at any time of year. The predominant floodplain soils are silty clay loams that are poorly drained and have low permeability (Crews 1976).

Current vegetation in the CNP includes large areas of mature deciduous forest (Jones 1997), with many trees of near record-size (Sharitz et al. 1992). More than 155 tree, shrub, and woody vine species are known to occur in the CNP (Thompson 1998; Gaddy and Nelson 2006). Stand composition is influenced by flooding frequency, depth, and duration. The largest portion of the National Park is occupied by old-growth bottomland hardwood forest ecosystems that are often flooded for short periods in winter but are usually dry during the growing season. Dominant tree taxa include sweetgum (*Liquidambar styraciflua* L.), oaks (*Quercus* spp.) (at least 9 species), sugarberry (*Celtis laevigata* Willd.), green ash (*Fraxinus pennsylvanica* Marsh.), red maple (*Acer rubrum* L.), and loblolly pine (*Pinus taeda* L.). The understory is dominated by American holly (*Ilex opaca* Ait.), deciduous holly (*I. deciduas* Walt.), American hornbeam (*Carpinus caroliniana* Walt.), red maple, and pawpaw (*Asimina triloba* (L.) Dunal.). Forests occurring in more low-lying areas and old oxbows (sloughs) are flooded for more extended periods and are dominated by water tupelo
(Nyssa aquatica L.) and bald-cypress (Taxodium distichum (L.) L.C. Rich.). The dominant understory species are water elm (Planera aquatica J.F. Gmel.), red maple, and Carolina ash (Fraxinus caroliniana P. Mill.). Areas near the adjacent upland that are fed by springs and seeps experience relatively little variation in water level, and the forests there are dominated by swamp tupelo (Nyssa biflora Walt.). There are at least 27 woody vine taxa in the Congaree floodplain (Allen et al. 1997), with trumpet creeper (Campsis radicans (L.) Seemann.), Virginia creeper (Parthenocissus quinquefolia (L.) Planchon.), eastern poison ivy (Toxicodendron radicans (L.) Kuntze.), and grape (Vitis spp.) (primarily muscadine (V. rotundifolia Michaux.) and Simpson’s grape (V. cinerea var. floridana Munson.)) among the most common vine species to reach 2.5 cm dbh.

On 21-22 September 1989, high winds associated with Hurricane Hugo caused extensive damage to the forest canopy within the CNP. Wind effects differed within and among forest types. In bottomland forests, 37% of trees were moderately to severely damaged, while only 10% of trees in sloughs were seriously damaged (Sharitz et al. 1992). In bottomland hardwood forests, more and larger gaps in the canopy were formed from snapped and uprooted trees and broken branches. In the sloughs, species characteristic of bottomland hardwood forests (e.g., Acer rubrum) were more heavily damaged than Taxodium or Nyssa (Putz and Sharitz 1991).

Three sources of vegetation data from the CNP are utilized for this dissertation. The first data set includes long-term data from permanent plots established after
Hurricane Hugo impacted the CNP. During fall of 1989 and winter of 1990 (immediately after the hurricane), ten 100 x 100 m plots were established in locations varying in vegetation, hydrology, and intensity of wind damage. Six plots were placed in bottomland hardwood forests, three in sloughs, and one in a seep near the adjacent upland. Discussions will be limited to the 6 bottomland hardwood plots and two slough plots where there is a sufficient level of replication and where lianas were present. In all plots, all trees (stems ≥10 cm diameter) obviously alive prior to the hurricane were tagged, identified to species, mapped within the plot, and measured for diameter. Trees and woody vines were measured at 1.4 m in height except for *Nyssa aquatica*, *Nyssa biflora*, and *Taxodium distichum*, which were measured at 2.0 m height (or 0.5 m above basal swell) to avoid their enlarged buttresses. Stems were mapped and assessed for hurricane damage. In the bottomland hardwood plots and the seep plot, saplings (stems < 10 cm but ≥ 2.5 cm dbh) were sampled in five randomly selected 20 x 20 m subplots per hectare plot. In slough plots, saplings were tagged and measured over the entire plot. During winter and spring 1993-4 (four growing seasons after Hurricane Hugo), 1997-8 (eight growing seasons after Hurricane Hugo), 2001-2 (twelve growing seasons after Hurricane Hugo), and 2005-6 (sixteen growing seasons after Hurricane Hugo) all woody stems were recorded as alive, dead, or missing, live stems were re-measured, and newly recruited stems (in-growth) were tagged, mapped, and measured. Vine occurrence rates were recorded as well as the number of vines larger than 2.5 cm. These
measurements provide some indication of the difficulty of accurately measuring tree diameters as concerns for vine health impeded accurate tree diameter measurement at times.

Because trees alive prior to the hurricane were included, the 1989-1990 data closely approximate pre-hurricane conditions. Thus, not only was variation in degree of hurricane damage apparent, but also the post-hurricane mortality, recruitment, and basal area increment could be directly quantified. Post-hurricane mortality was predicted based on severe damage, stems that were tipped-up or snapped-off after the hurricane and dead in 1994. Severe branch loss rarely resulted in tree death.

The second set of vegetation data from the CNP were collected in 1996 as part of a vegetation-mapping project. In 1996, teams lead by A.J. Thompson and L.L. Gaddy (Thompson 1988) established plots in contiguous forest blocks in representative stands based upon classification of aerial photography. Most of the plots were 0.1 ha (20 x 50 m) but some were smaller in area or had different shapes, in order to remain within a homogeneous community. The original data consist of stem counts for all woody species with a diameter at breast height (dbh) of at least 2.5 cm that were grouped into eight diameter classes. We used only fourteen of the total 126 plots that were situated on bottomland sites that had been harvested (partially or completely) between 1974 and 1976. The total number of stems in each diameter class was tallied by species in each plot and expressed as density (stems ha\(^{-1}\)) and basal area (m\(^2\) ha\(^{-1}\)).
The third data set from the Congaree, liana radial increment cores, were collected during the winter of 2005-6. After examining several cores form each of six liana species of the CNP, two species were selected, trumpet creeper (*Campsis radicans* (L.) Seemann) and poison ivy (*Toxicodendron radicans* (L.) Kuntze), which have distinct annual rings. One hundred cores were collected for each species across disturbance and size-class gradients. In addition to the increment core, we also identified the host-tree species and measured the liana diameter at core height (usually 1.3 m above the ground) and vine load (the number lianas $\geq$ 2.5 cm dbh) for each cored liana and its location within the floodplain.

**References**


Fig. 1.1. Locations of the Congaree National Park and the Savannah River floodplain, South Carolina. The shaded areas indicate the distribution of river floodplain forests in the region, located primarily on the Atlantic and Gulf Coastal Plains.
CHAPTER 2

TWELVE YEARS POST-HURRICANE LIANA DYNAMICS IN AN OLD-GROWTH SOUTHEASTERN FLOODPLAIN FOREST

2.1. Introduction

The role lianas, or large woody vines, play in forested ecosystems is coming under increased scrutiny (Philips et al. 2002; Schnitzer and Bongers 2002; Perez-Salicrup et al. 2004; Wright et al. 2004). Lianas have been suggested as a mechanism for the maintenance of species richness in tropical forests (Schnitzer and Bongers 2002). A recent study speculates that increases in liana size and density in the Brazilian Amazon, possibly in response to increased atmospheric carbon, is changing the composition of tropical forests and likely negatively influencing global carbon sequestration rates (Philips et al. 2002). Wright et al. (2004) reported that stem density and litter fall were increasing over time in long-term plots in Barro Colorado Island, Panama, and this was consistent with reports from the Amazon. In North America, lianas are most abundant and species rich in the southeastern United States, a region with warm temperatures, long growing seasons, and high precipitation (Teramura et al. 1991; Allen et al. 1997). Furthermore, in many temperate floodplain forests in this region, lianas are conspicuous features of wetland vegetation; however, research on the structure and dynamics of natural liana communities in temperate forests is limited (Monsi and Ogawa 1977; Friedland and Smith 1982; Carter and Teramura 1988; Gartner 1991; Collins and Wein 1993; Putz 1995; Talley et al. 1996; Allen...
et al. 1997). Questions remain about the role of natural disturbances in liana community dynamics, particularly in temperate forests.

Disturbances to the forest canopy affect lianas by altering the light environment, increasing establishment opportunities, and providing trellises (downed limbs or boles) for climbing. However, damage to a liana’s host tree may have negative consequences for the vine, and competition between lianas and tree seedlings at the ground layer may play a vital role in post-disturbance forest stand dynamics. These patterns may reflect the different ways liana species colonize their hosts, mechanisms used to ascend their host, and species specific growth and longevity. Under a closed canopy, liana growth is often limited by low light availability and lack of suitable natural trellises (Putz 1980). The abundance and distribution of lianas in tropical forests have been linked to the availability of trellises furnished by fallen trees in gaps (Hegarty and Caballé 1991). On a community scale, invasion of vines may be determined by the size and frequency of canopy gaps and by the type and persistence of disturbances. While disturbance may play an important role in liana population dynamics, lianas may also influence the nature and extent of canopy damage associated with disturbance (Allen et al. 1997).

Numerous studies have shown that major wind disturbances have lasting effects on forest structure and composition, and are critical to the dynamics of many forest ecosystems (Bormann and Likens 1979; Foster 1988; Oliver and Larson 1990; Lodge and McDowell 1991; Peart et al. 1992; Sheffield and Thompson 1992; Rice et al. 2004).
Hurricanes are normal features of the southeastern United States and have a repetitive influence on forest structure (Putz and Sharitz 1991; Allen et al. 1997; Battaglia et al. 1999). However, the relationship of lianas to the forest disturbance patterns associated with hurricane winds and the effect of such disturbances on vine dynamics are poorly understood.

The objective of this study was to revisit sites established in 1989 following Hurricane Hugo in the Congaree National Park and examine liana population dynamics in these old-growth floodplain forests. Specific questions we address are: 1) How have liana densities changed over the twelve years following the hurricane? 2) Have the patterns of vine occurrence on host trees observed prior to the hurricane changed since the hurricane? 3) How fast are lianas growing in diameter and do species, size, host tree damage, and colonization pattern influence diameter growth rates?

2.2. Study Site

The 9953 ha Congaree National Park (CNP) contains the last major remnant of mature bottomland hardwood forest in the southeastern U.S. (Gaddy et al. 1975). The floodplain consists of two broad forest types which are influenced primarily by hydrologic regime. Areas flooded infrequently (primarily November – March) or for short periods support a bottomland hardwood forest composed of *Liquidambar styraciflua* L., *Ilex opaca* Aiton., *Quercus* spp., *Celtis laevigata* Willd., *Fraxinus pennsylvanica* Marshall, *Ulmus* spp.,
Acer rubrum L., and other hardwood species, as well as some Pinus taeda L. Frequently flooded sloughs are dominated by Nyssa aquatica L. and Taxodium distichum (L.) Richard. Large areas of the floodplain have unlogged old-growth forests with many record or near record-sized individuals (Jones 1997). There are at least 27 woody vine taxa in the Congaree floodplain (Allen et al. 1997), with Campsis radicans (L.) Seemann, Parthenocissus quinquefolia (L.) Planchon, Toxicodendron radicans L., and Vitis spp. (primarily V. rotundifolia Michaux. and V. cinerea var. floridana Munson) among the most common vine species to reach 2.5 cm dbh.

Hurricane Hugo struck the forests of the CNP on Sept 21-22, 1989 with wind speeds approaching 155 km hr\(^{-1}\) (Putz and Sharitz 1991). The hurricane affected the forest types of the floodplain differently: 37% of trees in bottomland hardwood forests were moderately to severely damaged, while only 10% of trees in sloughs were similarly damaged (Sharitz et al. 1992). In the hardwood forests, more and larger gaps in the canopy were formed from snapped and uprooted trees and broken branches. In the sloughs, those species characteristic of hardwood forests (e.g., Acer rubrum) were more heavily damaged than were T. distichum and N. aquatica, which suffered mainly branch loss (Putz and Sharitz 1991).
2.3. Methods

2.3.1. Sampling

During the winter and spring following Hurricane Hugo (1989-90), eight 100 x 100 m (1 ha) plots (Fig. 2.1) were established in different forest communities within the CNP in areas where little or no previous logging was evident (Sharitz et al. 1992, Allen et al. 1997, Allen and Sharitz 1999). Plots were re-sampled during the winter and spring of 1994, 1998, and 2002. Six plots were located in bottomland hardwoods and two in shallow slough forests. All woody stems, including lianas, ≥10 cm diameter at breast height (dbh) were tagged, identified to species, measured, and mapped. Diameters were measured using a diameter tape or calipers at 1.4 m above the ground which was also 10 cm below a permanent tag. Thus, dbh was measured at the same point on the stem at each sampling period. The numerous aerial roots produced by Toxicodendron radicans necessitated averaging two caliper readings for an accurate dbh measurement of this vine species. For each tree, the number of attached large vines (≥2.5 cm) was noted as well as vine infestation level (low, medium, and high), whether vines reached the canopy, and degree of hurricane damage. Damage to the trees was categorized by the degree of tip-up (partial or full), snap-off height, and degree of branch loss (high >50% branch loss, medium – 25-50% branch loss, low <25% branch loss). In sloughs, all woody stems ≥ 2.5 cm dbh were sampled in a similar manner except for Nyssa aquatica, Nyssa sylvatica var. biflora (Walter) Sargent, and Taxodium distichum, which were measured at 2.0 m height (or 0.5 m above basal
swell) to avoid their enlarged buttresses. In bottomland hardwood plots, woody stems ≥ 2.5 cm but <10 cm were sub-sampled in five 20 x 20 m subplots per ha plot due to much higher sapling and vine densities. Because the initial sampling was performed immediately following the hurricane, trees damaged and killed by the storm were easily distinguished. Thus, the 1989-1990 data provide a reasonable measure of pre-hurricane conditions. Based on previous work (Allen and Sharitz 1999; Allen et al. 1997), we have divided the bottomland hardwood plots into either a high- or low-damage category. In the high damage plots (three of the 1-ha plots) severe tree damage (snapped-off, tipped-up, or suffered high or medium branch loss) on overstory individuals (≥40 cm dbh) ranged from 58-68% of the trees while in low damage plots (3 1-ha), the proportion of severely damage trees ranged from 21-46%.

2.3.2. Statistical Methods

Changes in the proportion of trees with vines present and the number of vines per tree were examined using t-tests. Changes in the patterns of liana species and host tree species were examined with a Chi-square (χ²) analysis: a sequential Bonferroni test was used to evaluate table-wide significance (α=0.05). A General Linear Model analysis of variance (GLM procedure, SAS Institute Inc. 1999) was constructed for liana diameter increment as a function of initial diameter, species, and hurricane damage to the host tree for the most common vine species. Because of small sample sizes, the effects of vine size and host damage could not be elucidated in a single model.
2.4. Results

2.4.1. Changes in liana composition, structure, and distribution

Although the hurricane reduced densities of lianas and host trees, especially in heavily damaged forests, twelve years later the proportion of trees with vines present and the number of large vines increased in the bottomland hardwood forests above pre-hurricane levels (Figure 2.2). Lianas, 11.5% of the woody stems >2.5 cm in the bottomland hardwood forests in 1989 (pre-hurricane), comprised 12.4% of the woody stems in 2002. The largest changes occurred in heavily damaged areas where the proportion of trees supporting vines increased steadily from 54.4% in 1989 to 79.2% in 2002. In the shallow slough forests, there was little change in the number of lianas or the number of trees supporting them.

We observed considerable change in liana density and species composition over the twelve years since the hurricane (Table 2.1), however, in all cases changes in vine density were not significant due to high variability between plots. Despite this variability, a few general trends have emerged. In both heavily damaged and low damage bottomland hardwood plots, liana density (which initially dropped 40% in heavily damaged areas following the hurricane) has surpassed pre-hurricane levels (Table 2.1). In the slough forests, liana densities have not surpassed pre-hurricane levels but they have recovered most of the losses. Finally, *Campsis radicans* density increased in both forest types and *Toxicodendron radicans, Vitis* spp., and *Parthenocissus quinquefolia* increased in hardwood plots (Table 2.1).
Vines were not distributed randomly among tree species in bottomland forests prior to the hurricane ($X = 43.2 > 29.59_{10(0.001)}$) or 12 years following the hurricane in 2002 ($X = 40.9 > 29.59_{10(0.001)}$) (Table 2.2). In particular, the canopy-dominant *Liquidambar styraciflua* individuals supported significantly more vines than expected before the hurricane and twelve years later. Similarly, in 1989, vines were not distributed randomly in slough forests ($X = 36.6 > 27.88_{9(0.001)}$), but this pattern was not significant in 2002 (Table 2.3).

2.4.2. Impacts on liana diameter growth and mortality

The impact of host tree damage and vine diameter class on liana diameter growth was modeled for each sample interval for the three most common liana species. Because of small sample sizes, the effect of liana size class and host tree damage could not be examined in a single model. While liana diameter growth was highly variable, several patterns have emerged. Models of diameter growth (PROC GLM, SAS 8.1) as a function of host tree damage indicated that hurricane branch loss affected liana diameter growth and that the pattern changed over time following the hurricane. Changes in diameter growth were significant ($P=0.0298$) only for *Vitis* sp.; vines growing on host trees that suffered severe branch loss did not grow for the first four years while those on less damaged host trees grew slowly (Figure 2.3). This pattern was reversed in subsequent time periods. Similar patterns in diameter growth were observed for *Campsis radicans*, although these differences were not significant ($P=0.2777$). Diameter growth patterns were reversed for *Toxicodendron*
radicans which grew more rapidly on heavily damaged trees from 1990-94 and showed virtually no differences in subsequent time periods. However, these differences were not significant (P=0.0705).

Few differences were observed related to the influence of liana diameter class on growth rate (Figure 2.4). Small (2.5-3.5 cm dbh) Campsis radicans stems grew significantly faster than large size classes immediately following the hurricane (1990-94). In later time intervals, the larger size classes grew as rapidly as the smaller size classes with no significant differences between them. Small Toxicodendron radicans consistently grew more rapidly than larger size classes but the differences were significant only during the second time interval four to eight years following the hurricane (1994-1998). Vitis sp. was the slowest growing species group and the only significant effect of size occurred during 1994-1998 when small stems grew significantly slower than medium sized stems (3.5-5.0 cm dbh) stems.

Stem mortality patterns for different woody plant life forms (liana, subcanopy tree species, and canopy species) appear to be a function of size and susceptibility to hurricane winds (Figure 2.5). Mortality refers to stem mortality for trees, shrubs, and lianas, no attempt was made to determine if the entire organism died. Post-hurricane mortality of trees was determined by whether the tree was snapped-off, tipped-up, or suffered severe branch loss as a result of the hurricane and was dead by the 1994 survey. Because it was difficult to detect direct hurricane damage to vines, lianas that were dead in 1994 and were located on
host trees that were killed by the hurricane were also assumed killed by the hurricane.
Lianas in bottomland hardwood forests had greater initial post-hurricane mortality (25%) than the other life forms regardless of size (4-15%; Figure 2.5). In subsequent years, mortality rates declined, but those of lianas (~5-6%/year) continued to exceed those of canopy and subcanopy trees of all sizes (~1-4% per year). Finally, species specific mortality patterns for lianas provide some insight into the demographic changes within the liana community (Table 2.4). Mortality rates were extremely variable following Hurricane Hugo, but in general, they indicate that mortality rates peaked after the hurricane and gradually decreased over the next twelve years.

2.5. Discussion

Liana communities in the Congaree National Park suffered a mortality episode in the aftermath of Hurricane Hugo in September 1989 associated with host tree mortality. Within twelve years after the hurricane, however, liana stem densities and basal areas exceeded pre-hurricane levels in the bottomland hardwood forests by greater than 50%, regardless of the level of hurricane damage. The proportion of trees with vines has increased in both bottomland hardwood forests and shallow slough forests. However, in slough forests, liana densities continued to decline for at least eight years following the hurricane. Recovery of pre-hurricane liana stem densities has not occurred within twelve years suggesting that factors other than hurricane damage appear to control vine communities in shallow slough
forests, and lianas may be limited by hydrologic regime. Finally, unlike many tree species, where the shade intolerant canopy species are being recruited only in areas heavily damaged by the hurricane (Allen and Sharitz 1999), our results show that lianas have responded across the entire range of forest damage. This suggests that lianas appear to be responding to some of the same environmental stimuli as shade tolerant tree and shrub species.

There is mounting evidence that lianas in temperate and tropical forests are not distributed randomly on host trees (Talley et al. 1996; Allen et al. 1997; Carsten et al. 2002; Rice et al. 2004). Twelve years following Hurricane Hugo, vines are still not randomly distributed on tree species in the Congaree, however the patterns seem to be less distinct than prior to the hurricane. This may represent a saturation effect, where an increase in the number of trees with vines has obscured the pattern. Tally (1996) found that *Toxicodendron radicans* was not randomly distributed among host tree species and had a preference for *Quercus rubra* and *Carya ovata* in mixed mesophytic forests in north Alabama. Similarly, Allen et al. (1997) found a positive association between *R. radicans* and *Liquidambar styraciflua* in the Congaree National Park. Carsten et al. (2002) found associations between lianas and host tree species in Australia, but determined that host diameter and liana climbing mechanism were also important.

While our results clearly demonstrate the importance of lianas in floodplain forests of the southeastern United States, liana mortality patterns have not been the focus of extensive research. Only Gerwing et al. (2004) and Putz (1990) have reported liana
mortality rates, and these are studies of tropical vines. Putz (1990) reported an annual mortality rate of 1.5% for climbing ramets (referring to stems rather than individuals), while Gerwing et al. (2004) found an average of 6.7%/yr ramet mortality for all species and ranged between 1.3 and 13.3%/yr on a species basis. In the Congaree, morality rates of 4.4-8.5%/yr were observed. Furthermore, liana mortality rates appear to be decreasing through time following hurricane disturbance in the CNP (Table 2.4). These rates may reflect delayed mortality or detection of mortality after the hurricane and shifts in size class distribution or species composition.

Unfortunately, the extent of published liana diameter growth data for comparison purposes is very small (Table 2.5), and this study represents fully one quarter of the published diameter growth data for lianas. While liana diameter growth rates have not been the subject of much study by forest ecologists in temperate forests, stem area to leaf area ratios of lianas have been shown to be highly correlated and substantially higher than those of trees in tropical forests (Putz 1983; Gerwing and Farias 2000; Gehring 2004). Diameter growth rates appear to have increased following Hurricane Hugo in the Congaree (Table 2.5), ranging from 1.29 mm yr\(^{-1}\) from 1990-94 to 1.71 mm yr\(^{-1}\) from 1998-2002. As a comparison, Gerwing (2004) found liana diameter growth rates for six Amazonian species to be 1.3 mm/yr based on three years of growth measurement of 1142 stems, by far the largest study to date. In the Congaree, increase in diameter growth following the hurricane may result from a shift in the size class distribution where the proportion of stems in the
smallest size classes has increased. Gerwing and Farias (2000) found that leaf mass to stem ratios for lianas in eastern Amazonian forests was 4-5 times greater than for trees. In addition, lianas have been shown to make up 19% of the leaf area in tropical forests (Putz 1983).

Species specific responses in growth rate reflect both the extent of damage to the host tree and the colonization patterns of the liana. Species that overtop their host tree, *Vitis* spp. and *Campsis radicans*, grew very slowly after the hurricane if their host tree suffered severe branch loss. This pattern was significant (P=0.05) only for *Vitis* spp., but the pattern was reversed in subsequent time periods (Figure 2.2). *Toxicodendron radicans*, which colonizes only the main stem and large branches of its host, grew more rapidly, though not significantly (P=0.05), on trees that suffered severe branch loss. This pattern disappeared in subsequent time periods (Figure 2.2).

Increases in liana density and basal area in the Congaree appear to reflect long-term (20 year) increases like those observed in the Amazon basin (Phillips et al. 2002) and across the Neo-tropics (Wright et al. 2004). Unlike the Amazon, there has not been a corresponding increase in mean diameter of lianas in the Congaree. Schnitzer and Bongers (2002) noted that liana abundance in tropical forests varied with total rainfall, soil fertility, and disturbance. Unlike the forests described by Phillips et al. (2002) and Wright et. al. (2004), the bottomland hardwood forests of the Congaree have been subject to a major wind disturbance; liana density has increased even in areas of low damage.
This study represents the first long-term demographic study that has examined liana density, diameter growth, recruitment, and mortality patterns in temperate floodplain forests. Long-term studies are needed to observe how forest communities are changing through time. Clearly, temperate lianas respond to large scale disturbance. Increased competition with trees for water, light, and soil nutrients will reduce tree growth rates, increase their susceptibility to wind damage, and may influence tree species composition. Unlike tropical forests where increases in liana density have been documented, the Congaree National Park was subject to severe wind disturbance prior to increases in density. Liana diameter growth following wind disturbance reflect species specific colonization patterns and host damage.

References


<table>
<thead>
<tr>
<th>Species</th>
<th>Low Damage Bottomland Hardwood Forests (n = 3)</th>
<th>High Damage Bottomland Hardwood Forests (n = 3)</th>
<th>Shallow Slough Forests (n = 2)</th>
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<tbody>
<tr>
<td>$T. radicans$</td>
<td>87.0±47.8 78.7±43.7 88.3±42.5 110.0±43.6 116.7±55.8</td>
<td>90.0±60.6 43.3±22.5 40.0±17.3 71.7±53.9 100.0±73.7</td>
<td>28.0±17.0 23.5±10.6 8.0±1.4 6.0±0.0 12.0±1.4</td>
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<tr>
<td>$Vitis$ spp.</td>
<td>35.0±56.3 33.3±57.7 28.3±49.1 30.0±52.0 41.7±52.0</td>
<td>29.3±11.5 27.3±10.0 27.3±7.1 47.0±15.7 63.7±17.0</td>
<td>12.5±16.3 12.5±16.3 10.0±12.7 7.0±8.5 9.5±10.6</td>
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<tr>
<td>$Parthenocissus$</td>
<td>$P. quinquefolia$</td>
<td>10.0±17.3 6.7±11.5 3.3±5.8 16.7±28.9 18.3±31.8</td>
<td>20.0±11.3 19.0±9.9 21.0±7.1 25.5±3.5 33.5±7.8</td>
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<tr>
<td>$C. radicans$</td>
<td>13.3±15.3 13.3±15.3 20.0±22.9 25.0±22.9 31.7±23.6</td>
<td>5.3±5.5 2.0±3.5 10.3±17.9 19.0±32.9 27.7±43.7</td>
<td>20.0±11.3 19.0±9.9 21.0±7.1 25.5±3.5 33.5±7.8</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>139.0±42.9 129.0±48.8 147.0±30.2 182.0±33 212.0±30.6</td>
<td>134.3±77.4 79.3±37.5 84.3±29.5 159.3±90.6 214.7±124.6</td>
<td>62.5±47.5 57.0±39.6 40.0±22.6 39.5±13.4 55.5±20.5</td>
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Table 2.1. Changes in liana densities (stems/ha ± SD) in the Congaree National Park from 1990 to 2002. Some liana species did not occur in all bottomland hardwood or shallow slough plots.
<table>
<thead>
<tr>
<th>Tree species</th>
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<td></td>
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<td># of trees w/vines</td>
</tr>
<tr>
<td></td>
<td># of trees</td>
<td>Observed</td>
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<tr>
<td>Ilex spp.</td>
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<td>470 (&gt;exp.)*</td>
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<td>84 (&lt;exp.)*</td>
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<td>121</td>
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<tr>
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<td>68</td>
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<tr>
<td>Fraxinus spp.</td>
<td>79</td>
<td>62 (&gt;exp.)*</td>
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<tr>
<td>Pinus taeda</td>
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<td>9</td>
</tr>
<tr>
<td>Nyssa spp.</td>
<td>37</td>
<td>5 (&lt;exp.)*</td>
</tr>
<tr>
<td>Other</td>
<td>71</td>
<td>35</td>
</tr>
<tr>
<td>Total</td>
<td>2593</td>
<td>1331*</td>
</tr>
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</table>

Table 2.2. Vine distribution on trees based on presence/absence data in bottomland hardwood forests in the CNP. *P<0.001. Other = Asimina triloba, Carya spp. (C. aquatica, C. cordiformis, C. ovata), Crataegus spp., Liriodendron tulipifera, Morus rubra, Platanus occidentalis, and Populus heterophylla
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<th>Tree species</th>
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<th>2002</th>
<th></th>
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<td># of trees w/vines</td>
</tr>
<tr>
<td><strong># of trees</strong></td>
<td>Observed</td>
<td>Exp.</td>
<td>Observed</td>
<td>Exp.</td>
</tr>
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<td><strong>Nyssa spp.</strong></td>
<td>844</td>
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<td>803</td>
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<td><strong>Quercus spp.</strong></td>
<td>37</td>
<td>21 (&gt;exp.)*</td>
<td>10</td>
<td>48</td>
</tr>
<tr>
<td><strong>C. caroliniana</strong></td>
<td>29</td>
<td>6</td>
<td>8</td>
<td>25</td>
</tr>
<tr>
<td><strong>Planer a aquatica</strong></td>
<td>25</td>
<td>5</td>
<td>6</td>
<td>24</td>
</tr>
<tr>
<td><strong>L. styraciflua</strong></td>
<td>20</td>
<td>9</td>
<td>5</td>
<td>18</td>
</tr>
<tr>
<td><strong>Ulmus spp.</strong></td>
<td>12</td>
<td>5</td>
<td>3</td>
<td>22</td>
</tr>
<tr>
<td><strong>Celtis laevigata</strong></td>
<td>4</td>
<td>4</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td><strong>Other</strong></td>
<td>4</td>
<td>2</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>1300</td>
<td>338*</td>
<td>1291</td>
<td>386*</td>
</tr>
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</table>

Table 2.3. Vine distribution on trees based on presence/absence data in shallow slough forests in the CNP. *P<0.001. aOther = Asimina triloba, Carya spp. (C. aquatica, C. cordiformis, C. ovata), Crataegus spp., Liriodendron tulipifera, Morus rubra, Platanus occidentalis, and Populus heterophylla
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<thead>
<tr>
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<tr>
<td></td>
<td>(%)</td>
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<tr>
<td><em>Campsis radicans</em></td>
<td>41</td>
<td>7.3</td>
<td>38</td>
<td>0.7</td>
<td>42</td>
<td>2.4</td>
</tr>
<tr>
<td>BLH – Low</td>
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<td>0.0</td>
<td>3</td>
<td>0.0</td>
<td>7</td>
<td>0.0</td>
</tr>
<tr>
<td>BLH - High</td>
<td>4</td>
<td>50.0</td>
<td>2</td>
<td>0.0</td>
<td>7</td>
<td>0.0</td>
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<tr>
<td><em>Parthenocissus quinquefolia</em></td>
<td>8</td>
<td>0.0</td>
<td>8</td>
<td>0.0</td>
<td>12</td>
<td>8.3</td>
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<tr>
<td>BLH – Low</td>
<td>6</td>
<td>33.3</td>
<td>4</td>
<td>12.5</td>
<td>2</td>
<td>0.0</td>
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<tr>
<td>BLH - High</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td><em>Toxicodendron radicans</em></td>
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</tr>
<tr>
<td>BLH – Low</td>
<td>53</td>
<td>9.4</td>
<td>48</td>
<td>6.3</td>
<td>53</td>
<td>7.1</td>
</tr>
<tr>
<td>BLH - High</td>
<td>54</td>
<td>51.9</td>
<td>26</td>
<td>6.7</td>
<td>24</td>
<td>11.5</td>
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<tr>
<td><em>Vitis spp.</em></td>
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<tr>
<td>BLH – Low</td>
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<td>20</td>
<td>7.5</td>
<td>17</td>
<td>2.9</td>
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<tr>
<td>BLH - High</td>
<td>20</td>
<td>5.3</td>
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<td>8.3</td>
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<td>295</td>
<td>17.3</td>
<td>243</td>
<td>8.5</td>
<td>221</td>
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Table 2.4. Liana mortality rates in slough (two 1-ha plots) and in bottomland hardwood (BLH) forests with low damage (three 1-ha plots) and high damage (three 1-ha plots) forests in CNP over the twelve year period 1990-2002. *Includes *Ampelopsis arborea, Decumara Barbara*, and *Berchemia scandens.*
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<tr>
<th>Study Location</th>
<th>Size Range (cm)</th>
<th>n</th>
<th>#Species</th>
<th>Time Period</th>
<th>MAI (SD) (mm/year)</th>
</tr>
</thead>
<tbody>
<tr>
<td>La Selva, Costa Rica (Ewer et al. 1991)</td>
<td>10.2 -20.3</td>
<td>60</td>
<td>11</td>
<td>1969 - 82</td>
<td>1.60 (0.2-1.1)</td>
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<tr>
<td>Barro Colorado Island, Panama (Putz 1990)</td>
<td>0.4-50.8</td>
<td>189</td>
<td>15</td>
<td>1979 - 87</td>
<td>1.36 (0.23)</td>
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<tr>
<td>Amazon, Brazil (Gerwing 2004)</td>
<td>0.3-19.4</td>
<td>1142</td>
<td>6</td>
<td>1996 - 99</td>
<td>1.3</td>
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<tr>
<td>Congaree Swamp, USA (Allen et al. 1997)</td>
<td>2.5-40.0</td>
<td>157</td>
<td>7</td>
<td>1990 - 94</td>
<td>1.29 (0.65)</td>
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<tr>
<td>Congaree Swamp, USA - present study</td>
<td>2.5-40.0</td>
<td>167</td>
<td>7</td>
<td>1994 - 98</td>
<td>1.48 (1.38)</td>
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<tr>
<td></td>
<td></td>
<td>239</td>
<td></td>
<td>1998 - 02</td>
<td>1.71 (1.59)</td>
</tr>
</tbody>
</table>

Table 2.5. Published liana diameter growth rates (mean annual increment, MAI) to date. For purposes of calculating MAI, negative increments were treated as zero.
Figure 2.1. Map of the location of the Congaree National Park, south of Columbia, South Carolina. The National Park avoided the most severe damage associated with Hurricane Hugo.
Figure 2.2. Changes in tree density (stems ≥ 10 cm), trees supporting vines, and the number of lianas (≥ 2.5 cm) in three forest types over 12 years following the hurricane in 1989. BLH = bottomland hardwood forests.
Figure 2.3. Diameter growth rate (mean ± SE) for lianas by species and host damage. MAI (mean annual increment) based on changes in diameter at four year intervals. Shrinking dbh is treated as zero growth. Different upper case letters indicate significantly different mean diameter growth rates based on a GLM analysis of variance ($\alpha = 0.05$).
Figure 2.4. Diameter growth rate for lianas by species and size class. MAI (mean annual increment) based on changes in diameter at four year intervals. Shrinking dbh is treated as zero growth. Different upper case letters indicate significantly different mean diameter growth rates based on a GLM analysis of variance (α = 0.05).
Figure 2.5. Mortality rates based on life form and potential size within bottomland hardwood forests in the Congaree National Park. Post-Hurricane mortality is assumed to have occurred within one year after Hurricane Hugo. Post-hurricane mortality was based on severe hurricane damage (Snapped-off, tipped-up, or severe branch loss and stem dead in 1994. Post-hurricane liana mortality was based on death of the host tree.
CHAPTER 3

ARE LIANAS INCREASING IN IMPORTANCE IN TEMPERATE FLOODPLAIN FORESTS IN THE SOUTHEASTERN UNITED STATES?

3.1. Introduction

The use of understory and epiphytic vegetation as indicators of ecosystem health requires an understanding of how forests are changing through time. This is particularly true for many tropical and neo-tropical forests where increases in the size and density of woody climbing plants (lianas) has spurred interest in liana ecology and elicited questions about the causes of this change in forest structure and composition (Phillips et al. 2002, 2005; Wright et al. 2004). Mechanisms for these shifts are not known, but could include changes in global temperature or atmospheric chemistry (Condon et al. 1992; Granados and Korner 2002), as well as shifts in disturbance regimes (Laurance et al. 2001; Pérez-Salicrup et al. 2001; Schnitzer and Bongers 2002).

A growing body of literature supports the theory that lianas are increasing in importance, as measured by density, basal area, and the proportion of stems, across widely scattered research sites. Using forest plot data from throughout the Neotropics, Phillips et al. (2002) found that lianas were increasing in size and density in old-growth forests over the last two decades of the twentieth century. Similarly, in Panama, Wright et al. (2004) reported a 100% increase in liana importance over a similar time period in old-growth forests at Barro Colorado Island and surrounding areas. Evidence for similar patterns in
temperate forests is much more limited. In upland old-growth forests in Arkansas, Bragg (2004) observed the absence of lianas in historical photos when compared with current photos and attributed increases in liana density over the twentieth century to the exclusion of fire.

Lianas are direct competitors with trees for nutrients, moisture, and sun light, and they also reduce tree growth rates (Dillenburg et al. 1995) and increase their host trees’ susceptibility to wind damage (Allen et al. 1997). Dillenburg et al. (1995) reported that photosynthesis and biomass allocation of sweetgum (Liquidambar styraciflua L.) were reduced by above and below ground competition with two vines species (Lonicera japonica Thunberg and Parthenocissus quinquefolia (L.) Planchon). Competition resulted in reduced photosynthetic capacity and lower carbon allocation to leaves compared with stems. Allen et al. (1997) found that trees with three or more lianas were significantly more likely to die during a hurricane than trees with no lianas regardless of tree size. Despite these important influences on forest composition and structure, long-term studies of forest dynamics have, until recently, ignored large woody vines (Foster 1988; Halpern 1988; Jones et al. 1994; Bellingham et al. 1995; Bell 1997; Conner et al. 2002). Recent evidence from data on increases in liana density in the absence of disturbance seems to contradict the accepted theory that lianas are most abundant in disturbed forests. In tropical forests, DeWalt et al. (2000) reported significantly lower liana density and species richness in forests older than 70 years; however, they also found that basal area of vines remained the same as lianas increased in size in mature forests. Additionally, Shear et al. (1996) reported that poison
ivy (*Toxicodendron radicans* L.), the most abundant species in the understory in the bottomland forests in Kentucky, was much more abundant in mature forests than in 50-year-old restored bottomland forests where native tree species had been planted.

The objective of this study was to examine long-term trends in liana size and density in old-growth and second-growth floodplain forests located in the Congaree National Park and the Savannah River Site of the southeastern United States. Specifically, we asked the following questions:

1) How have liana densities changed over 12 years in old-growth forests and 22 years in second-growth floodplain forests?

2) Do patterns observed in temperate liana communities reflect patterns observed in tropical forests?

### 3.2. Study Sites

We used data from two long-term studies of floodplain forests in South Carolina. Both forest sites are located just below the fall line on the upper Atlantic Coastal Plain along floodplains of major river systems, the Savannah River and the Congaree River (Fig. 3.1). The first site, the Savannah River and its tributary, Upper Three Runs Creek, is on the U.S. Department of Energy’s Savannah River Site (SRS). Five 1-ha permanent plots were established at SRS, two 1-ha plots in the river floodplain and three 1-ha plots along Upper Three Runs Creek. Access to the SRS has been restricted since 1950 and no active forest management activities have taken place in the areas of these plots during that time period.
The floodplain forests were harvested in the late 1800s (Good and Whipple 1982) but have not been significantly disturbed in more than a hundred years. The second site, the Congaree National Park (CNP), contains the last major remnant of mature bottomland hardwood forest in the southeastern U.S. (Gaddy et al. 1975) and has many record or near record-sized individuals (Jones 1997). The Congaree, unlike the Savannah River floodplain, was impacted by Hurricane Hugo in 1989, a category 4 hurricane that killed 20% of the trees ≥10 cm in its bottomland hardwood forests (Putz and Sharitz 1991).

At both sites, the liana communities are located primarily in the seasonally flooded bottomland hardwood forests. These highly productive forests are composed of sweetgum (Liquidambar styraciflua L.), American holly (Ilex opaca Aiton.), a mixture of oaks (Quercus spp.), sugarberry (Celtis laevigata Willd.), green ash (Fraxinus pennsylvanica Marshall.), elm (Ulmus spp.), red maple (Acer rubrum L.), and other hardwood species, as well as scattered loblolly pine (Pinus taeda L.). Major liana species include Campsis radicans (L.) Seeman, Parthenocissus quinquefolia, Toxicodendron radicans and Vitis spp. (Good and Wipple 1982; Allen et al. 1997; Allen and Sharitz 1999).

3.3. Methods

3.1. Field methods

In the SRS floodplain, five 100 x 100 m or 50 x 200 m (1 ha) permanent plots were established in 1979 in the most mature forests available (Good and Whipple 1982). All woody stems ≥ 4.5 cm diameter at breast height (dbh) were measured, mapped,
permanently tagged, and identified to species. No effort was made to determine if stems were sprout or genetically distinct individuals. Diameter was measured at 1.4 m above the ground (10 centimeters below the permanent tag). Thus, dbh was measured at the same point on the stem at each sampling period. Plots were re-sampled in 1989, 1995, and 2001.

Lianas stems were included in the plot if they crossed 1.4 m within the plot boundaries. If liana stems returned to the ground after crossing 1.4 meters (primarily *Vitis* spp.) a determination was made whether it should be classified as one stem or two (or more). If the stem had no branches before returning to the ground, it was only tagged the last time it crossed 1.4 meters in height. If branches were present, stems were tagged each time the liana crossed 1.4 meters. When liana stems touch the ground, they formed adventitious roots and were more likely to decay. The majority of lianas in this study climb by adhesive roots or tendrils and did not survive falls from their host.

In the CNP, plots were established during the winter and spring following the hurricane (1989-90). Six 100 x 100 m (1 ha) plots were placed in different forest communities along a disturbance gradient in areas where no previous logging was evident (Sharitz et al. 1992; Allen et al., 1997; Allen and Sharitz 1999). Plots were re-sampled during the winter and spring of 1993-4, 1997-8, and 2001-2. All woody stems ≥10 cm dbh were measured, mapped, permanently tagged, and identified to species. Woody stems ≥ 2.5 cm but <10 cm were sub-sampled in five 20 x 20 m subplots per ha plot. Diameters were measured using a diameter tape or calipers at 1.4 m above the ground (10 cm below the permanent tag). The numerous aerial roots produced by poison ivy necessitated averaging
two caliper readings for an accurate dbh measurement for this vine species. Because the initial sampling was performed immediately following the hurricane, trees damaged and killed by the storm were easily distinguished. Thus, the 1989-90 data provide a reasonable measure of pre-hurricane conditions (Sharitz et al. 1992). Post-hurricane liana mortality was based on host death from tip-up or snap-off and liana death by 1994. Hurricane damage in the form of branch loss by lianas was difficult to assess during the initial survey.

3.3.2. Statistical Methods

Repeted-measures analysis of variance models (ANOVA; PROC GLM, SAS Institute Inc., 2005) where time was the repeated measure were used to determine if changes in liana density and proportion of stems over time were significant in both SRS and CNP. McHughly’s sphericity was used to test whether the covariance matrix met Type-H covariance structure. If the sphericity statistic was lower than our alpha level (0.05) the Type-H covariance structure had not been met and adjustments to the degrees of freedom were needed. Greenhouse-Geisser (G-G) and Huynh-Feldt (H-F) provide adjusted F-values when the sphericity test is not met (Huynh and Feldt, 1976). Additionally, we used regression analysis (PROC REG, SAS Institute Inc., 2005) to examine trends in the mean proportion of lianas, mean liana density, and mean liana basal area over time for the two study sites. Regressions were conducted on both site means and on individual plot data with an alpha of 0.05. Regression values were considered significant at 0.05. Mean Annual Increment (MAI) was calculated for each
site and sample interval. Growth rates were placed on an annual basis for comparison purposes. Negative diameter growth was treated as zero growth to be consistent with existing published liana growth data. Negative diameter growth occurs when lianas do not have intact cambium surrounding the stem and have heart rot. The proportion of woody stems composed of lianas was calculated by dividing the total number of lianas by the density of all woody stems greater than the minimum size class for the site.

3.4. Results

3.4.1. Changes in liana density

Mean liana density was not significantly different (n=5, F = 2.67, P = 0.11) between 1979 and 2001 in Savannah River Site (Table 3.1). Conversely, liana density increased significantly (n=6, F=9.48, P=0.005) in the Congaree floodplain between 1989 and 2002 (Table 3.1). However, we observed considerable variability among plots with liana density ranging from 0 to 293 stems ha\(^{-1}\). In 1979, only one liana was found in the permanent plots on the SRS but 22 years later in 2001, liana density ranged from 1 to 34 stems ha\(^{-1}\). While there were higher densities in the CNP, liana density ranged from 50 to 202 stems ha\(^{-1}\) in 1989 and increased to 71 to 293 stems ha\(^{-1}\) in 2002.

Despite the high variability among plots, linear regression on mean liana density provides some insight on liana trends through time. In the Savannah River floodplain system (Fig. 3.2A), regression indicates a linear increase in liana density when the means of all five plots are used (R\(^2\)=0.99, P=0.02). The inconsistency between the two analyses
becomes clear in an examination of changes in individual plot densities over time. The two plots in the lower portion of Upper Three Runs Creek in an area with a wide floodplain had much greater increases in liana density then two plots along the headwater stream and one plot on a terrace of the Savannah River.

In the Congaree River floodplain, the changes in mean liana density reflect the disturbance history of the site (Fig. 3.3A). Prior to Hurricane Hugo in 1989, mean (± SE) liana density was 137.7 (± 20.8) stems ha\(^{-1}\). Immediately following the hurricane stem density decreased to 104.1 (± 17.7) stems ha\(^{-1}\) and by 2002 mean liana stem densities were 213 (± 30.2) stems ha\(^{-1}\). Despite the initial decrease in liana stems following the hurricane, mean liana stem density significantly increased over time from 1989 to 2002 in the CNP (\(R^2=0.76, P=0.05\)) (Fig. 3.3A). This trend was even stronger (\(R^2=0.95, P=0.026\)) when we examined only the mean liana density from 1990 to 2002 to remove the immediate effect of Hurricane Hugo (Fig. 3.4A).

3.4.2. Changes in the proportion of lianas

Changes in the proportion of lianas reflect not only changes in liana density but changes in overstory tree density as well. At SRS, the proportion of lianas increased from 0.001 (range 0.0 to 0.001) to 0.012 (range 0.001 to 0.026) from 1979 to 2001 (Fig. 3.2B); however, a repeated measure ANOVA indicated that differences in mean proportions of lianas were not significant (n = 5, F = 3.54, P = 0.061). Despite the high variability among sample plots, regression analysis of the mean proportion of lianas indicates a significant
linear increase over time ($R^2=0.99$, $P=0.0075$). In the Congaree, the mean proportion of lianas increased from 0.10 (range 0.046 to 0.131) to 0.12 (range 0.033 to 0.184) from 1989 to 2002 (Fig. 3.3B). As with the SRS sites, the data were highly variable but differences in the mean proportion of lianas from 1989 and 2002 were significant ($n = 6$, $F = 3.71$, $P = 0.027$). Conversely, regression analysis on the mean proportion of lianas over time does not indicate a linear increase in the proportion on lianas ($R^2=0.40$, $P=0.24$) between 1989 and 2002 in the CNP (Fig. 3.3B). When the immediate effects of the hurricane are removed, regression analysis on the proportion of lianas were still not significant ($R^2=0.86$, $P=0.065$)(Fig. 3.4B).

3.4.3. Changes in liana growth rates and basal area

At the SRS, liana diameter growth rates have not changed over time (Table 3.2); however, the sample size is limited as very few lianas survived any of the intervals between samples. The single liana tagged in 1979 did not increase in diameter by 1989. On average ($\pm$ 1 SE), the diameter growth rate of lianas varied from 0.57 (0.11) mm yr$^{-1}$ to 0.50 (0.11) mm yr$^{-1}$ from 1979 to 2001 (Table 3.2). Nevertheless, regression analysis revealed a significant linear increase ($R^2 = 0.99$, $P = 0.0131$) in liana basal area (Fig. 3.2C). In the CNP floodplain, diameter growth rates have increased from 1.29 (0.05) mm yr$^{-1}$ to 1.71 (0.10) mm yr$^{-1}$ from 1990-4 to 1998-2002 (Table 2). This may be influenced by the reductions in mean sizes associated with recruitment of smaller diameter stems. Regression analysis on changes in liana basal area through time in the CNP were not significant ($R^2 =$
0.64, $P = 0.11$) (Fig. 3.3C). If the effects of the hurricane are removed by starting the analysis in 1990, significant ($R^2 = 0.92, P = 0.039$) linear increases in liana basal area were detected (Fig. 3.4C).

### 3.5. Discussion

#### 3.5.1 Development of liana communities

Although highly variable, our data suggest that there are important changes occurring in liana communities of bottomland forests of the southeastern U.S. Because of high variability, we detected significant increases in mean liana density only in the Congaree National Park. However, based upon our regression analyses, liana densities, the proportion of lianas, and liana basal area in these forest ecosystems appear to be increasing at a linear rate in both the second-growth and old-growth bottomland forests along similar river systems in South Carolina. The fact that liana diameter growth rates have increased over time in the bottomland forests of the Congaree, in conjunction with decreased liana mortality rates and increased subcanopy tree mortality rates (Allen et al. 2005), may indicate why lianas are increasing in density relative to other life forms. However, this relationship appears to be dynamic as these forests respond to disturbance, specifically wind damage associated with hurricanes. Our data from the Congaree National Park demonstrate this relationship, as increases in subcanopy tree density resulting from the increased sunlight and other resources following the hurricane have
lowered the rate of increase in the proportion of lianas in the old-growth bottomland forest.

Do the trends observed in liana communities in South Carolina over time compare to those observed in the tropics and neotropics? Phillips et al. (2002) and Wright et al. (2004) have documented significant increases in liana density and size in tropical forests, similar to the patterns we have observed in the bottomland forests of the southeastern U.S. Additionally, Wright et al. (2004) reported that while lianas increased by 100% during the 1980’s and 1990’s, understory shrubs steadily declined. Subcanopy trees and shrubs have exhibited similar patterns in both disturbed old-growth and second-growth floodplain forests in South Carolina (Jones et al. 1994; Sharitz and Allen, unpublished data)

While these long-term trends in liana density, proportion of lianas, and mean liana diameter are informative, there are some limitations to the sample design that may inhibit our ability to adequately quantify liana dynamics in these floodplain forests. These include a small sample size of large plots, and the lack of adequate replication in large-scale vegetation plots. Long-term studies of forests provide unique insights into how forests change through time, and often these studies utilize large research plots (1 ha or larger) to examine forest stand dynamics. The conflict between adequate plot size and the number of plots sampled can limit statistical power, especially in forests that are species rich and highly variable in tree and vine composition such as those in
southeastern U.S. river floodplains. This fact, when combined with the clustered distribution of lianas (Allen et al. 1997), can mean that larger plot sizes as well as greater replication are required to clearly identify long-term trends.

3.5.2 Future research needs

Currently, discussions of old-growth forest characteristics, forest development patterns, and bottomland forest management do not adequately address the role lianas play in southeastern floodplain forests (Davis 1996; Oliver and Larson 1991). If lianas make up more than 10% of the stems in floodplain forests as our results indicate, then liana leaf areas comprise a significant fraction of the total leaf area and should not be ignored. If lianas are increasing in density, proportion of woody stems, and basal area, they are likely influencing tree species composition, growth, and mortality. Consequently, we argue that the role of lianas in forest stand development should be explored and incorporated into stand development models of bottomland hardwood forests.

While increases in liana abundance have been associated with disturbed systems (Laurance et al. 2001), our data seem to indicate lianas are increasing with forest age in a second-growth forest where the last major disturbance occurred over 100 years ago. In addition, the old-growth floodplain forests at the CNP have some of the highest reported densities of lianas in any temperate forests both prior to and 13 years after the hurricane.
These facts are interesting as many historical photographs from the Congaree National Park, as well as other studies in forests of the southeastern U.S. do not show a well developed liana community (Quarterman and Keever 1962; Bragg 2004). If this is the case and lianas are becoming more important components of southeastern bottomland forests as our data would indicate, then more information on the role of disturbance and specific mechanisms that regulate the development of liana communities is needed. This includes using techniques that have historically not been applied to lianas, including historical reconstructions and dendroecological studies. Additionally, the influence of river regulation and subsequent changes to the hydrologic regime should be examined as these factors may have influenced the competitive interactions among lianas, overstory trees, and subcanopy trees.

References


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Table 3.1. Liana ANOVA results by site through time for the Savannah River Site and the Congaree National Park, South Carolina, USA. Plots (5 1-ha) in the Savannah River Site include lianas ≥ 4.5 cm dbh. Plots in the Congaree National Park include lianas ≥ 2.5 cm dbh. § Repeated-measure adjusted probability (G-G = Greenhouse-Geisser and H-F = Huynh-Feldt). Mauchly’s sphericity test examines the form of the covariance matrix. If the P-value is lower than the alpha level, the sphericity assumption has been violated and either G-G or H-F (preferred) adjusted P-values is appropriate.

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<th>P</th>
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<td>0.181</td>
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<td>Proportion lianas</td>
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<td>3.54</td>
<td>0.061</td>
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<td>Liana density</td>
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<td>4</td>
<td>9.48</td>
<td>0.0004</td>
<td>0.021</td>
<td>0.005</td>
</tr>
<tr>
<td>Proportion lianas</td>
<td>0.029</td>
<td>4</td>
<td>3.71</td>
<td>0.025</td>
<td>0.0818</td>
<td>0.027</td>
</tr>
<tr>
<td>Site</td>
<td>Size Range (cm)</td>
<td>n</td>
<td>#Species</td>
<td>Time Period</td>
<td>MAI (SE) (mm/year)</td>
<td></td>
</tr>
<tr>
<td>-------------------------------</td>
<td>-----------------</td>
<td>----</td>
<td>----------</td>
<td>-------------</td>
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<td></td>
</tr>
<tr>
<td>Savannah River (unpublished)</td>
<td>5.0</td>
<td>1</td>
<td>1</td>
<td>1979-89</td>
<td>0.00 (-)</td>
<td></td>
</tr>
<tr>
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<td>4.5-6.8</td>
<td>25</td>
<td>4</td>
<td>1989-95</td>
<td>0.57 (0.11)</td>
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<tr>
<td>Savannah River (unpublished)</td>
<td>4.5-8.1</td>
<td>40</td>
<td>3</td>
<td>1995-01</td>
<td>0.50 (0.11)</td>
<td></td>
</tr>
<tr>
<td>Congaree Swamp, USA (Allen et al. 1997)</td>
<td>2.5-40.0</td>
<td>157</td>
<td>7</td>
<td>1990 - 94</td>
<td>1.29 (0.05)</td>
<td></td>
</tr>
<tr>
<td>Congaree Swamp, USA (Allen et al. 2005)</td>
<td>2.5-40.0</td>
<td>167</td>
<td>7</td>
<td>1994 - 98</td>
<td>1.48 (0.11)</td>
<td></td>
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<tr>
<td>Congaree Swamp, USA (Allen et al., 2005)</td>
<td>2.5-40.0</td>
<td>239</td>
<td>7</td>
<td>1998 - 02</td>
<td>1.71 (0.10)</td>
<td></td>
</tr>
</tbody>
</table>

Table 3.2. Changes in liana diameter growth rates (mean annual increment, MAI) through time in the Congaree National park and the Savannah River floodplain. For purposes of calculating MAI, negative increments were treated as zero.
Figure 3.1. Locations of the Congaree River and the Savannah River floodplains, South Carolina.
Figure 3.2. Changes in mean liana density (A), proportion of lianas (B), and liana basal area (C) in five 1-ha plots in the Savannah River floodplain and its tributary. Minimum size is 4.5 cm dbh. Bold regression lines, error bars (±SE), and summary statistics are for the mean of five 1-ha plots. Symbols and pale regression lines reflect trends in individual plots.
Figure 3.3. Changes in mean liana density (A), proportion lianas (B) and liana basal area (C) in six 1-ha plots in the Congaree River floodplain. Minimum size is 2.5 cm dbh. Bold regression lines, error bars (±SE), and summary statistics are for the mean of six 1-ha plots. Symbols and pale regression lines reflect trends in individual plots.
Figure 3.4. Changes in mean liana density (A), proportion lianas (B) and liana basal area (C) in 6 1-ha plots post-hurricane, 1990-2002, in the Congaree River floodplain. Minimum size is 2.5 cm dbh. Bold regression lines, error bars (±SE), and summary statistics are for the mean of six 1-ha plots. Symbols and pale regression lines reflect trends in individual plots.
4.1. Introduction

Although the principles of ecological forestry have been promoted for over 60 years (e.g., Spurr and Cline 1942), recently there has been an increased emphasis on the use of ecological forestry in forest ecosystems of North America (Franklin et al. 2002; Seymour et al. 2002; Mitchell et al. 2003; Crow and Perera 2004; Larson and Nielsen 2007). These efforts began with the promotion of “New Forestry” in the late 1980s (Franklin 1989; Swanson and Franklin 1992), and continued with the “sustained yield” and “ecosystem management” paradigms in the 1990s (Seymour and Hunter 1999). While there are a variety of definitions and synonyms for ecological forestry, the basic premise of the paradigm is the application of ecological principles to the management of forest ecosystems, with a primary focus on emulating natural ecosystem patterns and processes (Seymour and Hunter 1999; Mitchell et al. 2003; Crow and Perera 2004; Larson and Nielsen 2007).

One of the basic tenets of ecological forestry is based upon the increasing evidence that the characteristics of managed forests are inherently different than those which develop following natural disturbances (e.g., McRae et al. 2001; Palik et al. 2002;
Crow and Perera 2004). For example, harvesting operations typically remove more carbon, and historically have resulted in simplified species compositions and structures (Crow and Perera 2004). Consequently, the most appropriate silvicultural systems in an ecological forestry context will be those that best emulate the processes and outcomes of natural disturbance. Natural ecosystems are thought to be more resilient and diverse than their intensively-managed counterparts, in part, because of the increased compositional and structural complexity that results from recurring natural perturbations (Seymour and Franklin 1999; Franklin et al. 2002; Seymour et al. 2002; Mitchell et al. 2003; Crow and Perera 2004; Larson and Nielsen 2007). The increased complexity, often in the form of biological legacies (e.g., organisms, organic matter, and the biologically created patterns and structures that persist post-disturbance), provides important functional roles in forest ecosystems as the forest ecosystem recovers following disturbance (Franklin et al. 2003; Mitchell et al. 2003).

Silvicultural systems implemented within the context of the ecological forestry paradigm require a comprehensive understanding of natural disturbance and the associated biological legacies (Franklin et al. 2002). Unfortunately, our understanding of how many forest ecosystems recover from disturbance and develop over time is lacking. This is particularly true for bottomland hardwood forest ecosystems of the southeastern United States, which have been extensively modified over the past 200 years (Brinson 1990; Kellison et al. 1998) and are currently managed across the southeastern United States with intensive forestry practices (e.g., clearcutting).
Unlike in upland forests, autogenic processes such as sediment deposition and the associated changes in soil chemistry and hydrologic regime are thought to be the primary mechanisms that drive successional patterns in bottomland hardwood forests (Hodges 1997). In these forest ecosystems, small changes in elevation can influence flood depth and duration on a seasonal or annual basis, which regulate forest composition and structure (Wharton et al. 1982; Brinson 1990; Sharitz and Mitsch 1993; Kellison et al. 1998; Bendix and Hupp 2001). The interaction of flood- and shade-tolerance differences in the vegetation results in increased structural complexity and diversity of plant lifeforms (including lianas) and of forest community types (Hall and Harcombe 1998; Thompson 1998; Battaglia et al. 2004; Battaglia and Sharitz 2006).

Less frequent and more catastrophic disturbances, such as strong winds associated with tropical storms and hurricanes also strongly influence forest development and successional patterns in bottomland hardwood forests (Haymond et al. 1996; Webb 1999; Batista and Platt 2003; Zhao et al. 2006). Hurricanes create a mosaic of forest damage from catastrophic blowdowns to scattered treefalls based on winds speeds and associated tornadoes (Webb 1999). Species found in hurricane-prone regions have adapted to repeated wind damage by resisting wind damage, shedding limbs, sprouting, and taking advantage of establishment opportunities (Batista and Platt 2003). For example, in South Carolina, Hurricane Hugo disproportionately uprooted oaks and loblolly pine while sweetgum and green ash suffered extensive branch loss (Putz and Sharitz 1991; Sharitz et al. 1992). Consequently, the interaction of these different types of natural disturbance
regimes operating at different spatial and temporal scales results in late successional forests dominated by a mosaic of both shade-intolerant and flood-tolerant species (Zhao et al. 2006).

Before we can develop silvicultural systems for bottomland hardwood forests of the southeastern Coastal Plain that better emulate natural disturbance processes and implement ecological forestry principles, we need to not only understand how these forest ecosystems respond to natural disturbances, but we also need to examine how these forests respond following different types silvicultural activities. Forest stands that experience only natural disturbances can serve as controls for harvested forests to help determine if harvests are being conducted in a sustainable manner (Frelich et al. 2005). Fortunately, areas in the Congaree National Park, perhaps the largest and best remaining example of an old-growth bottomland hardwood forest ecosystem in the southeastern United States (Davis 2003) provides an excellent opportunity to examine forest development patterns following both natural disturbance and silvicultural activities. For instance, there are old-growth areas within the bottomland hardwood forests of the Congaree National Park that are recovering from a large-scale, natural disturbance in 1989 (i.e., Hurricane Hugo) and old-growth stands that were subjected to a partial harvest in 1974-76 and commercial clearcuts in 1976. The objective of this research was to compare the composition and structure of bottomland hardwood forests that have experienced different types and levels of disturbance.
4.2. Study Area

The 9,953-ha Congaree National Park (CNP) is located on the Atlantic Coastal Plain just below the “fall line”, south of Columbia, South Carolina (33°50’ north latitude, 81°45’ longitude) (Fig. 4.1). Although the CNP contains the largest major remnant of old-growth bottomland hardwood forest in the southeastern U.S. (Davis 1996; Davis 2003), approximately 1,500 ha of the CNP had been clear-cut or selectively cut in the 1970s prior to the formation of the park in 1976 (Davis 2003). In fact, it was these harvesting activities that hastened the formation of the Congaree National Monument in 1976, and later the Congaree National Park in 2003.

The physiography of the CNP is complex, with a network of small stream, levees, sloughs, and terraces. Elevations range from 25.6 to 32.0 m above sea level across the floodplain, gradually declining from the northwest to southeast (Wiggins-Brown et al. 2000). The Congaree River watershed in western North and South Carolina receives an average of 122 cm of precipitation annually (Rudell 1984). The predominant floodplain soils are silty clay loams that are poorly drained and have low permeability (Crews 1976).

The current vegetation includes large areas of mature deciduous forest (Jones 1997). Many trees of near record-size occur in the CNP (Sharitz et al. 1992; Jones 1997). More than 155 tree, shrub, and woody vine species are known from the CNP (Thompson 1998; Gaddy and Nelson 2006). The old-growth portions of the CNP are very diverse with over 80 tree species (Davis 2003), and the CNP has been described as one of the tallest temperate deciduous forests in the world with an average canopy height of
between 40-50 meters in the old-growth forests (Jones 1997). Along the creeks and sloughs that flow through the CNP, baldcypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*) dominate while the natural levees and higher elevations where lianas proliferate are dominated by sweetgum (*Liquidambar styraciflua*), green ash (*Fraxinus pennsylvanica*), loblolly pine (*Pinus taeda*), nine species of bottomland oaks (*Quercus* spp.), and three species of hickories (*Carya* spp.). These old-growth forests also contain a dense and diverse liana community (Allen et al. 1997; Allen et al. 2005).

On September 21, 1989 Hurricane Hugo, a category 4 hurricane, made landfall in South Carolina north of Charleston in the Francis Marion National Forest. Wind speeds of up to 155 km·hr⁻¹ were recorded near the CNP and these winds affected the various forest types differently (Putz and Sharitz 1991). Areas dominated by bald-cypress (*Taxodium distichum* (L.) L.C. Rich.) and water tupelo (*Nyssa aquatica* L.) experienced primarily branch loss though species less tolerant of flooding were disproportionately up-rooted. In bottomland hardwoods forests, 37% of the trees suffered severe damage (snap-offs, tip-ups, or severe branch loss) (Putz and Sharitz 1991; Sharitz et al. 1992; Zhao et al. 2006). Hurricane winds caused extensive damage, sometimes intense, but the damage was variable as large areas suffered only extensive branch loss.
4.3. Methods

4.3.1. Study design and data collection

Two vegetation data sets were used to address our research questions. The first data set included data from six of the ten permanent 1-ha plots in the old-growth bottomland hardwood forests in 1989-90 established to monitor the response of these forests to Hurricane Hugo. Plots were established during the winter and spring following Hurricane Hugo. Plots were placed in different forest communities along a disturbance gradient in areas where no previous logging was evident (Sharitz et al. 1992; Allen et al. 1994; Allen et al. 1997; Allen and Sharitz 1999; Allen et al. 2005; Zhao et al. 2006). Plots were grouped in low (21-46%) and high damage (58-68%) based on the percentage of damaged to stems over 40 cm dbh (Zhao et al. 2006). All woody stems ≥10 cm dbh were measured, mapped, permanently tagged, and identified to species. Woody stems ≥ 2.5 cm but <10 cm, including lianas, were sub-sampled in five 20 x 20 m subplots per ha plot. Diameters were measured using a diameter tape or calipers at 1.4 m above the ground (10 cm below the permanent tag). Plots were re-sampled during the winter of 2005-6 providing a sixteen year record of forest development.

The second source of plot data was from vegetation mapping dataset from CNP collected by crews led by A.J. Thompson and L.L. Gaddy (Thompson 1988). We utilized fourteen of the 125 0.1 ha plots located in old-growth areas that had either been clearcut in 1976 (five plots) and selectively logged between 1974 and 1976 (fourteen plots) prior to National Park Service acquisition. Selective logging was designed to be sustainable on
Foresters described the forests as being overmature and prescribed removal of all overmature, mature, or cull trees, a large fraction of the existing timber (Kinzer and Cely, In prep.). Most of the plots were 0.1 ha (20 x 50 m) but some were smaller in area or had different shapes, in order to remain within a homogeneous community. The original data consist of stem counts for all woody species, including lianas, with a diameter at breast height (dbh) of at least 2.5 cm, grouped into eight diameter classes. The total number of stems in each diameter class was tallied by species in each plot and expressed as density (stems/ha) and basal area (m²·ha⁻¹). Plots were re-sampled in 1996, providing a 20-22 year record of post-cutting forest development.

4.3.2 Data analysis

For all analyses we considered the different source and intensity of disturbance to be an individual treatment (hereafter referred to as disturbance type). These included two categories of old-growth (those with low damage and high damage) and two categories of forest management (selectively cut and clearcut). For the purposes of our analyses, the old-growth stands represent a control or benchmark with which to compare the composition, structure, and diversity of the managed stands. Differences in species composition, diversity, and structure were determined by summarizing plot data and expressing results on per hectare basis. Comparisons of species composition were based
on relative basal area standardized on plot maxima after placing on a per hectare basis to correct for unequal sample plot sizes.

Multi-response permutation procedure (MRPP in PC-ORD; McCune and Mefford 1995) using the relative basal area data was used to test the hypothesis that the species composition was not different among the different disturbance types. A natural weighting factor recommended by Mielke (1984) and Sørenson distances (McCune et al. 2000) were used in the calculations. Sørenson distances, although very similar to Euclidian distances, are less likely to emphasize the influence of outliers (McCune and Mefford 1995). We supplemented the MRPP with Wilcoxon tests to examine difference in relative basal area by species between the different disturbance types. For the Wilcoxon tests, we included only those species that occurred on 10% of the plots (39 out of 51 species) in an effort to reduce the noise often associated with community datasets.

Ordination techniques were used to explore systematic trends in species composition among the four disturbance types using basal area as a measure of species abundance. Prior to analysis, the data were standardized by the species maximum (Faith et al. 1987) to equalize the potential contributions of species to dissimilarity among sample units and ordinated with nonmetric multidimensional scaling (NMDS; Kruskal 1964) using the Bray-Curtis dissimilarity index (Bray and Curtis 1957). The NMDS was conducted using ten starting positions with a maximum of 200 iterations in DECODA software (Minchin 2006). Only species or genre present in two or more plots (39 out 55) were included in the ordination. Environmental variables were related to ordination axis.
by vector fitting. These environmental variables included level of disturbance (proportion of basal area removed), distance from the river, and down river distance. The proportion of basal area removed was known for hurricane damage plots but was estimated for clearcuts (100%) and partial cuts (50%). In partially harvested areas, as much as 50% of the overstory was removed (Nix and Barry 1992). Distance from the river was measured in kilometers from the river. Down river distance was quantified by acquiring river miles from the junction with the Wateree River. To minimize the effects of local meanders, linear distances were measured from the 8 kilometer mark from the Wateree River near the former (prior to 2006) southeastern boundary of the park.

Finally, we examined density, basal area, and size-class distributions to examine changes in stand structure among the different disturbance types. Stem density reflect all woody stems \(\geq 2.5\) cm. In areas subject to harvesting where stem diameters were collected in 5 cm dbh classes, basal area values were calculated by using the midpoint value of each dbh class.

4.4. Results

4.4.1 Differences in species composition

Forest composition among the four disturbance types has been influenced by the type and extent of disturbance events (Table 4.1). The results of the MRPP suggest that
species composition is not significantly different among the four disturbance types ($T = -1.57, P=0.069$), indicating differences in species composition at the community-level among the different disturbance types may be difficult to detect in this species-rich forest. Of the 39 species that occurred in at least 10% of the plots, three had significantly different distributions among disturbance types (Table 4.2 and 4.3). Only *Ilex opaca* ($P < 0.05$) was present in all four disturbance types but was more common in old-growth forests in areas that suffered minimal hurricane damage. Though marginally insignificant ($P=0.051$), *Liquidambar styraciflua* appears to be more common in old-growth forests, particularly areas the suffered minor hurricane damage. The presence of some of the least flood-tolerant (*Fagus grandifolia, Liriodendron tulipifera, and Quercus shumardii*) species in the old-growth forests that suffered minimal hurricane damage may indicate a relatively higher elevation within the floodplain.

The NMDS in two dimensions adequately summarized (stress = 0.277) the bottomland hardwood overstory community data (Fig. 4.2). Grouping of plots on Axis 1 and 2 suggest that beyond similarities among low damaged old-growth sites, sample plots are not grouped by disturbance history. This supports the results of the MRPP, that there are no significant patterns in species composition. Three environmental variables were significantly correlated with the ordination. Disturbance level ($P < 0.001$), defined as the proportion of basal area removed and estimated for clearcut and selective cut areas, was closely correlated with the first NMDS axis. Two environmental variables not associated with recent disturbance history were also significantly correlated with the ordination:
distance from river \((P < 0.001)\) and up-river distance \((P < 0.001)\). When we examined the NMDS results from the perspective of species (i.e., species center or a weighted average of plot scores) the ordination indicates where species were most prevalent (Fig. 4.3). Areas that were disturbed, partially or completely harvested, or suffered high levels of hurricane damage, had higher relative basal areas of *Fraxinus pennsylvanica*, *Celtis laevigata*, and *Pinus taeda*. *Berchemia scandens* was also most common in these areas (Table 4.3).

Liana density reflected disturbance history in the old-growth and harvested areas of CNP (Table 4.3). *Vitis* spp. was most common in areas that were clearcut in 1976 and progressively less dense in partially harvested forests, areas heavily and minimally damaged by Hurricane Hugo. *Toxicodendron radicans* was most common in areas heavily damaged by the hurricane and least common in clear cut areas. Lianas, however, were not associated with disturbance type in the NMDS ordination. Lianas species centers were mostly centrally located on Axis 1 and 2. Some of the least flood-tolerant species were located in southeast quadrant of the ordination possibly indicating an elevational gradient.

### 4.4.2 Differences in stand structure

Stem densities \((2,538 \text{ stems·ha}^{-1})\) and basal area \((45.3 \text{ m}^2\cdot\text{ha}^{-1})\) were highest in areas that had been clearcut twenty years prior to sampling. Areas that were subject to
severe hurricane damage also had high stem densities (1868.7 stems·ha⁻¹) but had the lowest basal area (35.4 m²·ha⁻¹). Areas that were selectively harvested 20-22 years prior to sampling has the lowest stem density (1156.7 stems·ha⁻¹) but also had a basal area of 35.6 m²·ha⁻¹. Areas that suffered only minor hurricane damage had both low stem density (1259 stems·ha⁻¹) and high basal area (44.7 m²·ha⁻¹).

The size class distributions of all woody stems (Figure 4.4) reflect both the intensity and type of disturbance. Areas that suffered minimal hurricane damage and areas that were partially harvested had very similar size-class distributions. Areas that experienced more intense disturbance (i.e., high hurricane damage or clearcutting) had higher densities of stems less than 10 cm dbh. The primary differences between the old-growth forests that experienced natural disturbance versus those old-growth forests that were either partially harvested or clearcut are the rare (≤ 4·ha⁻¹) large stems ≤ 130 cm dbh and lack of stems > 60 cm in areas that were clearcut.

4.5. Discussion

The application of ecological forestry principles requires a better understanding of forest development patterns following both natural and anthropogenic disturbance. Historically, there has been the assumption that even-aged silvicultural systems that have been applied within bottomland hardwood forests of the southeastern United States are analogous to stand-replacing disturbances associated with intense windstorms. Our
analysis from the Congaree National Park not only provides one of the first analyses of early stand development in floodplain forest ecosystems of the southeastern United States, but also is unique in that it examines how old-growth floodplain forests respond to different types of disturbances at different intensity levels.

The major forms of disturbance affecting floodplain forests in the southeastern U.S. are floods, tornadoes, hurricanes, severe wind storms, fires, and mammalian herbivory (Frelich 2002). The frequency and severity of large-scale wind disturbances such as hurricanes varies with distance from the coast and patterns of hurricane storm tracks. Hurricanes weaken upon land-fall or movement over colder ocean waters. Hurricanes frequently spawn tornadoes when they make landfall. Heavy rains are also associated with hurricanes and tropical storms, 35 cm average for a moderate hurricane, can produce flood events (Foster and Boose 1995). Conner (1996) reported that hurricanes occur about once every 20 years in south Florida and are more common on the Gulf Coast. The southern Atlantic Coast has 1-16% yr\(^{-1}\) probability of being struck by a hurricane and 0-7% yr\(^{-1}\) probability of being struck by a severe hurricane (>125 mph winds), a high category 3 to 5 hurricane on the Saffir-Simpson hurricane scale (>125 mph winds) (Bellis 1995).

4.5.1. Differences among disturbance types

The primary differences in forest composition between the stands that experienced natural disturbance versus those that were either selectively-cut or clearcut
were the proportions of relative basal area of the dominant tree and vine species. Although the NMDS ordinations of species composition did not reveal differences between the four disturbance types, the analyses do suggest that the areas that experienced natural disturbance were more compositionally complex than those which experienced disturbance associated with forest management. For example, areas with minor hurricane damage graded into areas that suffered more severe damage with more gradual edges and boundaries. However, no patterns were evident for areas subject to partial harvesting or clearcutting. Finally, the NMDS indicated that the liana community composition was similar across all disturbance types.

There were also significant differences in stand structure suggesting that the areas recovering from natural disturbance were more complex. For example, areas subject to partial or complete cutting had a lower mean relative basal area of *L. styraciflua* and *I. opaca*, while *I. opaca* was more common in those areas that experienced minimal hurricane damage. There were also differences in stand structure that indicate that the stands that experienced natural disturbances were more complex, despite being relatively similar in the amount of time since disturbance (16-22 years). For example, areas that have been clearcut in the 1970s have distinct structures from the old-growth forests, including areas that were heavily disturbed by Hurricane Hugo. Visually, the presence of clumps of trees that originated from stump sprouts and the prevalence of light-demanding lianas like *A. arboria* are different from less disturbed old-growth areas. The relative absence of *I. opaca* in the subcanopy of harvested areas, the most common stem
in old-growth areas, provide a much sparser subcanopy and midstory. These results are similar to those of Thompson (1998) who noted that old-growth floodplain forests are characterized by greater structural and functional complexity than younger forests.

4.5.2 Management implications

In terms of restoring floodplain forest ecosystems, the first and most important step is restoring the hydrologic regime. The depth, duration, and timing of floods is a critical component that regulates the structure the plant community by causing species specific mortality. Changes to the hydrologic regime have resulted in shifts in plant community composition (Junk et al. 1989; Shartiz et al. 1992; Rice and Peet 1997; Minchin and Sharitz 2007). During the accuracy assessment of Congaree vegetation map, Gaddy (2000) noted that half the ‘Ampelopsis-Vitis’ vegetation type was located in harvested areas, possibly indicating a need for post harvest control. However, in order to emulate natural disturbance in floodplain forests, the disturbance regime needs to be defined.

A major difference between managed forests and disturbed old-growth forest is the structural complexity, a reflection of the biological legacy present in the old-growth. In these highly productive forests, the diverse subcanopy, liana, and shrub communities as well as the lack of invasive herbs and shrubs differentiate old-growth from harvested forests.
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### Table 4.1. Tree and woody vine density in the Congaree National Park (dbh ≥ 2.5 cm).

<table>
<thead>
<tr>
<th>Damage Level</th>
<th>Density (stems/ha)</th>
<th>Basal Area (m²/ha)</th>
<th>n</th>
<th>Year Sampled</th>
<th>Total Area Sampled</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low Damage in 1989</td>
<td>1259</td>
<td>44.7</td>
<td>3</td>
<td>2005-6</td>
<td>3.0 ha</td>
</tr>
<tr>
<td>High Damage in 1989</td>
<td>1868</td>
<td>35.4</td>
<td>3</td>
<td>2005-6</td>
<td>3.0 ha</td>
</tr>
<tr>
<td>Selective cuts 1974-76</td>
<td>1156</td>
<td>35.6</td>
<td>9</td>
<td>1996</td>
<td>0.9 ha</td>
</tr>
<tr>
<td>Clearcut 1976</td>
<td>2538</td>
<td>45.3</td>
<td>5</td>
<td>1996</td>
<td>0.5 ha</td>
</tr>
<tr>
<td>Species</td>
<td>Old-growth forest 2006</td>
<td>Second-growth forest 1996</td>
<td></td>
<td></td>
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<tr>
<td>-------------------------------</td>
<td>------------------------</td>
<td>---------------------------</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Low Damage</td>
<td>High Damage</td>
<td>Partial cut 1974-6</td>
<td>Clear cut 1976</td>
<td></td>
</tr>
<tr>
<td>Liquidambar styraciflua</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ilex opaca</td>
<td>15.7*</td>
<td>1.2</td>
<td>0.9</td>
<td>0.3</td>
<td></td>
</tr>
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<td>Ulmus americana</td>
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<td>2.5</td>
<td>7.1</td>
<td>2.4</td>
<td></td>
</tr>
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<td>7.3</td>
<td>9.6</td>
<td>28.8</td>
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<td>Quercus pagoda</td>
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</tr>
<tr>
<td>Carpinus caroliniana</td>
<td>2.1</td>
<td>5.6</td>
<td>3.0</td>
<td>5.4</td>
<td></td>
</tr>
<tr>
<td>Fraxinus pennsylvanica</td>
<td>2.0</td>
<td>10.2</td>
<td>12.1</td>
<td>9.4</td>
<td></td>
</tr>
<tr>
<td>Fagus grandifolia</td>
<td>2.0*</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Q. michauxii</td>
<td>1.2</td>
<td>0.3</td>
<td>2.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acer rubrum</td>
<td>1.2</td>
<td>3.8</td>
<td>5.0</td>
<td>2.7</td>
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<td>0.7</td>
<td>0.9</td>
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<td>5.2</td>
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<tr>
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<td>33</td>
<td>37</td>
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<td>35.4</td>
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<td>Density, # of trees/ha</td>
<td>1259</td>
<td>1869</td>
<td>1115</td>
<td>2538</td>
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Table 4.2. Tree species composition and relative basal area of old-growth and managed bottomland hardwood forests in the Congaree National Park. Asterisk indicates significant difference in distribution (Wilcoxon test: *P* < 0.05).
<table>
<thead>
<tr>
<th>Species</th>
<th>Old-growth forest 2006</th>
<th>Second-growth forest 1996</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Low Damage</td>
<td>High Damage</td>
</tr>
<tr>
<td>Ampelopsis arborea</td>
<td>-</td>
<td>6.7*</td>
</tr>
<tr>
<td>Anisosticus capriolata</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Berchemia scandens</td>
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<td>6.7</td>
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<tr>
<td>Campsis radicans</td>
<td>23.7</td>
<td>26.0</td>
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<td>Parthencissus quinquefolia</td>
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<tr>
<td>Toxicodendron radicans</td>
<td>75.0</td>
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<td>Vitis spp.</td>
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</tr>
<tr>
<td>Density, # of lianas/ha</td>
<td>195.3</td>
<td>238.0</td>
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</table>

Table 4.3. Liana density (stems $\geq$ 2.5 cm; ha$^{-1}$) in old-growth and harvested bottomland hardwood forests in the Congaree National Park. Asterisk indicates significant difference in distribution (Wilcoxon test: $* P < 0.05$).
Figure 4.1. Location of the Congaree National Park south of Columbia, South Carolina. Hurricane Hugo damage occurred in September 1989. Plot locations reflect two distinct disturbance histories, plots in old-growth forests (■) were 1-ha in size and sampled during the winter 2005-6, 16 years post-disturbance. Plots in areas that were subject to partial or complete harvest prior to park formation (●) were sampled in 1996, 20-22 years post harvest.
Figure 4.2. Projection of Axis 1 v 2 of Nonmetric Multidimensional Scaling (NMDS) ordination of vegetation plots from areas of low (♦) and high (■) hurricane damage old-growth, clear cut in 1976 (Δ) and selectively cut in 1974-6 (○) in the Congaree National Park.
Figure 4.3. Projection on Axis 1 v 2 of Nonmetric Multidimensional Scaling (NMDS) ordination for species centers in the Congaree National Park based on vegetation plots sampled in 1996 and 2006.
Figure 4.4. Size-class distribution of trees and vines in the Congaree National Park south of Columbia, South Carolina. Sampled forests reflect four distinct disturbance histories; old-growth forests with low hurricane damage (A.), forests selectively logged in 1976 (B.), old-growth forests that suffered high hurricane damage (C.), and forests that were clear cut in 1976 (D).
CHAPTER 5

DENDROECOLOGY OF TWO LIANA SPECIES IN AN OLD-GROWTH FLOODPLAIN FOREST IN SOUTH CAROLINA, U.S.A.

5.1. Introduction

Lianas are important components of temperate and tropical forests that compete directly with trees and reduce tree establishment, growth rates, and survival (Dillenburg et al. 1993; Allen et al. 1997; Schnitzer and Bonger 2002). Lianas have been suggested as a mechanism for the maintenance of species richness in tropical forests (Schnitzer and Bongers 2002) and recent studies suggest that lianas are increasing in size, density, and dominance in tropical forests of the Amazon and Panama (Phillips et al. 2002; Wright et al. 2004). In temperate forests, trends in liana size and density are mixed (Bragg 2004; Londré and Schnitzer 2006; Allen et al. 2007). There are a variety of mechanisms that may be responsible for liana increases including changes in disturbance regimes, forest structures, or in climate and the associated increases in the concentrations of atmospheric CO₂. Elevated levels of CO₂ have been shown to stimulate liana growth more than tree growth (Granados and Korner 2002; Mohan et al. 2006; Zotz et al. 2006). Temperate liana growth rates responded to elevated CO₂ by accelerated growth for both poison ivy (Toxicodendron radicans) (Mohan et al. 2006) and English ivy (Hedera helix) (Zotz 2006) in controlled exposure studies.
An alternative explanation for increases in liana density in temperate forests relates to changes in land-use patterns and fragmentation (Londré and Schnitzer 2006). Changes in disturbance regimes, forest fragmentation, and land conversion to nonforest may also be responsible for increases in liana dominance as these activities often increase both light levels and edge habitat (Schnitzer 2005; Londré and Schnitzer 2006). It is likely that changes in the natural disturbance regimes that increase the frequency and intensity of disturbance will have a similar effect.

Another factor that may affect liana dynamics in tropical and temperate forests are large-scale disturbances such as hurricanes. Rice et al. (2004) documented higher densities of lianas in areas less intensely disturbed by hurricanes and showed that abundance varies not only with disturbance frequency but also with biogeography, seasonality of rainfall, and host tree features in Puerto Rican forests. Following Hurricane Hugo in 1989, Allen et al. (1997) found that the initial response of the liana community in the old-growth bottomland hardwood forests of the Congaree National Park, was an increase in liana mortality rates associated with host tree deaths. In a follow-up study, Allen et al. (2005) found that initial liana diameter growth rates reflected host tree damage and colonization patterns, and that overall growth rates increased through time while mortality rates decreased.

Dendroecological methods have traditionally been used to study the ecology, disturbance history, climate history of long-lived forest trees (e.g., Druekenbrod 2005; 108
Fraver and White 2005; McEwan et al. 2006). Although these methods have been used to study the effects of disturbances on stand development, the application of dendroecological techniques to examine longevity in lianas is in its early stages of development (Schnitzler and Heuze, 2006). The primary impediment to the application of these methods to lianas is the short life-expectancy, generally small size, and high rates of heart rot. Recent reports of mortality rates for lianas support the short life expectancy, but large lianas may not be ‘average’ in growth or mortality rates (Allen et al. 2005).

In North America, lianas are most abundant in the forests of the Atlantic and Gulf Coastal Plains where warm temperatures, long growing seasons, and high precipitation rates favor liana community development (Teramura et al. 1991). Despite liana abundance, few studies have examined the factors influencing the development of liana communities in these forests. Little is known about liana longevity, long-term growth, or how large they grow. As a functional group, lianas may comprise more than 10% of the stems in temperate floodplain forests (Allen et al. 2007), yet little is known about their ecology. The objective of this chapter is to apply dendroecological techniques to better understand the influence of disturbance intensity on liana communities in an old-growth bottomland hardwood forest. Specifically, there are two questions: 1) how long do lianas live in temperate floodplain forests? and 2) how do liana species respond to different types of both natural and anthropogenic disturbance?
5.2. Study Site

The 9,953-ha Congaree National Park (CNP) is located in the Atlantic Coastal Plain just below the “Fall Line”, south of Columbia, South Carolina (33°50’ north latitude, 81°45’ longitude) (Fig. 5.1). Although the CNP contains the largest major remnant of old-growth bottomland hardwood forest in the southeastern U.S. (Davis 1996; Davis 2003), approximately 1,500 ha of the CNP had been clearcut or selectively cut in the 1970s prior to the formation of the park in 1976 (Davis 2003). In addition, more recent acquisitions include areas that were salvage logged in 1990 or harvested as recently as 2005.

The old-growth portions of the CNP are very diverse, with over 80 tree species (Davis 2003), and the CNP has been described as one of the tallest temperate deciduous forests in the world with an average canopy height of between 40 and 50 m in the old-growth forests (Jones 1997). Along the creeks and sloughs that flow through the CNP, baldcypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*) dominate, while the natural levees and higher elevations where lianas proliferate are dominated by sweetgum (*Liquidambar styraciflua*), green ash (*Fraxinus pennsylvanica*), loblolly pine (*Pinus taeda*), nine species of bottomland oaks (*Quercus* spp.), and three species of hickory (*Carya* spp.). These old-growth forests also contain a dense and diverse liana community (Allen et al. 1997, 2005). Twenty-eight species of woody vines are known to occur in the CNP, however, only six species of lianas exceed 10 cm in diameter.

On September 21, 1989 Hurricane Hugo, a category 4 hurricane, made landfall in South Carolina north of Charleston in the Francis Marion National Forest. Wind speeds of up to 155 km·hr⁻¹ were recorded near the CNP and these winds affected the various forest types differently (Putz and Sharitz 1991). Areas dominated by bald-cypress (*Taxodium distichum* (L.) L.C. Rich.) and water tupelo (*Nyssa aquatica* L.) suffered primarily branch loss though species less tolerant of flooding were disproportionately up-rooted. In bottomland hardwoods forests, 37% of the trees suffered severe damage (snap-offs, tip-ups, or severe branch loss) (Putz and Sharitz 1991; Sharitz et al. 1993; Zhao et al. 2006). Hurricane winds caused extensive damage, sometimes intense, but the damage was variable as large areas suffered only extensive branch loss.

5.3. Methods

After examining several cores from each of six liana species of the CNP, we decided to focus our efforts on trumpet creeper and poison ivy, two liana species that
have distinct annual rings (Fig. 2). During the fall and winter of 2005-2006, I collected 100 cores of each species distributed across disturbance- and size-class gradients. Additionally, we identified the host tree species and measured the liana diameter (cm; measured at core height, usually 1.3 m above the ground) and vine load (the number lianas ≥ 2.5 cm dbh) for each cored liana.

Sampling along transects from the upland-floodplain interface to the Congaree River were prevented by persistent high water and the extensive network of deep channels and sloughs. The highly patchy nature and relative rarity of large liana distribution also influenced increment core collection. In general, the search for large lianas meant searching for large trees. GPS coordinates were taken for liana locations. Hurricane Hugo damage level was assessed based on large coarse woody debris and 16-year-old regeneration (Allen and Sharitz 1999; Allen et al. 2005; Zhao et al. 2006). Areas subject to logging were noted and the dates assigned using a map with locations and dates of logging operations using records obtained from the CNP (J. Cely 2004).

Cores were stored in plastic straws and transported to the laboratory at The Ohio State University for processing and analysis. Cores were prepared using standard techniques (McCarthy 2001) and sanded with increasingly fine sand paper and steel wool until a smooth surface was achieved and anatomical features were visible under low magnification. Cores were then scanned into high resolution image files (200-600 dpi). We measured annual increments of each liana core to the nearest 0.01 mm using
WINDENDRO® software (Windendro™ 2002). We did not cross-date cores; however this study represents only the second study overall and the first in North America to examine liana increment cores in temperate forests, and no suitable radial increment data set exists for cross-dating liana cores.

Growth increases were documented using an absolute increase method described by Fraver and White (2005):

\[ \text{Mean}_{t2} - \text{Mean}_{t1} - \]

where \( \text{Mean}_{t2} \) is the mean radial growth during the time window prior to the event and \( \text{Mean}_{t1} \) is the mean radial growth for the time window following the event.

This method requires that a temporal window be defined to filter out short-term changes in radial growth due to changes in temperature or precipitation (Lorimer 1980). Although the most common floating window, the period used to determine pre- and post-event growth, ranges used to determine release events is 10-15 years for trees (Lorimer 1980; Lorimer and Frelich 1989; Nowacki and Abrams 1997; Fravor and White 2005), the relatively short chronology length (19.3 – 22.6 years) for the lianas sampled in the current study dictated that we use a shorter floating window. Consequently, we used the four year floating window that has been used in other dendroecological studies (Henry and Swan 1974; Merrens and Peart 1992). Due to the short floating window, three consecutive years with an absolute increase greater than 0.5 mm was the criteria used to
define release events; this threshold represents a 25-100% increase in relative growth. Relative growth increases as low as 25% have been used to identify growth releases in trees (Nowacki and Abrams 1997). The absolute increase method was selected over the percent increase method \[\left[\frac{\text{Mean}_{t2}-\text{Mean}_{t1}}{\text{Mean}_{t1}}\times100\right]\] because the percent increase method is overly sensitive to growth release at slow growth rates and insensitive at high growth rates (Fraver and White 2005).

Differences in cored liana diameter, number of lianas per host tree, and host tree diameter associated with disturbance type and species were examined using General Linear Models (SAS 2005). In order to statistically examine the long-term trends in liana radial growth rates on a decadal basis, we used Wilcoxon two-sample tests (SAS 2005).

Of the 200 collected cores, 100 \textit{T. radicans} (Fig. 5.2A) and 96 \textit{C. radicans} (Fig. 5.2B) had distinct annual rings that could be interpreted. Liana stems cored ranged in size from 4.2 to 14.6 cm dbh. Those stems smaller than 4 cm were prone to splitting during core extraction and all stems larger than 14.6 cm suffered from heart rot and had discontinuous cambium. In areas logged in 1974-1976, seventeen \textit{Campsis} and thirteen \textit{Toxicodendron} cores were collected. Thirty-nine \textit{Campsis} and 54 \textit{Toxicodendron} cores were collected in areas of low Hurricane Hugo damage, while sixteen and twenty cores, respectively, were collected from sites that experienced moderate damage. Sixteen \textit{Campsis} and eight \textit{Toxicodendron} cores were extracted in areas of high hurricane damage.
damage. In addition, one *Campsis* core was collected along a logging road, four *Campsis* and one *Toxicodendron* were located in an area acquired by CNP in 2005 that had been managed forests.

The asymmetric nature of liana stems required the use of a pith locator (Applequist 1958) to estimate total age at dbh for 63% of the stems.

5.4. Results

5.4.1 Liana Characteristics

The mean (± 1 SE) size of cored lianas ranged between 7.4 (± 0.2) to 8.5 (± 0.5) for the two species in the four disturbance categories in CNP (Fig. 5.3). No significant differences were observed in cored liana diameters among disturbance types ($P=0.592$). However, cored *Campsis* stems were significantly larger than *Toxicodendron* stems ($P=0.025$).

The mean liana age was 22.6 yr old; the mean of the *Toxicodendron* stems was 26.0 yr old and the mean of the *Campsis* stems was 19.3 yr. Initial analysis of the data revealed that *Campsis* cores occasionally had indistinct ring patterns. Consequently, attempts to locate large *Campsis* stems required searches of somewhat lower portions of the floodplain.
5.4.2 Host tree characteristics

Host tree diameter was significantly different for both disturbance type ($P=0.0172$) and cored liana species ($P<0.0001$). Host tree diameter was significantly smaller in areas that suffered severe hurricane damage or were logged in the 1970s (Fig. 5.4). *Campsis* host trees were significantly smaller than *Toxicodendron* host trees.

General linear models of liana loadings (i.e., the number of competing liana stems on a host tree) indicate that both disturbance type ($P=0.0043$) and cored liana species ($P<0.0001$) were significantly different (Fig. 5.4). Liana loadings were significantly greater in areas that suffered high hurricane damage or were logged in the 1970s than in areas of low damage. There were significantly more competing lianas on *Toxicodendron* host trees than on *Campsis* host trees.

Host tree species reflected the difference liana species distribution within the CNP (Fig. 5.5). *Toxicodendron* was most frequently (31% to 70% of host trees) located on *Liquidambar styraciflua* regardless of disturbance type. This trend was the weakest (31% of host trees) in areas that were logged in the 1970s. A similar pattern was present for *Campsis* (12% to 36% of host trees) but at a lower percentage of host trees except in areas that suffered severe hurricane damage.
5.4.3 Liana longevity

Maximum age for *Toxicodendron* was 58 years and 38 years for *Campsis* (Fig. 5.6). Large *Campsis* stems were prone to heart rot and often had discontinuous cambium producing a lobed or braided appearance (Fig. 5.7). While the largest cored stem was 14.6 cm, stems frequently exceeded 20 cm in diameter with a maximum of 40 cm diameter observed. Large stems were usually hollow, often splitting into many stems.

*Toxicodendron* was less prone to heart rot or discontinuous cambium, but had a much smaller maximum diameter than *Campsis* stems. Cored *Toxicodendron* stems typically reached 10 cm in diameter, while the largest live stem observed reached 13.5 cm dbh. Large stems usually had intact cambium when they died.

5.4.4 Long-Term Growth Trends

Long-term trends in *Toxicodendron* radial growth indicate a long-term steady increase in growth from the 1960s to the 1990s (0.54 ± 0.11 mm·yr⁻¹ to 1.32 ± 0.05 mm·yr⁻¹); however, growth rates dropped slightly by the 2000s (1.18 ± 0.04 mm·yr⁻¹) (Fig. 5.8). In contrast, *Campsis* radial growth patterns have remained relatively constant.
through time, ranging from $1.52 \pm 0.09 \text{ mm yr}^{-1}$ in the 1980s to $1.72 \pm 0.08 \text{ mm yr}^{-1}$ in 1990s. *Campsis* consistently grew more rapidly than *Toxicodendron* ($P<0.0001$).

5.4.5 Liana Release Events And Growth Rates

Evidence for growth release events from the increment cores indicated the importance of disturbance history on radial growth rates (Fig. 5.9). Additionally, long-term radial growth patterns reflected differences in species and disturbance history (Fig. 5.10).

In areas that were logged in the 1970s, evidence for release events were weighted toward the late 1970s and 1980s following harvest operations, though sample sizes were small. Only *Toxicodendron* had evidence of radial growth release (23% of stems) between 1985 and 1989, and only *Campsis* had evidence of an increased growth response (13% of stems) between 1990 and 1994, directly after Hurricane Hugo. In areas logged in the 1970s, liana radial growth was more stable than in old-growth areas regardless of the level hurricane damage.

*Toxicodendron* radial growth increased from 1.0 mm·yr$^{-1}$ in 1975 to 1.2 mm·yr$^{-1}$ in 1978 then declined to 0.8 mm·yr$^{-1}$ and remained stable until 1988. Following Hurricane Hugo, radial growth increased 1.0 mm·yr$^{-1}$ and remained stable until 2005.
Campsis radial growth, however, fluctuated considerably between 1972 and 1984 but sample sizes were small. After 1984, Campsis radial growth declined from 2.0 mm·yr\(^{-1}\) to 1.4 mm·yr\(^{-1}\) in 1989. Post-hurricane radial growth increased to 1.7 mm·yr\(^{-1}\) in 1992 and steadily declined to 1.2 mm·yr\(^{-1}\) in 2005.

In heavily damaged areas, release events were more common between 1980 and 1994. Of the 8-15 stems, 11.1% to 12.5% exhibited release events for either five-year period. Sample size was extremely small prior to that time period and limited our ability to detect release events. Only Campsis had evidence of release events between 1995 and 2005. Of the sixteen stems present, 6.2% were released in both five-year periods. Toxicodendron consistently grew more slowly than Campsis, the only exception occurred during the five-year period following Hurricane Hugo. In areas of high damage, Toxicodendron radial growth increased from 0.6 mm·yr\(^{-1}\) in 1980 to 0.9 mm yr\(^{-1}\) in 1987 followed by a rapid increase to 2.2 mm·yr\(^{-1}\) in 1994. Radial growth then steadily declined to 1.0 mm·yr\(^{-1}\) in 2000 and remained stable until 2005. Campsis radial growth fluctuated considerably in 1970s and early 1980s, but sample sizes were extremely small. By the mid 1980s, Campsis radial growth stabilized at 1.3 mm yr\(^{-1}\) followed by a precipitous increase to 2.0 mm·yr\(^{-1}\) in 1991. Radial growth then declined to 1.5 mm·yr\(^{-1}\) in 1992 and continued to decline to 1.2 mm·yr\(^{-1}\) in 2005.

In areas that suffered moderate hurricane damage, evidence of growth releases were greatest between 1985 and 1989. During that period, 25% of all Toxicodendron
stems and 12.5% of Campsis stems exhibited a growth release event. Between 1990 and 2005, the proportion of lianas released ranged from 6.2 to 12.5% for Campsis and from 0 to 5% for Toxicodendron. Toxicodendron grew slowly (0.5 mm·yr\(^{-1}\)) from the 1950s to the 1970s, though sample sizes were small. In 1975, radial growth rates rose from 0.5 mm·yr\(^{-1}\) to 0.9 mm·yr\(^{-1}\) in 1988. After Hurricane Hugo in 1989, radial growth rose to 1.4 mm·yr\(^{-1}\) in 1990 followed by a steady decline to 1.0 mm·yr\(^{-1}\) in 2005. Campsis chronologies in areas of moderate damage were much shorter but had a similar pattern as Toxicodendron at a higher growth rate. Campsis radial growth rose from 0.9 mm·yr\(^{-1}\) in 1976 to 1.8 mm·yr\(^{-1}\) in 1987. Unlike Toxicodendron, Campsis radial growth declined to 1.4 mm·yr\(^{-1}\) in 1990. Growth then increase to 1.9 mm·yr\(^{-1}\) in 1991 followed by a steady decline to 1.5 mm·yr\(^{-1}\) in 2005.

In the least damaged areas, where sample sizes were larger, growth release events peaked between 1985 and 1989 when 13.3% of the Campsis and 28.3% of the Toxicodendron stems exhibited a detectible response. Toxicodendron diameter growth rates gradually increased from 0.25 mm·yr\(^{-1}\) in the late 1960s to 1.0 mm·yr\(^{-1}\) by 1990. From 1990 to 2005, Toxicodendron diameter growth rates fluctuated between 1.0 and 1.5 mm·yr\(^{-1}\) with a steady drop in growth rate from 2001 to 2005. Campsis radial growth fluctuate between 1.0 and 2.0 mm·yr\(^{-1}\) from 1970s to 2005. Periods of slow growth (< 1.5 mm·yr\(^{-1}\)) occurred from 1978 to 1982 and 1990 to 1993.
5.5. Discussion

The questions of liana stem longevity, long-term growth, and species-specific response to disturbance may have important implications to floodplain forest development patterns. Our analyses suggest that the size-age relationships for the two liana species examined appear to differ. *Toxicodendron* grew more slowly and reached a greater maximum age than *Campsis* in the bottomland hardwood forests of the CNP. However, the greater age appears to be an artifact of our ability to age the largest *Toxicodendron* vines but not the largest *Campsis* vines. *Campsis* stems larger than 15 cm diameter were common and one reached 40 cm dbh, but larger stems suffered from heart rot and stem shattering.

Size-age relationships appear to be influenced by disturbance history. In areas heavily damaged by hurricane winds in 1989, *Campsis* vines have grown more slowly than in areas where the canopy was not as disturbed. *Toxicodendron*, unlike *Campsis*, have grown more rapidly in areas of high hurricane damage. This difference in response to hurricane damage between species may again reflect the different host sizes, host species, and utilization patterns of the two species. *Toxicodendron* colonizes primarily the main trunk and a few large limbs of the host tree, displaying leaves below the host’s crown. *Toxicodendron* also had significantly more competition from other lianas and this pattern was strongest in area that were heavily disturbed, either logged in the 1970s or suffered high hurricane damage. *Campsis*, like *Vitis*, attempts to overtop the host
tree, competing directly for light. Diameter growth patterns also reflect host damage and colonization patterns. Size-age relationships support long-term trends in diameter growth as well. Further analysis is needed to determine if diameter growth rates of these lianas are increasing through time but long-term trends for *Toxicodendron* appear to support both physiological (Mohan et al. 2006) and demographic data (Allen et al. 2007).

The theory that liana abundance increases with disturbance and forest fragmentation (DeWalt et al. 2000; Schnitzer and Bonger 2002; Londré and Schnitzer 2006) seems to be at odds with recent studies that report increases in liana size and density in relatively undisturbed forests (Phillips et al. 2002; Wright et al. 2004; Bragg 2004; Allen et al. 2007). One explanation for this trend may be level of disturbance and the associated changes in temperature or light levels, limit liana growth as forests develop over time or latitude increases. While Londré and Schnitzer (2006) did not find increases in liana density in forest interiors in Wisconsin, they report2e ~250 liana stems·ha⁻¹ in forest edges at latitudes above 42° N, suggesting that lianas may be increasing in disturbed habitats of this region. While the mechanisms for increases in liana density in temperate floodplains has not been identified, increases in liana growth and decreases in mortality rates relative to trees and shrubs may indicate why lianas are increasing in density relative to other life forms in South Carolina (Allen et al. 2005; Allen et al. 2007).
Unlike prior studies, we now have pre-hurricane growth rates to compare with long-term post-Hugo data. Increment data from *Toxicodendron* indicate increases in radial growth rate extending back to the 1950s. Areas that were heavily damaged were the only areas where *Toxicodendron* radial growth ever exceeded *Campsis* radial growth, occurring between 1994-1998 five years following Hurricane Hugo. Long-term increases in liana diameter growth rates reported by Allen et al. (1997, 2005, 2007) were based on lianas with a smaller minimum diameters, included slower growing species, and reported somewhat lower diameter growth rates (1.29-1.71 mm·yr\(^{-1}\)) in the Congaree. Similarly, Allen et al. (2005) reported species-specific diameter growth rates for *Toxicodendron* (0.8 to 2.2 mm·yr\(^{-1}\)) and *Campsis* (1.0 to 1.9 mm·yr\(^{-1}\)) between 1994 and 2002 that were substantially lower than cored lianas. *Campsis* stems larger than 5 cm dbh, unlike *Toxicodendron*, grew more rapidly than smaller stems in permanent plots between 1998 and 2002. Converting radial growth rates from cored lianas of 1-2 mm·yr\(^{-1}\) to diameter growth rates of 2-4 mm/year reflect these differences; however, it does appear that the large liana stems cored in this study grew more rapidly than the same species observed in permanent plots (Allen et al. 2005).

The observed longevity patterns for *Toxicodendron* and for *Campsis* stems must be considered in the context of individual longevity. If these species reproduce clonally, individual longevity could exceed many trees species in the floodplain. In this forest, *Vitis* may be the oldest liana, with stems >24 cm dbh (observed and documented during
core collection) and lower growth (~1 mm·yr⁻¹) than *Campsis* or *Toxicodendron* (Allen et al. 2005). In the Congaree floodplain, lianas appeared to be patchy in distribution, with stems of a species often grouped together with patches widely spaced. Evidence for the clonal nature of lianas is limited, but includes estimates of 1.1-7.4 ramets per genet in the east Brazilian Amazon (Gerwing 2004). Foster and Sork (1997) suggested that large lianas (>10 cm dbh), might be the oldest woody plants in the upland forests in Cameroon, surviving several generations of their host trees. This does not appear to be the case for liana stems in the Congaree.

The link between large lianas and forest age has been a subject of growing acceptance (Schnitzler 1995; DeWalt et al. 2000; Hamilton et al. 2005; Phillips et al. 2005). In the Congaree, the presence of large trees of a wide range of species (Jones 1997) and the presence of large lianas may reflect disturbance history and stand development pattern. Prior to Hurricane Hugo, a category 4 hurricane when it struck South Carolina, the last major hurricane to strike Columbia, South Carolina area occurred in 1893 (Purvis 1989). Hurricane Gracie, a category 4 hurricane, made landfall in South Carolina between Hilton Head and Charlestown in 1959. Hurricane Gracie did enough damage to prompt salvage logging in parts of the Congaree (Kinzer and Cely, In prep.). This 100-year return interval allows lianas to reach large sizes after understory light level decrease following disturbance. The Congaree has been subjected to many lesser storms and wind events over this time period. In the Amazon, large
lianas (> 10 cm dbh) represented < 5% of the liana stems, but 80% of the liana biomass. Foster and Sork (1997) reported that lianas > 10 cm dbh were considered indicators of primary tropical forests. Philips et al. (2005) reported that large liana (>10 cm dbh) may be controlled by the availability of large tree supports (trellises) in lowland tropical forests.

Currently, discussions of old-growth forest characteristics, forest development patterns, and bottomland forest management do not adequately address the role lianas play in southeastern bottomland forests. Discussions on the role lianas play in forest development need to address emerging patterns of liana density increasing with forest age and changes in liana growth rates. If lianas are increasing in diameter growth rate through time as our data suggests, they are likely influencing tree species composition, growth, and mortality patterns. Additionally, if liana longevity approaches that of trees, demographic changes in growth and mortality will have long-term consequences for floodplain forests. Consequently, we suggest that the role of lianas in forest stand development should be explored more completely and incorporated into stand development models of bottomland hardwood forests.

5.6 Conclusions

Although liana growth was highly variable, our data suggest that diameter growth rates of lianas are responding to both large- and small-scale changes in bottomland forests of the Congarre National Park. Our data suggest that lianas are long-
lived components of Atlantic Coastal Plain floodplain forests that are influenced by changes in the forest as well. However, this relationship appears to be dynamic as these forests respond to disturbance, specifically wind damage associated with hurricanes and forest management activities.

References


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on the growth of the tree host *Liquidambar styraciflua*. Oecologia 93:48-54.


Figure 5.1. Cored liana locations (▲) within the Congaree National Park, South Carolina. Cores were collected during the winter 2005-6.
Figure 5.2. Radial increment cores from *Toxicodendron radicans* (A) and *Campsis radicans* (B) in the Congaree National Park, South Carolina.
Figure 5.3. Mean cored liana diameter (±SE) in four disturbance categories in the Congaree National Park. *Campsis* diameters were significantly larger than *Toxicodendron* diameters ($P=0.0251$). Asterisk indicated a significant difference between *Campsis* and *Toxicodendron* (Proc GLM, SAS 9.1; *P*<0.05).
Figure 5.4. Host characteristic for cored lianas in the Congaree National Park. Mean liana density (±SE) (>2.5 cm dbh) are presented for host trees in four disturbance categories (A.). Mean host tree mean diameter (±SE) for cored lianas are presented in the four disturbance categories (B). Asterisk indicated a significant difference between *Campsis* and *Toxicodendron* (Proc GLM, SAS 9.1; *P*<0.05).
Figure 5.5. Distribution of host trees for *Campsis radicans* and *Toxicodendron radicans* in the Congaree National Park in (A) areas logged in the 1970s, (B) areas that suffered severe hurricane damage in 1989, (C) areas that suffered moderate damage, (D) and areas that suffered low or minimal hurricane damage.
Figure 5.6. Establishment patterns for *Campsis radicans* (A) and *Toxicodendron radicans* (B) based diameter at 1.3 meters as a function of disturbance history in the Congaree National Park.
Figure 5.7. Large *Campsis* stem showing lobed surface and discontinuous cambium
Figure 5.8. Mean radial decadal increment (±SE) for *Campsis radicans* (◊) and *Toxicodendron radicans* (□) in the Congaree National Park in South Carolina. Asterisks indicate a significant difference between Campsis and Toxicodendron (Wilcoxon two-sample test; *** indicate $P<0.0001$).
Figure 5.9. Distribution of absolute radial growth increases expressed as a percentage for *Campsis radicans* and *Toxicodendron radicans* in the Congaree National Park in (A) areas logged in the 1970s, (B) areas that suffered severe hurricane damage in 1989, (C) areas that suffered moderate damage, (D) and areas that suffered low or minimal hurricane damage. A growth increase is defined as 0.5 mm increase in absolute growth with a four year floating window lasting at least three years. Numbers in upper part of the graph indicate sample size with *Toxicodendron radicans* on top and *Campsis radicans* below for that 5 year period.
Figure 5.10. Mean annual radial increment (±SE) for *Campsis radicans* (♦) and *Toxicodendron radicans* (□) in the Congaree National Park in South Carolina based on diameter in (A) areas logged in the 1970s, (B) areas that suffered severe hurricane damage in 1989, (C) areas that suffered moderate damage, (D) and areas that suffered low or minimal hurricane damage. Arrows indicate Hurricane Hugo’s passage.
CHAPTER 6

A NEW DEFINITION FOR OLD-GROWTH “RED RIVER” FLOODPLAIN FORESTS OF THE SOUTHEASTERN UNITED STATES

6.1. Introduction

Definitions for old-growth forest ecosystems typically include a minimum level of forest age and some limit on anthropogenic disturbance. In conservation terms, definitions should not be so exclusive as to eliminate all good candidate sites or so inclusive so as to accept a large fraction of forests. Red rivers (also called brown water rivers) originate in the Piedmont or Mountains of the eastern United States and during floods carry heavy loads of red clay sediment (Stanturf and Schoenholtz 1997). Examples include the Roanoke, Savannah, Alabama, Red, and Mississippi rivers. Existing definitions for red river old-growth floodplain forests do not meet these basic requirements because they either include most mature forests with native species (Lynch 1996) or conclude that none exist (Shear et al. 1997). Improving definitions requires finding more and better examples and incorporating an understanding of floodplain forest development patterns. If red river old-growth forests exist, and it is our contention that they do, a new definition is needed that not only uses improved models of forest development in these large river floodplains and fits the best examples of red river floodplain forests. In floodplains, the hydrologic regime is the primary factor regulating
species composition and structure (Wharton et al. 1982; Sharitz and Mitsch 1993; Jones et al. 1994; Hodges 1997; Hall and Harcombe 1998; Kellison et al. 1998; Battaglia and Sharitz 2005), definitions that require both the canopy dominant trees be shade-tolerant and the tree species composition to be stable, may not be appropriate. Trade-offs between flood- and shade-tolerance may prevent a shade-tolerant canopy from developing in floodplains that are not accumulation sediments at high rates.

Distinct forest types need unique definitions to adequately assess and manage current old-growth forests and those forests intended to be old-growth replacements. While old-growth floodplain forests in large river systems of the southeastern United States have been described by a number of authors (e.g., Lynch 1995; Meadows and Nowacki 1997; Shear et al. 1997), further refinements are needed. This is particularly true for red river floodplain forests. Red river floodplain forests occur along rivers that after flowing from the Piedmont, over the fall line and onto the Coastal Plain, where flow rates decrease, depositing sediments on to river floodplains downstream. These deposits form broad floodplains with predictable forest composition based on landform and hydrology (Wharton et al 1982; Hodges 1997; Kellison et al. 1998; Mitsch and Gosselink 2000). Most models of forest development on large river floodplains (Shelford 1954; Hosner and Minckler 1963; Hodges 1997) of the southeastern U.S. suggest that late-successional forests will consist of cherrybark oak (*Quercus pagoda* Raf.), Shumard oak (*Q. shumardii* Buckl.), swamp chestnut oak (*Q. michauxii* Nutt.), bur oak (*Q. macrocarpa* Michx.), and other white oaks and hickories. The mechanism driving
successional processes is thought to be sediment deposition (Hodges 1997), a surrogate for elevation and hydrologic regime. As sediments are deposited across the floodplain, relative elevation rises, allowing less flood-tolerant species to persist over time. This implies that if sediment deposition slows or ceases, species composition will stabilize. Hosner and Minckler (1963) noted that bottomland hardwoods appear to be maintained as sub-climax forests consisting of oaks, hickories, elms, and ashes and that progression to an oak-hickory climax depended on continued deposition of sediment at extremely slow rates. Species that would indicate progression to the next stage include American beech (Fagus grandifolia Ehrh.), yellow-poplar (Liriodendron tulipifera L.), white oak (Q. alba L.) and northern red oak (Q. rubra L.).

The deposition of clay sediments from the Piedmont creates some of the most productive sites in the southeastern United States (Shear et al. 1997; Kellison and Young 1997). The historical rates of sediment deposition between 1780 and 1930, sometimes as much as five meters since the 1700s, have led some authors to conclude that old-growth forests no longer exist (Trimble 1974; Shear et al. 1997). Historically, old-growth floodplain forests were found on most of the large river systems flowing across the Atlantic and Gulf coastal plains (Figure 6.1).

The objective of this paper is to review the available literature and produce a new definition for red river old-growth forests. Specifically, we: 1) review important ecosystem components that regulate the development of these floodplain forests including geomorphology, hydrology, disturbance regime, and successional patterns; 2)
review existing definitions of old-growth red river floodplains; 3) suggest a new
definition for old-growth red river floodplains; and 4) examine the characteristics of some
of the best remaining old-growth red river floodplain forests in the southeastern U.S.

6.2. Factors influencing red river floodplain forests

6.2.1. Geomorphology

Red rivers, so named for their heavy load of red clay sediment, are relatively new
to the Atlantic Coastal Plain landscape. Prior to 18th century, European explorers
described rivers in the southeastern United States that ran “crystal clear” (Shear et al.
1997; Trimble 1974). Clearing of land for agriculture, beginning in the late 1700s in
Virginia and migrating west to Georgia by the 1840s, exposed highly erodable soils.
Aggradation rates reflect this pattern; for example, the Roanoke River in North Carolina
has >5 m of sediment deposition directly below the fall line and the depth gradual lessens
as you approach Albemarle Sound (personal observation and R.K. Peet personal
communication). The reduction in forest cover in the watershed reduces
evapotranspiration and rain water interception, causing an increase in river flow volumes
as well as dramatic increases in sediment loads.

By the 1850s, sediment loads began to fill river beds, raising the floodplain
surface (Shear et al. 1997). Starting in the 1920s and 1930s abandonment of agricultural
land, the reestablishment of forests in the Piedmont, and reductions in erosive agricultural
practices eventually reduced sediments entering river systems (Trimble 1974). However,
sediments already in the river beds continue to move downstream and projected to be redistributed for at least another 100 years (Meade 1982). While erosion due to agriculture practices has decreased, river sediment loads remain higher than in the 18th century due to continued transport of sediments already accumulated in the river channel. The construction of large reservoirs for hydroelectric power production and flood control trap a significant portion of the river sediment load (Meade 1982). Reservoirs can trap 80-90% of the suspended sediments that flow into them (Meade 1982). Dams also alter flow regimes by capturing high flows and elevating low flows for flood control, electrical power generation, irrigation, recreation, and municipal water needs (Schneider et al. 1989; Poff et al. 1997).

6.2.2. Hydrology

Hydrologic regime, particularly flooding depth, duration, and frequency, are the primary forces shaping the plant communities in floodplains (Junk 1989). Shear (1997) concluded that in the southeastern U.S., high rates of floodplain aggradation followed by river channel downcutting through sediment deposits have resulted in streams with deeper channels. This has resulted in a decreased rate of bank overflow as compared to that prior to European settlement and a decreased frequency of overbank floods. The resulting changes have resulted in a shift toward less flood-tolerant tree species.
Alteration of hydrologic regimes by dam construction can interrupt and alter ecological processes of river systems (Ligon 1995; Leyer 2005). Dammed rivers have longer duration of moderate flow rates with fewer high and low flow periods. Dams also reduce sediment loads by slowing water speeds and retention times. Increased evaporation from reservoirs also reduces river discharges (Schneider et al. 1989). Most of the large river systems in the southeastern United States have been substantially altered by flow alterations (Dynesius and Nilsson 1994). Many dams were constructed between 1930 and 1970 in the mid-Atlantic states (Schneider et al. 1989).

Human intervention in natural flood regimes, including the construction of dams for flood control and electrical power generation, can have dramatic impacts on the size, duration, and seasonality of flood events, as well as minimum flow rates (Patterson 1985; Nilsson et al. 1991; Nilsson and Berggren 2000; Leyer 2005). Leyer (2005) examined species specific response of 30 grassland species to altered hydrologic regime in the Elbe River, Germany, and concluded that most species showed a significant preference for either highly fluctuating water levels or a stable water table, and that the probability of their occurrence was either reduced or increased along a gradient of reduced fluctuation. By altering flow rates, dams will also alter sedimentation rates and patterns.

6.2.3. Disturbance Regime

Disturbances, such as wind or flooding, play a dominant role in regulating the composition and structure of forests (Borman and Likens 1979). Forest succession, or
the predictable progression from light-demanding species to shade-tolerant tree species, continues until a major disturbance modifies these autogenic patterns. In southeastern floodplains, flood-tolerance interacts with shade-tolerance, producing substantially different and complex successional patterns than are observed in upland forests (Hall and Harcombe 1998; Lin et al. 2004; Battaglia and Sharitz 2006; Francis 2006; Niinemets and Valladares 2006). As in New England, strong cyclonic winds also impact southeastern floodplain forests and predictable interrupt autogenic processes by removing canopy dominant trees setting back successional processes (Foster 1988).

Disturbance regimes, i.e., the frequency and severity of disturbance events, determine successional patterns in floodplain forests. The major forms of disturbance affecting floodplain forests in the southeastern U.S. are floods, tornadoes, hurricanes, severe wind storms, fires, and mammalian herbivory (Frelich 2002). The frequency and severity of large scale wind disturbance like hurricanes varies with distance from the coast and patterns of hurricane storm tracks. Hurricanes weaken upon land fall or movement over colder ocean waters. Hurricanes frequently spawn tornadoes when they make landfall. Heavy rains are also associated with hurricanes and tropical storms (35 cm average for a moderate hurricane) can produce flood events (Foster and Boose 1995). Conner (1996) reported that hurricanes occur about once every 20 years in south Florida and are more common on the Gulf Coast. The southern Atlantic Coast has 1-16% yr⁻¹ probability of being struck by a hurricane and 0-7% yr⁻¹ probability of being struck by a
severe hurricane (>125 mph winds), a high category 3 to 5 hurricane on the Saffir-Simpson hurricane scale (Bellis 1995).

Fire, though present from frequent lightning strikes, does not represent a large scale disturbance in most floodplains. The high moisture levels, decomposition rates, and lack of persistent litter layer limit the abundance and connectivity of fuels.

Herbivory by members of the deer family, particularly the white-tailed deer (*Odocoileus virginana*) and moose (*Alces alces*) disturb forest by browsing on woody seedlings and sapling and herbaceous plants (Frelich 2002). Southeastern floodplain forests, while lacking moose, have an introduced mammalian herbivore, feral hogs (*Sus scrofa*), whose rooting are highly destructive to the seedling layer and represent an important component of the disturbance regime (Allen and Sharitz 1999). The long-term impacts of large populations of mammalian herbivores on the vegetation are not known, but their browsing and consumption of acorns and other seeds can alter tree regeneration patterns (Hough 1965; Anderson and Katz 1993; Boerner and Brinkman 1996; Rooney and Dress 1997; Wiegmann and Waller 2006; Pellerin et al. 2006).

Changes in global climate that increase ocean temperature in Caribbean and the Gulf of Mexico may produce more and larger hurricanes (Webster et al. 2005). Potential effects on forests could be a shortening of the return interval for major hurricanes and increasing the frequency of associated major flood events, further amplifying the disturbance-mediated processes like episodic reproduction. This could cause shifts in species composition by restricting establishment opportunities for some species.
6.2.4. Forest development patterns

In upland forests, autogenic process control successional patterns and plants often alter the environmental conditions resulting in shifts in species composition (Clements 1916; Odum 1969; Oliver and Larson 1990). Models of forest development for upland forests that are based primarily on shade tolerance and longevity must be adapted to fit floodplain forests. In floodplains, allogenic processes (i.e. changes in the environmental conditions such as sediment deposition) combine with autogenic processes to structure plant communities. In floodplains, shade tolerance interacts with flood tolerance at the seedling and sapling level, the primary filter for species composition. The interaction of hydrologic regime, sediment deposition, and disturbance regime often produces late-successional forests dominated by shade intolerant species (Table 6.1; Robertson and Weaver 1978; Brown and Paterson 1983; Devall and Ramp 1992; Shear et al. 1997; Allen and Sharitz 1999).

Within a floodplain, elevation is often the primary factor regulating species composition and structure and in floodplains the vegetation differs among levees, sloughs, and back swamps, as do soils and hydrology. Large river floodplain forests are species rich as described by Kellison et al. (1998). Based on published vegetation composition (Table 6.1) the vegetation of red river floodplain forests vary widely among sites. The few examples that do exist are primarily small with the Congaree National
Park in South Carolina being a rare exception. All have suffered some level of alteration to their hydrologic regimes.

Vegetation composition of the Congaree National Park can be used as example of red river forest vegetation composition. In the Congaree floodplain, stand composition is influenced by flooding frequency, depth, and duration. Large portions of the floodplain support bottomland hardwood forests that are often flooded for short periods in winter but are usually dry during the growing season. Dominant tree taxa include *Liquidambar styraciflua* L., *Quercus* spp. (at least 9 species), *Celtis laevigata* Willd., *Fraxinus pennsylvanica* Marsh., *Acer rubrum* L., *Ulmus americana* L., and *Pinus taeda* L. The understory is dominated by *Ilex opaca* Ait., *I. decidua* Walt., *Carpinus caroliniana* Walt., *Acer negundo* L., and *Asimina triloba* (L.) Dunal. Forests occurring in more low-lying areas and old oxbows (“sloughs”) are flooded for more extended periods and are dominated by *Nyssa aquatica* L. and *Taxodium distichum* (L.) L.C. Rich.. The dominant understory species are *Planera aquatica* J.F. Gmel., *A. rubrum* L, and *Fraxinus caroliniana* P. Mill.

6.3. Definitions

6.3.1 Existing definitions

Defining old-growth forests on red river floodplains is difficult because few pre-European forests exist and little data is available that describes forest composition and
stand dynamics. Existing definitions range from Lynch (1996) who required only mature forests dominated by native species to Shear et al. (1997) who concluded that they do not exist based on historically rates of sediment deposition. Shear et al. (1997)’s conclusion appear to be based primarily on the Devil Gut tract in the Roanoke River floodplain where sediment deposition were 3-5 meters since the 1700s.

Lynch (1995) presented a general description for southeastern floodplain forests that included four criteria to define old-growth; 1) old-growth must contain a canopy of native species with the average age of the canopy dominants near the common age maximum for that species; 2) understory and ground layers must be dominated by native plant species commonly associated with that natural community 3) soils and soil horizons show no evidence of “anthropomorphic” disturbance; and 4) there is no evidence of human-related disturbance such as grazing and logging. Shear (1997) further described old-growth red river floodplain forests for the eastern United States as those with the following characteristics: 1) the forest has reached an age at which species composition and net annual growth has stabilized; 2) the forest is older than the average interval between natural disturbances severe enough to lead to succession; 3) the dominant trees have reached their average life expectancy on that site type; 4) the annual growth rate is less than the average growth rate; and 5) the forest has never been cut or been converted to another type of ecosystem.

Of the examples given by Shear et al. (1997) of old-growth red river forests, none met all of the criteria. Only Devil’s Gut Tract on the Roanoke River in North Carolina
met most of the old-growth criteria and was considered a red river floodplain. Boiling Springs Natural Area is located on the floodplain of Lower Three Runs Creek, a blackwater stream whose headwaters are located along the fall line. The lack of alluvial sediments in blackwater streams produce distinctly different forest composition and forest development patterns (Hodges 1997). Other examples given for old-growth red river floodplain forests (Tennessee Valley Authority Tract, Falling Creek Tract, and Union Camp Track) were too small (three hectares or less) to maintain old-growth characteristics, were not red-river floodplain forests, or had a history of anthropogenic disturbance. The projected forest dominants were American elm (Ulmus americana L.), hackberry (Celtis occidentalis L.), and red maple (Acer rubrum L.). Shear (1997) further projected that the dominance of shade intolerant sweetgum (Liquidambar styraciflua L.) would diminish with time.

6.3.2. New Definition

The unique nature of old-growth red river floodplain forests requires a definition that takes into account an understanding of forest development patterns and the composition of the best examples available. We suggest a definition for old-growth red river forests needs to include the following criteria: 1) the forest is significantly older than the return interval for the major types of disturbance; 2) A significant portion of the dominant canopy species are approaching their maximum size or age for the forest type; 3) the forest has never been extensively cut or otherwise disturbed; 4) the forest has a
variety of age and size classes indicative of both small- and large-scale disturbance; 5) coarse woody debris and snags that reflect the size and species composition of the forest; 6) understory and herb layer is composed primarily of native species associated with floodplains; and 7) forest has a “diverse” woody vine communities and the associated structure and connectivity.

The primary difference with prior definitions are: 1) no requirement for stable species composition or slow growth, 2) requires an old forest rather than old trees, 3) incorporates disturbance regime, and 4) incorporates coarse woody debris, structural diversity and lianas.

Stable species composition may not be expected in a disturbance-mediated system. Of these criteria, 7) may be the most difficult to meet in floodplains where invasive species take advantage of the perpetually disturbed nature of the understory. Additionally, many of the criteria associated undisturbed forests (stable species, slow growth) may not be appropriate where the forest is older than the individual trees (Frelich and Reich 2003).

6.4. Examples of red river old-growth forests

A search of the existing literature for old-growth red river floodplain forests in the eastern United States quickly reveals the rarity of good examples (Robertson and Weaver
However, there are several good examples.

6.4.1 Congaree National Park, South Carolina

The Congaree National Park is one of the best examples of old-growth red river floodplain forest in the Southeast (Davis 1996). The large trees, while not particularly old, are nearing their species maximum for size. Loblolly pine have been aged using cores or stump counts as 143 (Gaddy et al. 1975), 156-180 (Putz and Sharitz 1991) and 227 years old (Pederson 1997). Many species may have greater longevity on less productive sites. Fast-growing trees that reach their species maximum for size at a relatively young age in floodplains may have a shorter life expectancy.

The Congaree has little record of anthropogenic disturbance in large portions of the bottomland hardwood forests. Cypress was cut in the sloughs by the Santee-Cypress Logging Company between 1895 and 1910 (Ricard 1988) and small portions of the floodplain, primarily adjacent to the river, were farmed. In the late 1960s and early 1970s, large portions of the Congaree National Park (~4500 of 9953 hectares) showed no evidence of human disturbance (Davis 1996). Evidence of sediment deposition is found in stump holes. An old cypress in the lower portion of the floodplain is hollow 1.5 meters below ground, indicating a substantial change in surface elevation over the last several centuries. Maps from the late 1700s show only minor changes in the river
channel and floodplain area. Historical reports of forest composition in the Congaree floodplain report that species composition, specifically the dominance of sweetgum (*Liquidambar styraciflua* L.), was similar to present day forests over 100 year ago (Chittenden 1906; Braun 1950).

Hurricanes have played a prominent role in structuring the floodplain forest of the Congaree (Putz and Sharitz 1991; Allen et al. 1997; Allen and Sharitz 1999; Zhao et al. 2006). The canopy dominant species (Table 6.1.) in this forest; sweetgum (*L. styraciflua* L.), loblolly pine (*P. taeda* L.), and bottomland oaks (*Quercus* spp.), are relatively shade-intolerant (Harlow et al. 1996). Re-establishment of these species is primarily occurring in areas heavily disturbed in 1989 by Hurricane Hugo (Allen and Sharitz 1999; Zhaoa et al. 2006). Hurricane Hugo disproportionately removed some late successional species, such as cherrybark (*Q. pagoda* Raf.) and Shumard oaks (*Q. shumardii* Buckl.). Loblolly pine regeneration has been extremely rare following the hurricane (Pederson 1997). The frequency of catastrophic events, particularly hurricanes, is not well described, but hurricanes are natural re-occurring events along the Atlantic and Gulf Coasts (Figure 6.2). Species indicative of late successional floodplain forests (*Fagus grandifolia* Ehrh., *Liriodendron tulipifera* L., and *Q. alba* L.) are present at the highest elevations in the floodplain (Table 1.)
6.4.2 Devil's Gut Tract, North Carolina

Devil's Gut tract is a 49.4 hectare forest on a ridge adjacent to Devil's Gut, a tributary of the Roanoke River on the Atlantic Coastal Plain located in Martin County, North Carolina (Shear et al. 1997). The dominant tree species is American beech (Fagus grandifolia Ehrh.), with loblolly pine (Pinus taeda L.), cherrybark oak (Quercus pagoda Raf.), and sweetgum (Liquidambar styraciflua L.) present (Table 1.). Loblolly pine individuals were aged 154-162 years while two American beech were aged 92 and 100 years old. Selective removal of pine occurred over the last 100 years; otherwise, the area has little evidence of human disturbance. The Roanoke River floodplain, by its location on the Virginia-North Carolina border, was subjected to extensive sediment accumulation during the 18th and 19th centuries as a result of the duration of erosive agricultural practices with up to five meters of accumulation below the fall line (R.K. Peet, Pers. Com.).

6.4.3 Big Oak Tree State Park, Missouri

Hodges (1997) suggests that the best example of late-successional forest for large river floodplains occurs in Big Oak Tree State Park in southeastern Missouri. Shelford (1954) described forest developed from “hackberry-elm or hackberry-gum” to “gum-oak”. The park is noted for its large trees with scattered extremely large bur and swamp chestnut oaks (McCarty 1999). The park is located in the floodplain of the Mississippi.
River and was established in 1938 to protect 405 ha of floodplain, 32 ha of which are considered old-growth. Dominant species include swamp white oak (*Q. bicolor* Willd.), American elm, (*U. americana* L.), shellbark hickory (*Carya laciniosa* (Michx.f.) G. Don.), bur oak (*Q. macrocarpa* Michx.), and pecan (*C. illinoinensis* (Wangenh.) K. Koch.) (Taylor 1995). While located within the historic floodplain of the Mississippi River, the park no longer receives floodwater from the Mississippi due the main line levee system but does flood regularly due to local rainfall events.

6.3.4 The Big Thicket, Texas

Located on the Gulf Coastal Plain between the Trinity and Neches Rivers in southeast Texas, the Big Thicket National Preserve protects floodplain forests on the terraces of the Neches River. Floodplain forests are dominated by sweetgum (*L. styraciflua* L.) and water oak (*Q. nigra* L.) (Marks and Harcombe 1981). Forests at slightly higher elevation include American beach (*F. grandifolia* Ehrh.) and loblolly pine (*P. taeda* L.) (Table 1). The stands sampled were the most mature in the region but did have some evidence of past logging.

6.3.5 Red Gum, Green Ash, and Overcup Oak Research Natural Areas, Delta National Forest, Mississippi

Located on the Delta National Forest in Mississippi, the three Research Natural Areas (RNA) established in 1943 are located in the historic floodplain of the Mississippi
River (Devall and Ramp 1992). Current floods occur from the Big Sunflower River. The RNAs protect ‘virgin forests’ 16-28 ha in size and are named after their dominant species (Table 6.1). In 1936, the U.S.D.A. Forest Service purchased 5342 ha of mostly virgin forest and began managing the forest in 1938 (Devall and Ramp 1992). Only the RNA’s avoided management activities. All the dominant species in the three RNAs have declined ~50 % in relative basal area between 1935 and 1990. Both the Green Ash and the Overcup Oak RNAs are still subject to annual flooding (Devall and Ramp 1992).

6.3.6 Potential additional sites

Additional sites that may contain old-growth large river floodplain forest include: Bayou DeView, Moro Creek Bottoms, and Sugarberry Natural Area in Arkansas; Bayou Bouef in Louisiana, and Horseshoe Island in Illinois (Davis 2003).

6.5. Conclusions

Definitions of red river old-growth forest must incorporate disturbance regimes and growth rates of dominant overstory species to accurately describe these disturbance-mediated forests. While sediment deposition and altered hydrologic regimes have dramatically influenced red river flood plain forest composition over the last two centuries, we argue that old-growth floodplain forests were not eliminated as suggested by other authors. Forest composition will be driven by the two dominant interacting
forces in these systems; the hydrologic and disturbance regimes. The disturbance regime will change as hurricane and tornado frequencies change from east to west, with distance from the ocean, and with global climate change.

Models of forest development for large river floodplain forests (Hodges 1997) noted that floodplain forest on the Atlantic Coastal Plain contain more of the shade intolerant red oaks and sweetgum. The Congaree National Park is one of the best example of red river old-growth forest in the southeastern U.S. (Davis 1995) and should be used as a model for floodplain forest development models specific to the Atlantic Coastal Plain. While wind disturbance is frequent, rapid tree growth rates have resulted in some of the largest specimens for their species (Jones 1997). Shade-intolerant canopy dominant species were disproportionately removed by the hurricane, and recruited only in areas of high damage. Disturbance regimes, particularly hurricanes, maintain the shade intolerant component of the forest canopy. The interaction of disturbance and hydrologic regimes will also act as a filter on species composition in floodplain forests.

References


<table>
<thead>
<tr>
<th>Species</th>
<th>Congaree 1998</th>
<th>Devils Gut</th>
<th>Red Gum RNA</th>
<th>Green Ash RNA</th>
<th>Overcup Oak RNA</th>
<th>Horseshoe Lake</th>
<th>Big Thicket FHP</th>
<th>Big Thicket FLH</th>
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Table 6.1. Species composition and relative basal area of eight old-growth red river bottom forests (Robertson and Weaver 1978; Devall and Ramp 1992; Shear et al. 1997; Allen and Sharitz 1999). ¹ includes only species with more than 0.05 m²/ha
Table 6.1. (Continued) Species composition and relative basal area of eight old-growth red river bottom forests (Robertson and Weaver 1978; Devall and Ramp 1992; Shear et al. 1997; Allen and Sharitz 1999). \(^1\) includes only species with more than 0.05 m\(^2\)/ha.

<table>
<thead>
<tr>
<th>Species</th>
<th>Congaree 1998</th>
<th>Devils Gut</th>
<th>Red Gum RNA</th>
<th>Green Ash RNA</th>
<th>Overcup Oak RNA</th>
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<th>Total basal area m(^2)/ha</th>
<th>Density, # of trees/ha</th>
<th>Diameter of largest tree (m)</th>
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<td>Total basal area m(^2)/ha</td>
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<td>Density, # of trees/ha</td>
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<td>Diameter of largest tree (m)</td>
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<td>Name</td>
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<td>Sample</td>
<td>Size (ha)</td>
</tr>
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<td>-------------------------------</td>
<td>-----------------</td>
<td>--------------</td>
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<td>Congaree National Park - bottomland hardwood forests</td>
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<td>6 stands (6 ha)</td>
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<td>Devils Gut</td>
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<td>Mississippi</td>
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<td>Trinity and Neches river floodplain</td>
<td>Texas</td>
<td>2 stands</td>
<td></td>
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<td>Big Thicket floodplain hardwood forest (FLH)</td>
<td>Trinity and Neches river floodplain</td>
<td>Texas</td>
<td>15 stands</td>
<td></td>
</tr>
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<td>Missouri</td>
<td>59 plots (380 m²/plot)</td>
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Table 6.2. Old-growth floodplain forests extent and locations.
<table>
<thead>
<tr>
<th>Name</th>
<th>Tree Ages</th>
<th>History</th>
<th>Date Established</th>
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<tbody>
<tr>
<td>Congaree</td>
<td>loblolly pine 83-227 Pawpaw 30</td>
<td>Used as a hunting preserve during the 20th century prior to becoming a National Monument in 1976</td>
<td>1976</td>
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<tr>
<td>Red Gum RNA</td>
<td>sweetgum 250-300</td>
<td>At least 50 years since major human disturbance prior to establishment</td>
<td>1943</td>
</tr>
<tr>
<td>Green Ash RNA</td>
<td>green ash 200-250</td>
<td>At least 50 years since major human disturbance prior to establishment</td>
<td>1943</td>
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<tr>
<td>Overcup Oak RNA</td>
<td>overcup oak 200-250</td>
<td>At least 50 years since major human disturbance prior to establishment</td>
<td>1943</td>
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<tr>
<td>Big Thicket FHP</td>
<td></td>
<td>In the 1850s economic exploitation began with the cutting of pine and cypress. Sawmills followed, using railroads to move out large volumes of wood. Ancient forests were felled and replanted with non-native slash pine</td>
<td>1974</td>
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<tr>
<td>Big Oak Tree State Park</td>
<td></td>
<td>Old-growth with many state and national champion trees</td>
<td>1938</td>
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Table 6.3. Old-growth floodplain forest tree ages and disturbance history in the eastern United States
Figure 6.1. Old-growth red river floodplain forests of the Southeastern U.S.A.
Figure 6.2. South Carolina hurricane history 1893-present. Hurricane tracks based on NOAA records. Hurricane Hugo’s track in 1989 is highlighted in gray.
CHAPTER 7

CONCLUSION

Old-growth floodplain forests are uniquely suited to study forest development patterns and response to disturbance. The Congaree Nation Park represents one of the best example of large river alluvial floodplain forests (Davis 1996). Long-term studies provide the opportunity to examine demographic and life-history characteristics that drive forest development patterns. The species-rich bottomland hardwood forests also have dense and diverse liana communities that have been largely ignored in studies of temperate forests. Understanding how lianas interact with disturbance type, both natural and anthropogenic, will allow predictions of how climate change will impact forest development patterns. This study has not only documented post-hurricane liana community dynamics, mortality rates, and long-term growth patterns but also documented long-term increases in liana density in both disturbed old-growth forests and second-growth forests. Changes in atmospheric chemistry and global climate will have wide reaching affects of forests. Increases in CO₂ have been shown to increase some temperate lianas growth rates to a much greater extent than some tree species.

Although highly variable, our data suggest that diameter growth rates of lianas are responding to both large- and small-scale changes in bottomland forests of the Congarre National Park. Our data suggests that lianas are long-lived components of
Atlantic Coastal Plain floodplain forests that are influenced by changes in the forest as well. However, this relationship appears to be dynamic as these forests respond to disturbance, specifically wind damage associated with hurricanes and forest management activities.

Definitions of red river old-growth forest must incorporate disturbance regimes and growth rates of dominant overstory species to accurately describe these disturbance-mediated forests. While sediment deposition and altered hydrologic regimes have dramatically influenced red river flood plain forest composition over the last two centuries, we argue that old-growth floodplain forests were not eliminated as suggested by other authors. Forest composition will be driven by the two dominant forces in these systems; the hydrologic and disturbance regimes and their interaction. The disturbance regime will change as hurricane and tornado frequencies change from east to west, with distance from the ocean, and with global climate change.

Models of forest development for large river floodplain forests (Hodges 1997) noted that floodplain forest on the Atlantic Coastal Plain contain more of the shade intolerant red oaks and sweetgum than forests in the Mississippi River drainage. The Congaree National Park has the best example of red river old-growth forest in the southeastern U.S. (Davis 1995), and should be used as an example for floodplain forest development models specific to the Atlantic Coastal Plain. While wind disturbance is frequent, rapid tree growth rates allow some of the largest specimens for their species (Jones 1997). Shade-intolerant canopy dominant species were disproportionately
removed by Hurricane Hugo, and recruited only in areas of high damage. Disturbance regimes, particularly hurricanes, maintain the shade intolerant component of the forest canopy. The interaction of disturbance and hydrologic regimes will also act as a filter on species composition in floodplain forests.
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APPENDIX A

LIANA DENDROGRAMS
Radial Increment (mm)

- C10
- C11
- C12
- C13
Radial Increment (mm)

C22

Radial Increment (mm)

C23

Radial Increment (mm)

C24

Radial Increment (mm)

C25
Radial Increment (mm)

- R9
- R10
- R11
- R12
Radial Increment (mm)