

**EFFECTS OF HURRICANES AND FIRES ON SOUTHEASTERN
SAVANNA-FOREST LANDSCAPES**

A Dissertation

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DEDICATION

In Memory of my Grandfather

Dr. Robert Richmond Bryden, Ph.D.
1916-2005

Ecologist, professor
and
always a wonderful Grandpa

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ABSTRACT

Sequential large-scale disturbances may produce interacting effects that differ from those predicted for each disturbance in isolation. These non-additive effects can strongly influence the composition and structure of plant communities. Hurricanes and natural lightning-season fires are large-scale, frequent disturbances in southeastern savanna-forest landscapes. Although interactive effects have been proposed, my research is the first to develop and experimentally test mechanistic hypotheses for hurricane-fire interactions. I develop a predictive conceptual model for interacting disturbances. I propose that hurricane-fire interactions depend on the relative timing of disturbances and the duration of effects. To predict the conditions under which hurricane-fire interactions are expected, my mechanistic hypotheses incorporate rates of fine fuel re-accumulation after a fire relative to decomposition of fine and coarse woody debris after a hurricane. This model suggests that the probability for disturbance interactions varies across savanna-forest landscapes. I predict that 1) hurricane-fire interactions are most likely in savannas, 2) they are least likely in forests, and 3) they may influence ecotones between savannas and forests by changing species composition and structure. Based on predictions, I implemented an experimental study in savanna-forest ecotone to test hypotheses of interactive effects. I hypothesized that effects of lightning-season fires differ when fires occur alone compared to when fires are preceded by hurricanes. I simulated two main effects of hurricanes as treatments— canopy disturbance and fine fuel deposition – by removing canopy trees and manipulating fuel loads. Compared to unaltered controls, I predicted hurricane treatments would influence fire intensity and vegetation response. Both canopy disturbance and fuel addition influenced the behavior of subsequent fires. In addition, the two main hurricane effects interacted to increase maximum fire temperatures. High fuel loads and fire resulted in

disturbance interactions that reduced stem density and species richness of woody plants.

Reduced hardwood density in areas of locally intense fires may decrease competition between species and increase establishment of pines and other fire-resistant species. Thus, hurricane-fire interactions influence vegetation structure in savanna-forest ecotones. Furthermore, over longer time scales interactions may result in landscape-level changes in southeastern savanna-forest ecosystems.

CHAPTER 1

INTRODUCTION

Disturbance is a central focus of modern ecological theory and research. Disturbances are temporally and spatially discrete events that alter the structure of populations, communities and ecosystems (*sensu* Pickett and White 1985). The magnitude of disturbance effects in forested landscapes may depend on the intensity, severity and frequency of the disturbance (Webb 1999). Disturbance effects can include mortality of individuals and local extirpation of species in a given area, changes in the size or biomass of living organisms and changes in the number and types of species present. Such changes produce short- and long-term alterations in community composition and structure.

Any single disturbance may influence the likelihood and effects of subsequent disturbances. Interactions between disturbances occur when effects of an initial disturbance are present when a later disturbance occurs, altering the probability or effects of the second event. Potential for interactions following disturbance are widely recognized and depend on the specific disturbance regime of an area (e.g., Bormann and Likens 1979, White 1979, Frelich and Reich 1999). For example hurricane effects in tropical forest are interconnected with subsequent herbivory, landslide, treefalls, flooding or drought (Willig and Walker 1999). Each interconnected event affects the structure and function of the forest.

In this dissertation I focus on interacting effects of two disturbances in southeastern ecosystems. I use both theoretical and experimental methods to explore the influence of hurricane effects on subsequent growing season fires. Hurricanes that develop in the North Atlantic often make landfall in coastal regions of the southeastern United States (Elsner and Kara 1999). Hurricanes in forested regions defoliate trees, snap branches and trunks, and uproot canopy trees (see Boucher et al. 1990, Gresham et al. 1991, Slater et al. 1995). The result is openings in the forest canopy and large quantities of downed biomass on the forest floor.

Lightning strikes in the southeastern United States frequently cause fires, at a rate of more than once a decade per given location historically (Platt 1999 and references therein). Lightning season fires in upland pine savannas consume foliage and fine fuels, but kill relatively few trees or understory plants. The nature and extent of hurricane-fire interactions should depend on multiple factors including the spatial and temporal overlap as well as the duration of their effects. Hurricane-fire interactions may have played an important role in shaping southeastern communities, landscapes and ecosystems.

Conceptual Models of Disturbance Interactions

Multiple large-scale disturbances may produce combined effects not predicted from studies of individual disturbances. I develop a predictive conceptual model for effects of interacting natural disturbances in southeastern North American coastal lowland landscapes containing pine savannas and warm-temperate/subtropical forests. Individually, neither hurricanes nor climate-driven lightning season fires typically produce large changes in savanna-forest landscapes (Platt 1993, Glitzenstein et al. 1995, Olson and Platt 1995, Slater et al. 1995, Platt et al. 2000, Drewa et al. 2002). Direct annual mortality attributed to hurricanes in old-growth pine savannas and forests rarely appears to be catastrophic. Savanna plant species typically survive lightning fires with minimal damage.

I propose that any interactions depend on the relative timing of disturbances and the duration of their effects. Large-scale fires typically occur during transitions from dry to wet periods in the early growing season (Olson and Platt 1995), while hurricanes occur later in the growing season (Simpson and Riehl 1981). The longevity of fire and hurricane effects should influence the likelihood that they interact in savanna-forest landscapes. Return of groundcover to a burnable state requires at least two years in savannas and more in ecotones and forests

(Glitzenstein et al. 1995, Slocum et al. 2003). Savannas and forests differ in the quantity and distribution of tree biomass on the ground after hurricanes, and in the rate of decomposition of that biomass (Brokaw and Walker 1991, Platt and Rathbun 1993, Ostertag et al. 2003).

Hurricane-generated fuels in old-growth savannas comprise discrete patches of slow-decomposing coarse fuels within a matrix of fine fuels. Coarse and fine downed fuels in warm-temperate/subtropical forests are more continuously distributed, but decompose more rapidly than savanna fuels because of higher moisture content.

My conceptual models suggest the likelihood of disturbance interactions differ for savannas compared to ecotones and forests. In savannas, interacting fire/hurricanes effects are likely, but interactions may be delayed if fires occurred in the year or two prior to a hurricane. Depending on tree densities and severity of hurricane damage in savannas, interactions may affect both groundcover and overstory vegetation. In ecotones and forests, hurricane-generated fine fuels are typically present throughout, but fuels decompose within a year, leaving primarily discontinuous woody fuels by the next lightning-season. For this reason, hurricane-caused fuels should not increase the likelihood that subsequent lightning fires burn from savannas into forests. Rare interactions, such as during periodic droughts, might facilitate invasion of ecotones by pyrogenic plant species and increase the likelihood of repeated fires and formation of unique ecotone plant communities.

Experimental Tests of Interactions

I propose that the design of experimental disturbance interaction studies should depend on the amount of prior knowledge of the ecosystem and of the disturbance regimes. To explore interactive effects of two disturbances in an unknown system, researchers may choose to test all the factorial combinations of both disturbances. I illustrate the factorial combinations of two

disturbance treatments labeled “D1” and “D2” in Figure 1.1. In such a study, questions would include: 1) what are the effects of D1 and D2 individually, 2) what are the interactive effects of D1 and D2 when they occur together, and 3) what are the effects of no disturbance? This design would allow researchers to understand effects of disturbances that may be novel or rare in an ecosystem, such as anthropogenic disturbances. I propose, however, that the full factorial approach is not necessarily the most informative approach within an individual ecosystem.

	+D1	-D1
+D2	(D1) + (D2)	(D2)
-D2	(D1)	Neither

Figure 1.1. Factorial treatment combinations for testing two disturbances and their interaction. The presence and absence of “Disturbance 1” are represented by +D1 and -D1 in the columns. Presence/absence of “Disturbance 2” is represented in the rows.

First, depending on the disturbance regime of the study system(s) researchers must first choose the appropriate disturbance(s) to test. The factorial design might be applicable on a broad geographical scale but not on the smaller scales where the number of disturbance types is limited. I illustrate these differences in scale in Figure 1.2 using hurricane and fire as the two disturbances. A broad-scale study might include a variety of disturbance regimes so the design could include all possible disturbance combinations. For example a study of disturbance effects in seasonally deciduous forests across a latitudinal gradient in Eastern N. America could include both hurricane and fire treatments because both disturbances occur but at very different frequencies among sites (e.g., Quigley and Platt 2003). To test disturbance effects on smaller scales the best experimental design might not include all factorial disturbance combinations. In

regions where hurricanes are relatively frequent but fires are very rare, such as New England forests, it makes sense to test the only hurricane vs. no-hurricane (e.g., Cooper-Ellis et al. 1999). Where only fire is important and hurricanes do not occur, like the Venezuelan llanos (plains), a legitimate comparison would be to test fire alone vs. no-fire (Silva et al. 1990). Where both disturbances are frequent, as in southeastern pine savannas, interactions may occur and experimental designs should include both disturbances.

	+Fire	-Fire
+Hurricane	(H) + (F) e.g., Pine Savanna	(H) e.g., New England
-Hurricane	(F) e.g., Venezuelan llanos	Neither e.g., many forests

Figure 1.2. Factorial combinations of fire and hurricane disturbances. Fires and hurricanes are both relatively frequent disturbances in southeastern longleaf pine savannas. New England forests are an example of an ecosystem where hurricanes are recurrent large-scale disturbances. The llanos (plains) of Venezuela are frequently burned but are not affected by hurricanes. Many forested ecosystems of the world are affected neither by hurricanes nor fires.

Specific hypotheses addressed by the factorial design would also depend on the relative frequency of both disturbances. Assume that two disturbances are not rare events in an ecosystem (Figure 1.1). Hypotheses of interest may include:

$$D1 + D2 \neq D1$$

$$D1 + D2 \neq D2$$

The factorial design would allow researchers to compare combined disturbance effects to individual effects. However, hypotheses should depend on whether the relative frequencies of

D1 and D2 differ. For example, if D1 were a more common event than D2 the question of interest would become: Does D2 (the rare event) alter the effects of D1 (the common event)? Finally, if the common disturbance event (D1) is inherent in the ecosystem then testing the absence of that event may not be ecologically meaningful.

My study concerns two frequent, large-scale disturbances in southeastern savanna-forest landscapes. I am specifically interested in interaction effects when hurricanes are followed by lightning season groundcover fires in the ecotone between savannas and forests. Both disturbances occur within the ecosystem, thus my experimental design incorporates hurricane and fire effects. However, in this system fires are frequent events without which the community composition and structure of pine savannas would change drastically (Gilliam and Platt 1999). Many experimental studies of fire effects in fire-frequented habitats have justified not testing the effects of no-fire, as it is not a true control in pyrogenic systems (see Platt et al. 1988a, Olson and Platt 1995). Hurricanes are less frequent events with effects that could potentially alter expected effects of lightning season fires. Thus, the question of interest in my study is: Do hurricanes modify the effects normally expected from growing season fires? Because I am not interested in testing the effects of no-fire the complete factorial design for two disturbances is not the best approach. In my study of hurricanes and fires in southeastern savanna-forest landscapes I limit my comparisons to the effects of hurricanes followed by fire vs. fire alone.

Dissertation Structure

In my dissertation, I approach questions of interacting disturbance effects in southeastern ecosystems from two directions. First, I explore interactions of hurricanes and fires in pine savannas and adjacent hardwood forests using conceptual models. Then I test resulting hypotheses using experimental field studies. This combined approach enables me to draw broad

conclusions about what might be expected in these ecosystems in the context of anthropogenic changes to forests, fire regimes, and climate-driven disturbance regimes.

In this Introduction I have summarized the roles of fires and hurricanes in southeastern landscapes, and I have explored experimental designs for testing disturbance interactions at different scales. In Chapter 2, I explore interacting effects of sequential disturbances by developing conceptual models of hurricanes followed by lightning-season fires in pine savannas. In Chapter 3 I review the results of an experimental study in which I tested interactions of two hurricane effects followed by prescribed fire in the understory of savanna-forest ecotones. Finally, in Chapter 4 I provide a general conclusion that links together the two approaches and highlights the significance of understanding disturbance interactions. In this chapter, I consider how anthropogenic changes to landscapes and effects on climate driven disturbances might alter the frequency or intensity of natural disturbances and thus alter interactions and effects of interacting large-scale disturbances.

CHAPTER 2

HURRICANE-FIRE INTERACTIONS IN FORESTED LANDSCAPES IN COASTAL SOUTHEASTERN NORTH AMERICA

Introduction

Large-scale disturbances influence ecological landscapes. Different types of large-scale disturbances commonly have different effects on vegetation and ultimately entire ecosystems (Turner et al. 1997, Turner and Dale 1998). Interactions between different disturbances might produce effects different from those produced in isolation (Elmqvist et al. 1994, Smith et al. 1994, Myers and Van Lear 1998, Paine et al. 1998, Willig and Walker 1999, Platt et al. 2002). Moreover, effects of interacting disturbances should vary with the frequency of the different disturbances, as well as the types of individual disturbance effects on the vegetation (Platt et al. 2002). We reason that interacting disturbances are most likely to influence landscape-level vegetation patterns in biogeographic regions where different large-scale disturbances occur frequently and influence common aspects of landscapes.

We develop hypotheses regarding short-term interactive effects of natural, lightning-season fires and hurricanes on savanna-forest landscapes in southeastern North America. Fires and hurricanes occur frequently in lowland coastal landscapes in this region of the continent (e.g., Whigham et al. 1991, Glitzenstein et al. 1995, Batista and Platt 1997, Platt 1999, Platt et al. 2000). We first compile known effects of each disturbance in isolation on old-growth pine savannas and warm-temperate/subtropical hardwood forests, as well as the ecotone between these plant communities. Second, we consider potential effects of juxtaposed fires and hurricanes based on differences in seasonal timing and direct effects of these disturbances, as well as post-disturbance changes in potential fuels following fires and hurricanes in savannas, ecotones, and forests. We then extend these hypotheses regarding short-term synergistic effects to propose potential long-term implications of fires and hurricanes in different habitats within the landscape, given a context of local climatic and site conditions and the presence of certain types of plant species. Finally, we modify our proposed model of hurricane-fire interactions to include anthropogenic fires, and we then consider how anthropogenic modifications of fire regimes

might influence restoration and management of southeastern North American landscapes containing savannas and forests. We attempt to develop general hypotheses, applicable to landscapes in coastal warm temperate regions of the Atlantic Ocean and Gulf of Mexico, as well as subtropical coastal regions of the Gulf of Mexico and Caribbean Sea.

Background

Pine Savannas and Hardwood Forests in Southeastern North America

Lowlands (< 1000 m elevation) predominate in coastal regions of southeastern North America along the Atlantic Ocean, Gulf of Mexico and Caribbean Sea (see reviews of Beard 1953, Clewell 1986, Murphy and Lugo 1986, Furley et al. 1992, Murphy and Lugo 1995, Platt 1999). Local topography typically involves subtle variation in elevations. Soils are primarily weathered porous sands or recently exposed substrates that are low in nutrients (Christensen 1976, Kellman 1984) and that change locally with elevation (Furley et al. 1992). The warm-temperate to subtropical climate is notable for pronounced seasonal patterns of precipitation that produce characteristic wet and dry seasons (e.g., Hutchinson 1977, Chen and Gerber 1990).

Historically, lowland forested landscapes in many coastal regions of southeastern North America were a mixture of savannas and warm-temperate or subtropical hardwood forests. Pines were a dominant feature of these savanna landscapes. The historical distribution of lowland warm temperate pine savannas in North America extended more or less continuously from southeastern Virginia westward to Texas and south to central Florida in the southeastern United States (Figure 2.1). Pine savannas (*sensu* Platt 1999) contained a discontinuous overstory of pines (primarily longleaf pine, *Pinus palustris*; (Platt et al. 1988b), some hardwoods (e.g., scrub oaks, Rebertus et al. 1993, Greenberg and Simons 1999) and a species-rich herbaceous-dominated groundcover (Walker and Peet 1983, Peet and Allard 1993, Platt 1999, Platt et al. 2005). Hardwood forests occurred within a background matrix of pine savannas, often in locally

edaphically variable sites and at lower elevations (Platt and Schwartz 1990, Harcombe et al. 1993, Batista and Platt 1997).

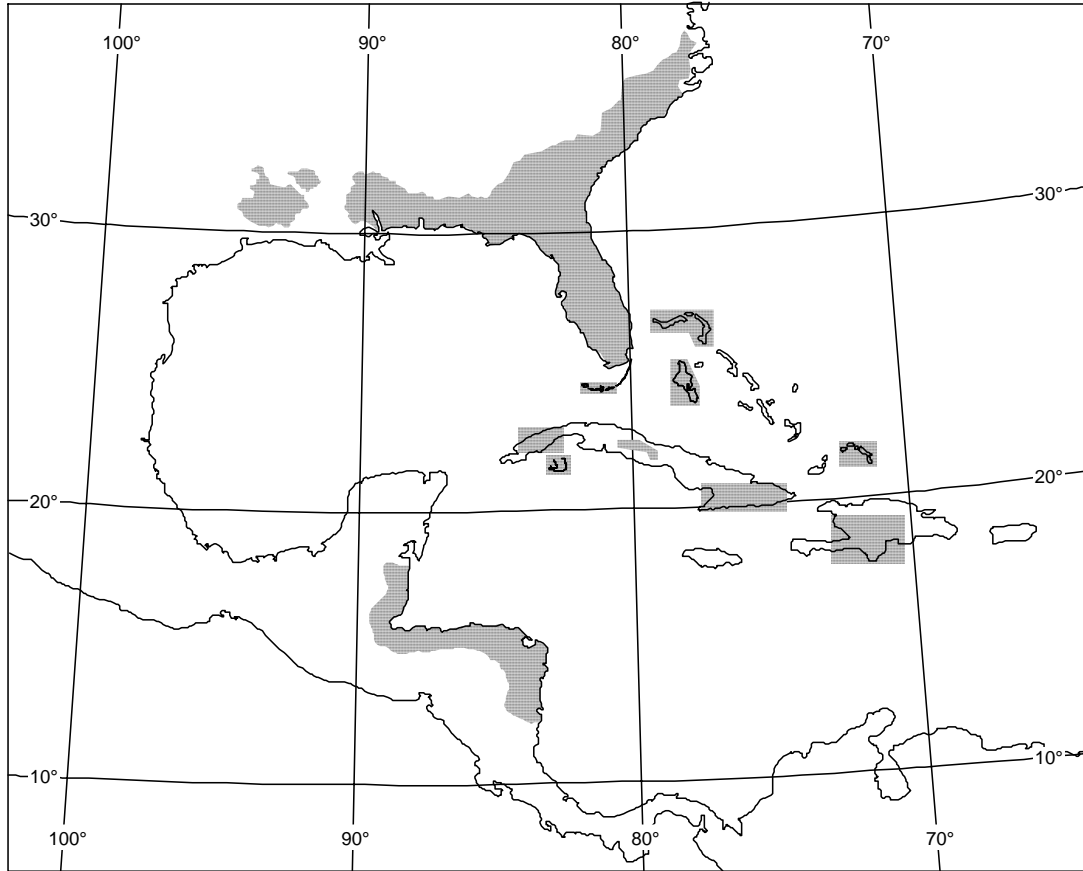


Figure 2.1. The historical distribution of pine savannas in lowland warm temperate and subtropical regions of North America and the Caribbean (shaded regions).

Similar patterns have been described for lowland, subtropical coastal regions. These landscapes extended from southern Florida through the western Caribbean as well as the eastern coast of Central America, from the southern tip of Mexico to central Nicaragua (Figure 2.1). Savannas with a discontinuous overstory of pines (e.g., *Pinus elliottii* var. *densa*, *Pinus caribaea*, *Pinus oocarpa*) and species-rich, graminoid-dominated groundcover were interspersed with subtropical hardwood forests in this region (Beard 1953, Munro 1966, Hutchinson 1977, Clewell 1986, Snyder et al. 1990, Doren et al. 1993, Mooney et al. 1995).

Large-Scale Disturbances in Pine Savanna-Hardwood Forest Landscapes

Fires. Natural climate-driven lightning fires have long been recognized as an integral part of the environment in pine savannas of both warm temperate and subtropical regions of coastal North America (Beard 1953, Robertson 1953, Munro 1966, Hutchinson 1977, Clewell 1986, Perry 1991, Doren et al. 1993, Platt 1999 and references therein, Beckage et al. 2003, Beckage et al. 2006). Lightning fires were inherently variable, but historically occurred more than once per decade (Table 2.1A). We diagram one randomly generated pattern of fire frequency for a hypothetical savanna-forest landscape in Figure 2.2A.

Other characteristics of lightning fires also tend to be predictable (Table 2.1A). Seasonal rainfall patterns (e.g., Hutchinson 1977, Chen and Gerber 1990) produce distinct transitions from dry to wet seasons, during which time thunderstorms and lightning strikes increase in frequency (Olson and Platt 1995, Hodanish et al. 1997, Platt 1999). This combination produces synoptic weather conditions (Johnson 1992) favoring ignition of fires in pine savannas during the early “lightning season” (March-June; Platt 1999, and references therein, Beckage et al. 2003, Beckage et al. 2005). The predominance of fine fuels (Table 2.1B) results in rapid drying and high likelihoods of ignition shortly after rainfall (Table 2.1A). Rates of spread of savanna fires usually are rapid, with fires being confined to the groundcover. High fire frequencies generally result in low intensities ($< 800^{\circ}\text{C}$), but increased fuel loads can result in “hotspots” in local areas (Thaxton 2003, Table 2.1A).

Savanna tree and understory species generally survive lightning fires with minimal damage (Table 2.1C). Savanna pines are fire-resistant (Platt 1999), and recruitment occurs even when fires occur frequently (Grace and Platt 1995). Frequent growing season fires have been shown to affect relative dominance and distribution of pines and hardwoods within savannas (Gilliam and Platt 1999, Platt et al. 2005). Such fires cause greater complete kill and top kill of hardwoods relative to pines (Glitzenstein et al. 1995). Moreover, effects of fires are greatest near

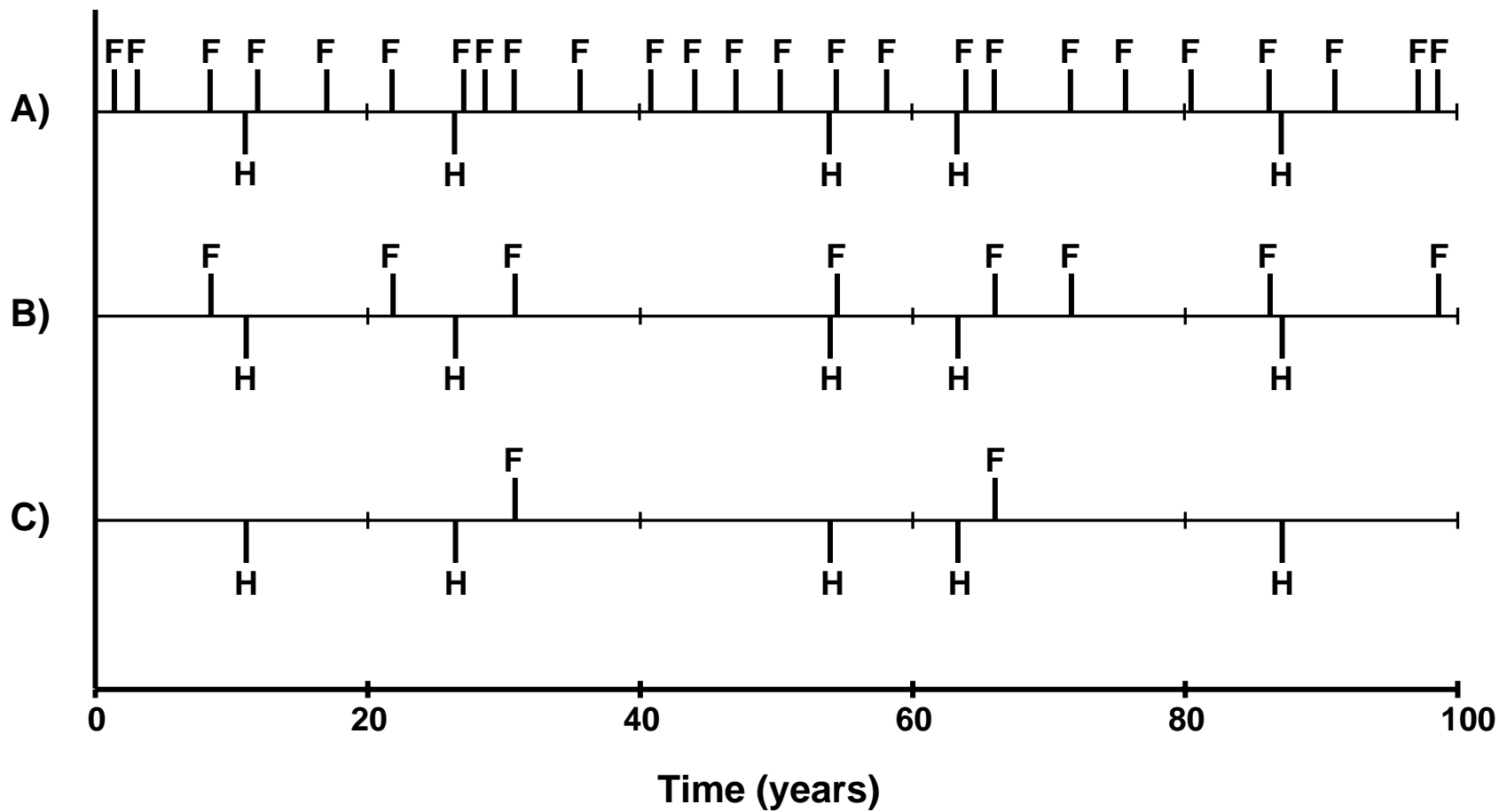


Figure 2.2A. A hypothetical century of lightning-initiated fires (F) and hurricanes (H) in a landscape containing adjoining pine savanna, ecotone, and hardwood forest. Each F represents a fire, and each H represents a hurricane. The hurricane return intervals, 4-6 per century, are the same in all three habitats. A) PINE SAVANNA: fires return at intervals of more than once per decade. B) SAVANNA-FOREST ECOTONE: fires occur much less frequently than in pine savanna, about once every 10 to 20 years on average. C) HARDWOOD FOREST: fires occur only rarely, once every 50 or more years, during severe droughts.

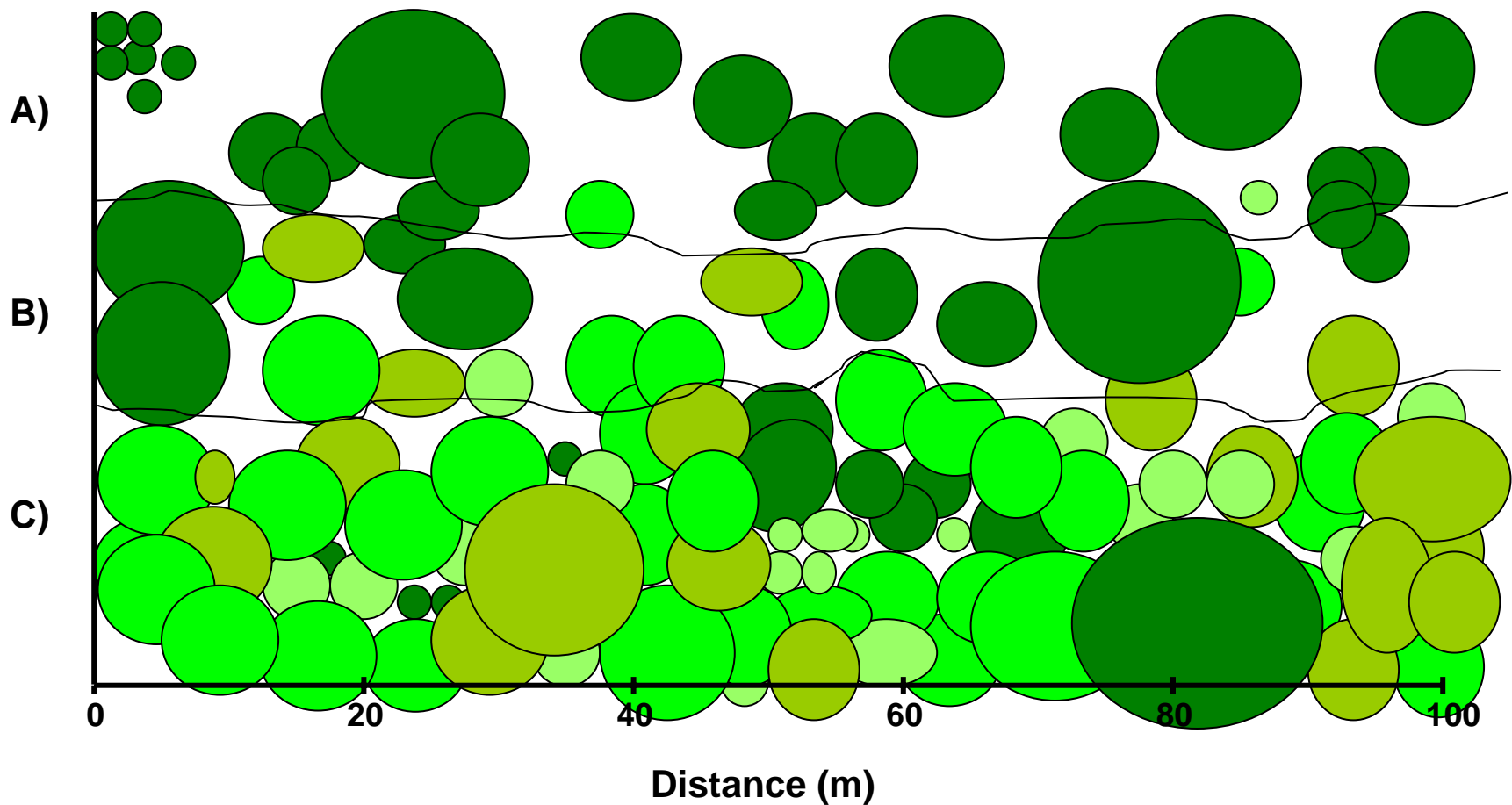


Figure 2.2B. A cartoon depicting the forest canopy as seen from above in a landscape containing adjoining pine savanna, ecotone, and hardwood forest. Relative sizes of shapes represent canopies of canopy trees (large), subcanopy trees (medium) and understory trees and shrubs (small). A) PINE SAVANNA: characterized by a discontinuous canopy of large pines with patchy distribution across the landscape, with seedlings as well as some hardwood shrubs in the understory. B) SAVANNA-FOREST ECOTONE: greater canopy cover compared to savannas, and woody species include a mixture of pine and hardwoods. C) HARDWOOD FOREST: closed canopy of adjacent hardwood forest results in decreased light levels in the understory. Woody species are predominantly hardwoods with occasional canopy pines.

Table 2.1A. Comparison of fire regimes in pine savanna, ecotone and hardwood forest communities of coastal North America.

Fire Regime	Pine Savanna	Source	Ecotone	Source	Hardwood Forest	Source
Frequency	More than one fire per decade	(Hutchinson 1977, Kellman 1984, Clewell 1986, Frost 1993, Platt 1999 and references therein, Beckage et al. 2003)	Once every 1 to 2 decades	(Myers 1990, Platt and Schwartz 1990, Snyder et al. 1990, Kellman and Meave 1997)	Once every 50 or more years	(Platt and Schwartz 1990, Snyder et al. 1990, Robertson and Platt 1992, 2001)
Timing/Season	Dry/wet transition during early growing season	(Olson and Platt 1995, DeCoster et al. 1999, Platt 1999 and references therein, Beckage et al. 2003, Slocum et al. 2003)	Early growing season during dry years	(Platt and Schwartz 1990, Snyder et al. 1990, Robertson and Platt 1992, Kellman and Meave 1997, Robertson and Platt 2001)	Early growing season during extreme drought years	(Platt and Schwartz 1990 and references therein, Robertson and Platt 1992, 2001, Slocum et al. 2003)
Behavior	Fast-moving surface fires; occasionally entering crowns	(Platt 1999 and references therein, Slocum et al. 2003)	Generally creeping surface fires, sometimes fast-moving	(Myers 1990, Platt and Schwartz 1990, Kellman et al. 1994, Kellman and Meave 1997)	Creeping surface fires, patchy	(Platt and Schwartz 1990 and references therein, Robertson and Platt 1992, Kellman et al. 1994, Kellman and Meave 1997, Robertson and Platt 2001)
Intensity	Generally low; higher in areas with increased fuels (i.e. treefalls)	(Platt 1999 and references therein, Slocum et al. 2003)	Generally low, higher in areas with flammable vegetation (i.e. cane, palmettos)	(Platt and Schwartz 1990, Kellman et al. 1994)	Low	(Barden and Woods 1974, Streng and Harcombe 1982, Platt and Schwartz 1990, Kellman and Meave 1997, Robertson and Platt 2001)

Table 2.1B. Fuel consumption during fires in pine savanna, ecotone and hardwood forest communities of coastal North America.

Fuel Type	Pine Savanna	Source	Ecotone	Source	Hardwood Forest	Source
Fine Fuels	Dry pine needles, grasses	(Rebertus et al. 1989b, Platt et al. 1991, Glitzenstein et al. 1995, Platt 1999 <i>and references therein</i> , Fonda 2001, Platt and Gottschalk 2001)	Dry leaves and pine needles, flammable vegetation (i.e. cane, palmetto)	(Streng and Harcombe 1982, Kellman 1984, Myers 1990, Platt and Schwartz 1990, Snyder et al. 1990, Kellman and Meave 1997)	Discontinuous fuels such as packed and moist leaves, root mats	(Streng and Harcombe 1982, Kellman 1984, Kellman and Meave 1997)
Woody Fuels	Branches and stems of some live shrubs and small trees; dead branches and stems	(Hermann 1993, Liu et al. 1997)	No live woody fuels consumed; dead woody fuels consumed	(Streng and Harcombe 1982, Myers 1990, Platt and Schwartz 1990, Snyder et al. 1990, Kellman and Meave 1997)	No live woody fuels consumed; dead woody fuels consumed	(Baker 1974, Platt and Schwartz 1990, Robertson and Platt 1992, 2001)

Table 2.1C. Comparison of fire effects in pine savanna, ecotone and hardwood forest communities of coastal North America.

Fire Effects	Pine Savanna	Source	Ecotone	Source	Hardwood Forest	Source
Canopy Trees	Low mortality of many stages due to fire-resistant grass stages and layered bark	(Platt 1999 <i>and references therein</i>)	Some mortality of species with thin-bark	(Myers 1985, Platt and Schwartz 1990, Kellman and Tackaberry 1993)	Mortality of thin barked species; trunk scarring	(Laessle and Monk 1961, Blaisdell et al. 1974, Myers 1985, Robertson and Platt 1992, 2001)
Groundcover	Very low mortality; Widespread top-kill followed by resprouting and reseedling; some mortality of seedlings	(Walker and Peet 1983, Abrahamson 1984a, b, Brewer and Platt 1994, Olson and Platt 1995, DeCoster et al. 1999, Drewa et al. 2002, Kirkman et al. 2004)	Top-kill and resprouting of most small trees and shrubs, extensive seedling mortality	(Myers 1985, Kellman and Tackaberry 1993, Kellman and Meave 1997)	Top-kill and resprouting of small trees and shrubs; high seedling mortality	(Monk 1960, Blaisdell et al. 1974, Abrahamson 1984a, b, Robertson and Platt 1992, Kellman and Tackaberry 1993, Kellman and Meave 1997)

pinus (Williamson and Black 1981, Rebertus et al. 1989a, b, Platt et al. 1991, Rebertus et al. 1993), resulting in hardwood patches in open areas away from canopy pines (Rebertus et al. 1989a, b, Harcombe et al. 1993, Platt 1999, and references therein). Groundcover plants are top-killed by fires, but resprout from dormant buds or recruit from seed (Table 2.1C). Pre-burn stem densities are reached shortly after fires (Olson and Platt 1995), although biomass re-accumulation takes at least one year and often longer (Platt 1999). Fire-related mortality generally is confined to very small plants or to areas of locally heavy fuel loads (e.g., Williamson and Black 1981, Hermann 1993, Glitzenstein et al. 1995, Olson and Platt 1995).

Repeated fires have been recognized to influence the local distribution of pine savannas and adjacent hardwood forests (Kellman 1984, Platt and Schwartz 1990, Harcombe et al. 1993, Kellman and Tackaberry 1993, Rebertus et al. 1993, Platt 1999, and other references therein). In both uplands and lowlands, pine savannas occur where fires burn most frequently. These areas typically contain nutrient poor soils that dry out frequently (Beard 1953, Alexander 1973, Kellman 1984, Mooney et al. 1995). Transitions occur from dry, nutrient-poor regions to adjacent areas of increasing soil moisture on lower slopes, areas of seepage or different soil types (e.g., Beard 1953, Furley 1974b, Furley 1974a, Kellman 1984, Meave et al. 1991, Kellman and Tackaberry 1993). Such ecotones or "tension zones" between pine savannas and adjacent hardwood forests occur throughout coastal landscapes in southeastern North America. We illustrate the distribution of tree and shrub canopies near the transition from savanna to hardwood forest in a southeastern landscape (Figure 2.2B).

Periodic fires entering hardwood forests can generate ecotones that contain distinct assemblages of plants (Platt and Schwartz 1990). Relative to forest interiors, these ecotones are characterized by increased light levels (MacDougall and Kellman 1992, Kellman and Tackaberry 1993), different nutrients and soils (Kellman 1984, Meave et al. 1991), and decreased moisture (Platt and Schwartz 1990). As a result, ecotones have been hypothesized to contain species that

are somewhat light-demanding and fire tolerant, but require longer fire-free intervals than savanna species (e.g., Platt and Schwartz 1990, MacDougall and Kellman 1992, Kellman and Tackaberry 1993, Kellman and Meave 1997). In the middle panel of Figure 2.2A, the fire frequency in the ecotone between a pine savanna and a hardwood forest is depicted as somewhat frequent, about once every 1-2 decades on average, but highly variable. The intervals between successive fires in ecotones depend, in large part, on rates of re-accumulation of fine fuels after fires. Fires in the ecotone are generally of lower intensity than pine savanna fires, except in areas with highly flammable vegetation (Table 2.1A, B). Ecotone fires top-kill many understory plants and cause widespread mortality of seedlings (Table 2.1C).

Lightning-season fires that originate in savannas should move through ecotones into areas containing hardwood forests at longer intervals and most often during drought years (Table 2.1A). In the lower panel of Figure 2.2A, fires are depicted as entering hardwood forests at intervals of about twice each century. These intervals are based on fire records for lightning-initiated fires burning from pine savanna into subtropical forest in Everglades National Park (Robertson 1953, Olmsted et al. 1983, Platt 1999, Robertson and Platt 2001). Other hardwood forests adjacent to pine savannas have experienced periodic fires (Platt and Schwartz 1990, Kellman and Tackaberry 1993, Kellman et al. 1994, Kellman and Meave 1997). Such fires do not burn intensely or become canopy fires, but creep across the forest floor, moving into lower-lying areas (Table 2.1A). These fires burn irregularly through discontinuous leaf litter and root mats and often result in patches of bare substrate. Although fuels may be present at ground level, they tend to be packed, moist and discontinuous (Table 2.1B), resulting in decreased fuel consumption and low intensity fires. Nonetheless, such fires can cause mortality of understory seedlings and saplings (Table 2.1C).

Hurricanes. Winds from hurricanes and tropical storms are known to damage forests in coastal regions of North America (e.g. Boucher et al. 1990, Brokaw and Walker 1991, Gresham

et al. 1991, Horvitz et al. 1995). These storms develop over the northern Atlantic Ocean and range in intensity when they make landfall (Table 2.2). Hurricane return periods vary for coastal regions within North America and decrease with distance inland from the coast (Table 2.2). Expected return periods for hurricanes in coastal counties from Florida's east coast to North Carolina range from 4.6 to 97 years with only 7 of the 43 counties having return periods longer than 30 years (Elsner and Kara 1999). Gulf coast counties from Florida to Texas have return periods from 3.7 to 48.5 years and only 4 of the 55 counties have expected returns greater than 30 years. In Figure 2.2A we depict a hurricane return period of 20 years (5 storms per century).

Table 2.2. Hurricane regime of the southeastern coastal region of North America.

Hurricane Regime	North Atlantic tropical cyclone basin	Source
Region	<ul style="list-style-type: none"> Atlantic coast of southeastern United States, the Gulf of Mexico, and the Caribbean Sea 	(Neumann et al. 1993)
Intensity	<ul style="list-style-type: none"> <u>Tropical storm</u>: maximum sustained winds 18-33m/s <u>Minor Hurricane</u> (Saffir/Simpson categories 1-3): maximum sustained winds 33 to 49m/s <u>Major Hurricane</u> (Saffir/Simpson categories 4-5): maximum sustained winds greater than 50m/s 	(Simpson and Riehl 1981)
Return Period	<ul style="list-style-type: none"> Return periods (annual-landfall-probability⁻¹) for coastal Florida counties range from 3.7 to 48.5 years Annual probability of Florida hurricane landfall is 62% 	(Elsner and Kara 1999)
Timing/Season	<ul style="list-style-type: none"> >97% of tropical activity from June 1 to November 30 78% of tropical storm days from August to October 87% of minor hurricane days from August to October 96% of major hurricane days from August to October 	(Landsea 1993)
Variability	<ul style="list-style-type: none"> Frequency varies over short and long time scales. Return periods vary between the Atlantic and Gulf coasts For example, variation in landfall of major hurricanes between the Atlantic and Gulf Coastal regions every 10 years is associated with an inverse correlation in activity between high and low latitudes 	(Simpson and Lawrence 1971, Landsea 1993, Henderson-Sellers et al. 1998, Liu 1999, Elsner et al. 2000, Liu and Fearn 2000, Emanuel 2005 and references therein)

Hurricanes typically damage trees in old-growth forests and savannas. Some savanna and forest trees are uprooted or snapped below crowns. Much larger proportions are damaged, but survive (Table 2.3), even in the most intense hurricanes (see studies following Hurricanes Hugo and Andrew: Finkl and Pilkey 1991, Walker et al. 1991, Stone and Finkl 1995, Platt et al.

2000). Savannas and forests differ, however, in the states of surviving trees. Most pines in old-growth savannas are intact, but may be leaning or have lost branches. Most needles survive and remain green during the year after the hurricane. In contrast, trees in hardwood forests often are severely damaged (e.g., Boucher et al. 1990, Slater et al. 1995). As a result of differences in effects on trees, spatial patterns of damage differ between old-growth pine savannas and hardwood forests. In old-growth pine savannas, based on limited studies (Platt and Rathbun 1993, Platt et al. 2000), individual trees may be damaged or killed, but multiple blowdowns appear uncommon. Much greater damage tends to occur in hardwood forests affected by the same hurricane (Slater et al. 1995, Batista and Platt 1997). The most notable direct effect of hurricanes in hardwood forests is the elimination of portions, or in major hurricanes, almost the entire canopy. Additional effects of canopy disturbance include large quantities of litter on the forest floor and increased light penetration to understory.

Direct annual mortality attributed to hurricanes in old-growth pine savannas and forests rarely appears to be catastrophic (*sensu* Platt and Connell 2003). Even major hurricanes (maximum sustained winds $\geq 50\text{m/s}$) rarely result in mortality that exceeds 30% of individuals (Platt et al. 2000). Although mortality of trees following hurricanes may increase transiently compared to background mortality (Lugo and Waide 1993, Platt and Rathbun 1993, Lugo and Scatena 1996), even major hurricanes appear not to be catastrophic. Direct mortality may be higher in old-growth pine savannas than in hardwood forests (Platt et al. 2000; Table 2.3) as a result of differences in resprouting (Boucher 1990, Boucher et al. 1990). Mortality during the year after a hurricane averaged 20-25% in old-growth pine savannas of the southeastern United States, but mortality of trees in hardwood forests during the same year was considerably less than 20% (Platt and Rathbun 1993, Slater et al. 1995, Platt et al. 2000, Batista and Platt 2003).

Table 2.3. Damage and mortality to trees in forests and savannas of coastal southeastern North America following major and minor hurricanes. Damage and mortality estimates were obtained from trees approximately ≥ 2 cm diameter at breast height (dbh) generally within one year of the hurricane except where indicated.

Hurricane	Year	Country	Forest	Damage	Mortality	Source
David	1979	Dominica	Wet and Dry Tropical	52% ¹	2%	Lugo et al. 1983
Kate	1985	USA	Pine Savanna	6% ²	3%	Platt and Rathbun 1993, Platt unpublished data
			Warm Temperate Hardwood	30% ²	3%	Batista and Platt 1997, Batista and Platt 2003
Gilbert	1988	Jamaica	Tropical	13% ¹	8%	Bellingham 1991, Bellingham et al. 1992, 1994
		Mexico	Dry Tropical	90% ¹	10%	Whigham et al. 1991
Joan	1988	Nicaragua	Wet Tropical	62% ¹	13%	Boucher et al. 1990
			Pine Forest	2% ¹	42%	Boucher et al. 1990
			Wet Tropical	80% ¹	23%	Yih et al. 1991
Hugo	1989	Puerto Rico	Wet Tropical	30% ³	1%	Frangi and Lugo 1991
			Tropical Hardwood	17% ²	9%	Zimmerman et al. 1994
			Tropical Hardwood	14-20% ²	7%	Walker 1991, Walker et al. 1992
		USA	Bottomland	49% ^{3,4}	11% ⁵	Putz and Sharitz 1991, Allen and Sharitz 1999
Andrew	1992	USA	Pine Savanna	>70% ²	17%	Platt et al. 2000
			Subtropical Hardwood	92% ²	32-67%	Horvitz et al. 1995
			Subtropical Hardwood	85% ²	12%	Slater et al. 1995

¹Percentage stems snapped/broken and uprooted

²Percentage of stems bent, snapped, and uprooted

³Percentage of stems snapped, uprooted, severe crown loss (>25%)

⁴Damage of trees > 20cm dbh

⁵Mortality of trees > 10cm dbh

Post-hurricane composition of pine and hardwood stands remains essentially unchanged. No direct evidence exists for large-scale changes (i.e., succession) in old-growth pine savannas following hurricanes (Platt and Rathbun 1993, Platt et al. 2000). Resprouting and recovery of hardwood forest trees also results in little change in forest composition following hurricanes (Vandermeer et al. 1990, Tanner et al. 1991, Yih et al. 1991, Basnet 1993, Slater et al. 1995). Resprouting and refoliation may be initiated within a few months of a hurricane (Yih et al. 1991, Walker et al. 1992, Bellingham et al. 1994). Rapid reformation of hardwood forest canopies, especially in subtropical forests, occurs close to the ground (Slater et al. 1995, W.J. Platt, pers. obs.). Direct regeneration results in little or no change from pre-hurricane species composition (Yih et al. 1991). Nonetheless, there may be recruitment of some pioneer and exotic species, especially in local disturbances such as tip-ups (Pascarella 1997, Horvitz et al. 1998, Kwit et al. 2000).

Hypotheses and Predictions

Hurricane-Fire Interactions

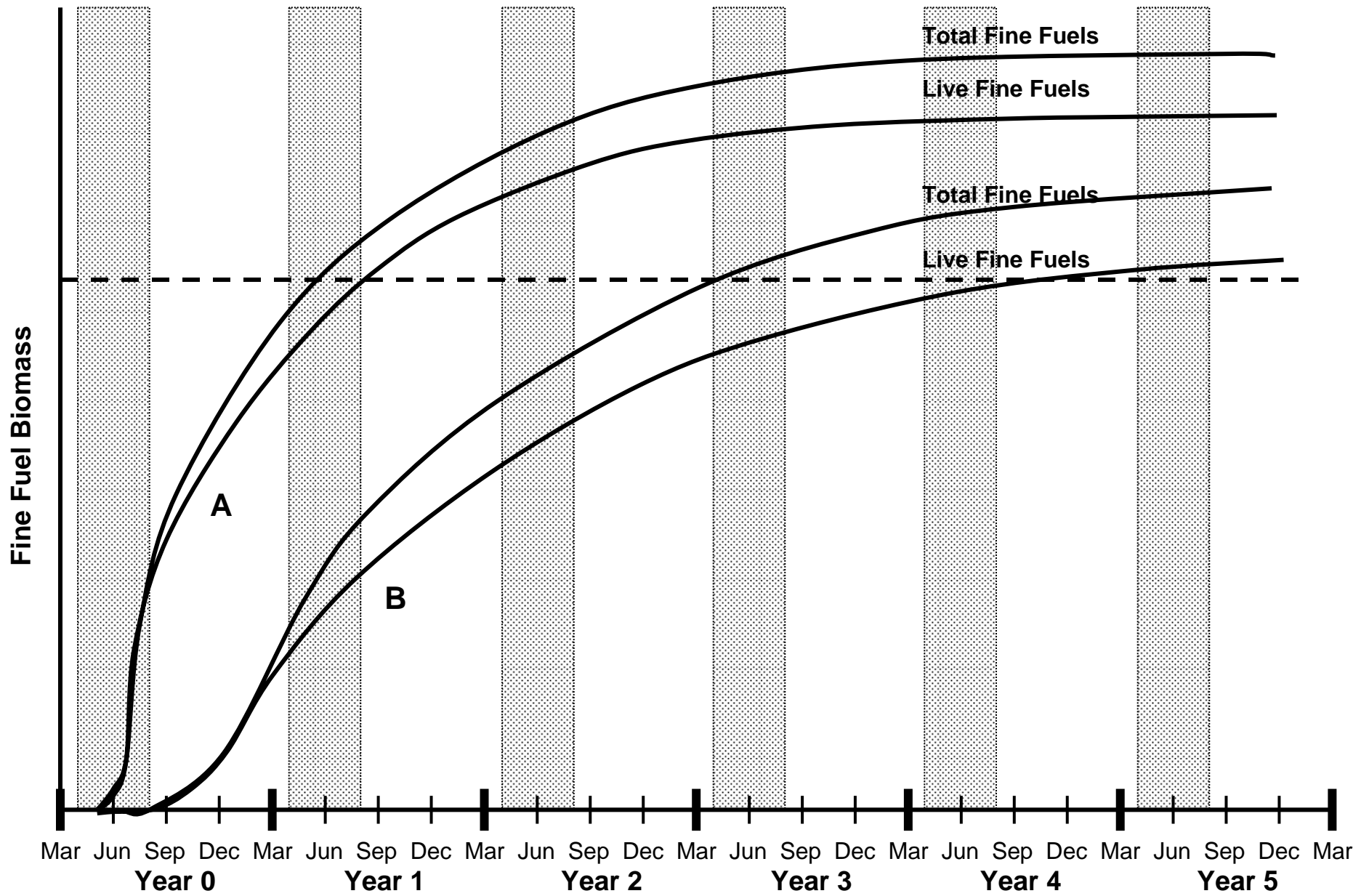
Interaction Hypotheses. Interactive effects of fires and hurricanes depend on the juxtaposition of these disturbances over short time periods of several years relative to changes in fine fuels during the intervening period. Any modification of the effects of a subsequent disturbance thus should depend on the longevity of effects produced by the initial disturbance. In addition, differences in seasonality of hurricanes and natural lightning fires will influence interactive effects when these disturbances occur in close association. More than 96% of major Atlantic hurricanes occur within three months (August - October), with the remaining 4% occurring during adjacent months (Landsea 1993). In contrast, most lightning fires occur earlier in the year (May-August in both the U.S. and Central America), and extensive fires (those likely to influence savanna-forest landscapes), are even more restricted in occurrence to the transition

from dry to wet seasons (May and June in the southeastern U.S.; Komarek 1964, Doren et al. 1993, Platt 1999).

We propose that the occurrence and magnitude of hurricane-fire interactions depend on the relative timing of hurricanes and fires in relation to the duration of effects produced by the different disturbances. For example, in Figure 2.2A, each hurricane is preceded and followed by a fire, but the relative timing is variable within and among landscape components (savanna, ecotone and forest). We use two sets of information to generate a mechanistic hypothesis for predicting the conditions under which hurricane-fire interactions are expected. First, patterns of fine fuel re-accumulation after any single fire influence the likelihood of subsequent fires. Second, fine and coarse woody debris produced by hurricanes decompose over time. The time scales of litter re-accumulation after a fire relative to decomposition after a subsequent hurricane should determine the likelihood that fuels in the different landscape components will be continuous and sufficient to burn during the next fire. Our empirically-derived conceptual model generates scenarios based on variations in fuels and time scales that we illustrate graphically for three components of the landscape.

Re-accumulation of Groundcover Biomass and Litter after Fire. Any single fire in a North American pine savanna will tend to consume most fine fuels (grasses, herbs, pine needles, fine litter). The likelihood of a subsequent fire burning the same area depends, in part, on re-accumulation of these fine fuels (Johnson 1992, Whelan 1995, Platt 1999). Increases in the quantity and continuity of fine fuels over successive years result in fires being likely to burn across savanna landscapes within a decade and often within 2-3 years of a previous fire (Table 2.1A). In mesic pine savannas, as groundcover vegetation grows back during the post-fire wet season, we predict that live biomass will re-accumulate across the landscape to levels that are above the fuel continuity threshold about one year after fire (as illustrated in Figure 2.3; W.J. Platt personal observation). However, unless severe drought occurs, fires are unlikely to burn

Figure 2.3. Patterns of fine fuel re-accumulation after a fire in pine savanna and savanna-forest ecotone. Gray-shaded bars denote the natural lightning fire season which coincides with late spring/early summer lightning season. Curves represent the regrowth of fine fuels following a fire in year 0. The upper pair of curves represent fine fuels in a mesic pine savanna (A). The lower pair of curves represents fine fuels in an adjacent mesic savanna-forest ecotone (B). The lower curve of each pair represents live fine fuels while the vertical space between the pair represents dead fine fuels. The horizontal dashed line represents the threshold level of fine fuel biomass: the “fuel continuity threshold.” Widespread fires are not expected to occur until fine fuels are sufficiently continuous to carry a flame through a respective plant community. In this mesic savanna, fine fuels reach the threshold during the first year after fire, whereas ecotone fine fuels do not reach the fuel continuity threshold for several years.



across landscapes one year after an extensive fire because, regrowth tends to have high moisture content and there is yet little dead fine fuel (Figure 2.3). By the second year after a fire, accumulation of biomass produces additional fine dead fuels, and ignition is likely to result in relatively low intensity and somewhat patchy fires that burn across mesic savannas. In areas without extensive groundcover, such as low nutrient or xeric savannas, fuel continuity 2-3 years after a fire may still be insufficient for the next fire to burn across a savanna.

We predict that fine fuels in savanna-forest ecotones will accumulate more slowly than in adjacent savannas (Figure 2.3). Available data (e.g. Kellman and Meave 1997, Biddulph and Kellman 1998) indicate that growth of herbaceous groundcover species (especially warm season grasses) may be slowed in the lower light conditions of the ecotone and that accumulation of leaf litter may also be slower. Thus in ecotones, fuel continuity may be insufficient to carry fires for several years. This suggests that intervals between successive fires in ecotones are longer than those in savannas. Quantity, moisture-content and structure of fine fuels in ecotones also are likely to differ from those in savannas (Streng and Harcombe 1982). Rates of leaf and litter production by woody species should influence re-accumulation of fuels in ecotones to states where re-burning is possible. We predict that fuels will reach continuity thresholds over longer time intervals in ecotones than savannas (Figure 2.3). Still, the more open canopy of ecotones might result in fuels that dry more quickly, thus shortening fire-intervals compared to forests (Kellman and Meave 1997). In addition, flammability of fuels produced by some tree species, as for example, by large pines in ecotones, might also shorten return intervals between fires.

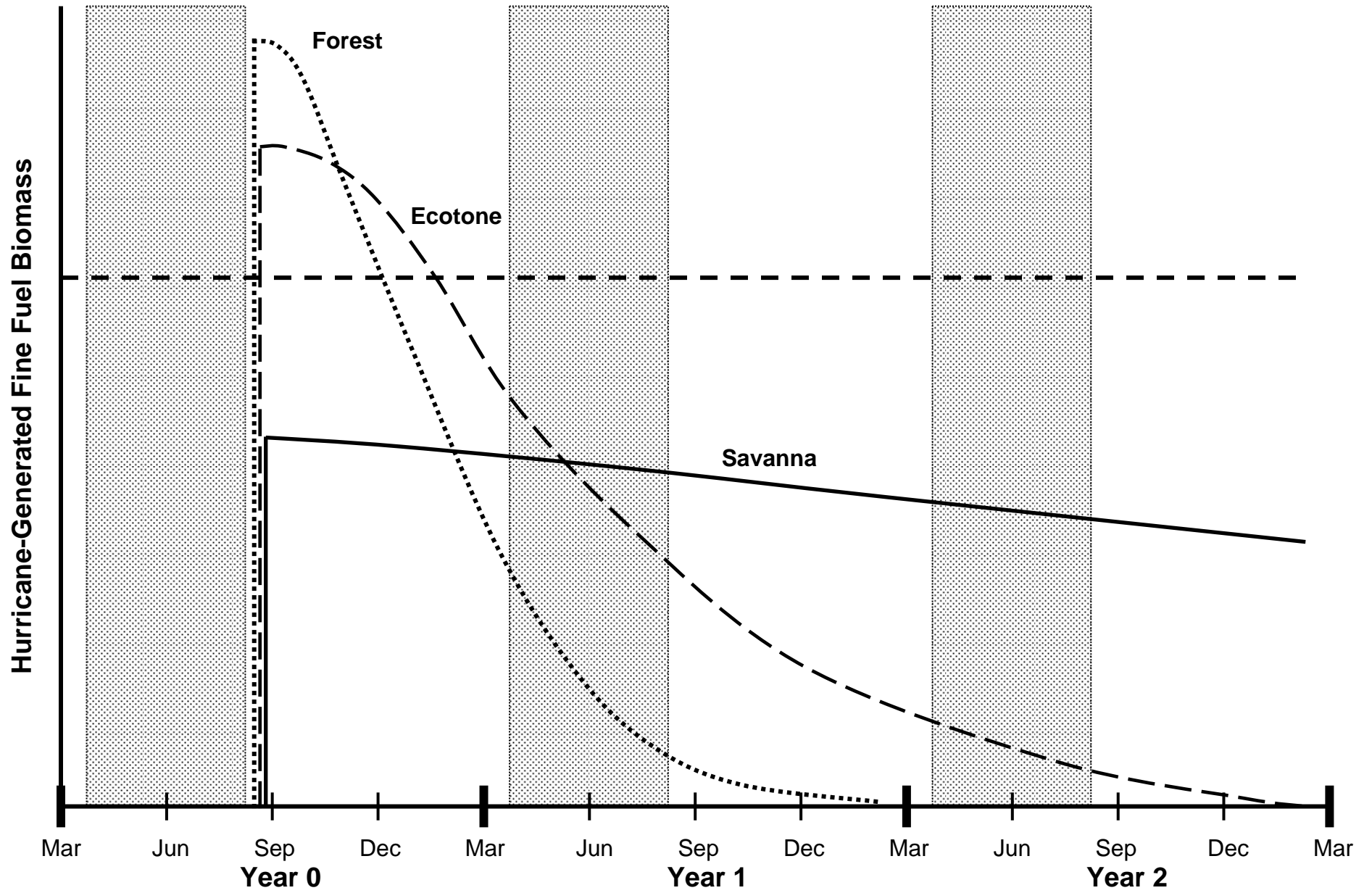
Post-Hurricane Conditions and Decomposition of Fuels after Hurricanes. The amount, composition and distribution of hurricane-produced litter differs between forest types (Brokaw and Walker 1991, Ostertag et al. 2003). In old-growth pine savannas, tall trees are widely spaced and there is not a continuous canopy (Figure 2.2B). Following hurricanes, downed large trees and branches with attached needles cause local, discrete increases in biomass (Platt and Rathbun

1993, Platt et al. 2000). These increases are not uniform or widespread, and thus hurricane-generated biomass would likely not cross the fuel continuity thresholds for entire savannas (Figure 2.4).

The deposition of fine fuel biomass by hurricanes occurs more consistently throughout hardwood forests than pine savannas (e.g., Boucher et al. 1990, Slater et al. 1995). The combination of many broken branches from abrading tree crowns and defoliation of most crowns results in increased leaf litter and woody debris of various sizes throughout forests (Ostertag et al. 2003). Hurricane Hugo created an influx of fine litter more than 400 times the daily input in a subtropical wet and lower montane forest of Puerto Rico (Lodge et al. 1991). Litter amounts added during the month following the hurricane were 2-3 times greater than that of a typical year, regardless of stream, riparian, or upslope topographies (Vogt et al. 1996). In subtropical hardwood forests, fine debris has been noted to comprise 15-33% of the total mass of hurricane-generated debris (Frangi and Lugo 1991, Zimmerman et al. 1995, Vogt et al. 1996). Even fairly moderate-intensity hurricanes might be expected to produce fine fuel pulses that exceed the fuel continuity threshold in both warm-temperate and subtropical hardwood forests (Figure 2.4).

The rate at which hurricane-generated fuels decompose depends on the type of biomass and on environmental conditions, such as moisture content and temperature. Post-hurricane decomposition of biomass in savannas has not been measured, but savanna fine fuels suspended in bunchgrass crowns above the soil surface are found to decompose half as fast as surface fuels (Hendricks et al. 2002). We depict slow decomposition of hurricane-generated fine fuels in savannas over a number of years in Figure 2.4. Coarse fuels decompose very slowly in pine savannas, with heartwood of fallen pines in old-growth savannas sometimes persisting for decades despite frequent fires. Although needles and small branches of downed pines burned within a few years after Hurricane Kate, >75% of downed large branches and tree trunks were still present 15 years later, despite 7-8 fires (W.J. Platt, pers. obs). Similar patterns have

Figure 2.4. Patterns of decomposition of hurricane-generated fine fuel biomass in savanna, savanna-forest ecotone, and forest. Gray-shaded bars denote the natural lightning fire season which coincides with late spring/early summer lightning season. Curves represent the input and subsequent decomposition of fine fuels following a hurricane during year 0. Fine fuel inputs in forests are greater than in the ecotone, but decompose more rapidly. In both forests and ecotones, fine fuel levels decrease below the fuel continuity threshold (horizontal dashed line) prior to the next fire season (gray shaded bars). Savanna fine fuel inputs do not cross the fuel continuity threshold and decomposition is slow.



occurred in Everglades pine savanna, with much coarse woody debris still present 10 years and several fires after Hurricane Andrew (W.J. Platt, pers. obs.).

Both fine and coarse woody biomass typically decomposes rapidly in warm temperate and subtropical hardwood forests (Batista and Platt 1997, Sullivan et al. 1999, Ostertag et al. 2003). Green and senescent leaves both decompose quickly on the forest floor (Brenner 1991, Ostertag et al. 2003, Fonte and Schowalter 2004). Litter and fine debris (twigs, small branches) >50 cm deep on the forest floor in Woodyard Hammock in Northern Florida had virtually disappeared within six months after Hurricane Kate (W.J. Platt, pers. obs.). Similar patterns were noted for subtropical forest in Everglades National Park after Hurricane Andrew (Slater et al. 1995, W.J. Platt, pers. obs.). Hurricane-generated leaf-litter on subtropical forest floors tends to decompose completely within 4-10 months (Frangi and Lugo 1991, Whigham et al. 1991, Ostertag et al. 2003). In seasonally-dry forest, leaf litter often decomposes more rapidly during rainy seasons than after the onset of dry seasons (e.g., Alvarez-Sanchez and Enriquez 1996). We depict post-hurricane fine fuel biomass (leaves and twigs) that declines below the fuel continuity threshold within a year in Figure 2.4.

Rates of decomposition for coarse woody debris are slower than for fine litter in warm temperate and subtropical forests, but are still more rapid than rates in pine savannas. Vogt and colleagues (1996) estimate that 7-16 years are needed for essentially complete decomposition of downed coarse woody debris (3-6 cm diameter) in subtropical forests. In a warm temperate forest, coarse debris from a hurricane was still present 9 years later (Batista and Platt 1997). Decomposition rates of woody debris in forests may be variable following hurricanes. Compared to undisturbed forest, understory light levels are significantly higher below single and multiple tree fall gaps in tropical and temperate forests (Canham et al. 1990) as well as in pine savannas (Battaglia et al. 2003). Drying of woody debris exposed to high light levels may slow local decomposition. As a result, more heavily disturbed areas may experience lower decay rates

(Rice et al. 1997, but see Alvarez-Sanchez and Enriquez 1996, Denslow et al 1998). As in pine savannas, coarse woody fuels do not count toward the fuel continuity threshold, because they are not continuously distributed.

Short-Term Implications of Hurricane-Fire Interactions. Individually, neither lightning season fires nor hurricanes typically produce large changes in savannas and forests. The longevity of effects of any single fire or hurricane will determine the likelihood of interactions in savannas and forests. Differences in the rates of re-accumulation of fine fuels following fires and decomposition of hurricane-produced fuels after hurricanes in savannas, ecotones and forests affect the probability of interactions within the savanna-forest landscape. We propose that the probability of short-term effects resulting in hurricane-fire interactions differs for pine savannas, ecotones, and forests.

The likelihoods of hurricane-fire interactions in pine savannas should be higher when decomposition rates of hurricane-generated fuels are slow. In savannas, hurricane-generated fuels should still be present for several years after a hurricane, when the first post-hurricane lightning fires occur. Whether such debris will ignite and burn depends on the state of the fine fuels and the environmental conditions at the time of the fire. Personal observations from the Wade Tract and Everglades National Park (W.J. Platt) indicate that lightning-season fires within the year following a hurricane often do not burn even the needles of pines downed by recent storms. The needles may still be green or matted on the ground, forming locally moist microclimates not conducive for the spread of fire. By two years after a hurricane, the needles of downed pines have dried; intense fires are likely in local areas containing tree crowns (Hermann 1993). These observations suggest that any hurricane-fire interactions in savannas will be delayed at least a year.

Hurricane-fire interactions should be unlikely immediately after fires or hurricanes, but should become increasingly likely over time, as post-fire and post-hurricane fuel conditions

increasingly favor locally hot fires. We illustrate hypothesized hurricane-fire interactions in a savanna in Figure 2.5A. First, assume that a lightning-initiated fire burns across a mesic savanna in year 0. Fine fuel biomass increases over time, crossing the fuel continuity threshold during year 1. Thus, if a hurricane also occurred in year 0, no fire as a result of an interaction would be predicted to occur in year 1. In our model the savanna fuels are not yet sufficient to produce a very intense fire, and the hurricane-generated fuels are matted and incompletely dried in the first year. By year 2, however, dried hurricane-generated fuels and larger amounts of dead savanna fuels should carry a fire across the landscape, producing local hot spots in the groundcover. If a hurricane instead occurred after year 0, then the hurricane-fire interaction may still be unlikely in the following lightning fire season if hurricane fuels are still moist. Fire frequencies of >2 per decade should result in hurricane-fire interactions being delayed only a few years. Nonetheless, delayed interactions could result in negative effects of dense fuel mats on the groundcover vegetation prior to fire, confounding direct hurricane effects with hurricane-fire interactions. Such confounding may be more likely if time intervals between successive fires are increased, as in xeric savannas and ecotones where fine fuels accumulate more slowly.

Conditions in savannas may continue to be favorable for hurricane-fire interactions at smaller spatial scales for years to decades. Downed branches and trunks directly kill vegetation beneath them. They also may burn intensely in stages (bark, before softwood, before heartwood) at variable intervals over several decades, creating “hot spots” (local elongate, open patches in the groundcover larger than the tree trunk diameter) over long time intervals. Once a fire has occurred, however, fuels for subsequent fires in these “hot spots” are reduced because plants in the groundcover are killed. Thus subsequent fires are likely to burn at lower intensity, if at all, within these areas (see Hermann 1993). Furthermore, blowdowns that produce large areas without pines may experience decreased fire intensity over long time intervals as a result of fewer pine needles present. Hardwood stems might become more prevalent (see Rebertus et al.

1989a, b, Rebertus et al. 1993) in such large localized areas in savannas (Harcombe et al. 1993, Platt and Rathbun 1993, Noel et al. 1998) that no longer burn as readily following removal of pine trees and needles (Liu et al. 1997). Thus hurricane-fire interactions potentially generate variability in both groundcover and tree components of savannas.

Hurricane-fire interactions appear less likely in ecotones and hardwood forests than in savannas. For hurricanes to affect patterns of fire behavior within savanna-forest ecotones and in forests, increased fuels produced by hurricanes must still be present when lightning fires enter these areas. The temporal disjunction between hurricane and natural lightning fire seasons, coupled with rapid decomposition of fine fuels in forests, reduces the likelihood of hurricane-fire interactions. By the time post-hurricane fires occur, most fine fuel increases produced by the hurricane are likely to have mostly disappeared. Although large coarse woody debris would be present, it is not likely to enhance fire spread without a continuous fine fuel matrix. More humid conditions and moist fuels also are likely in forests and ecotones than in savannas, especially if resprouting of trees results in a reformed canopy close to the ground (e.g., Fernandez and Fetcher 1991, Horvitz et al. 1995, Slater et al. 1995, Quigley and Platt 1996).

The potential for a hurricane-fire interaction in ecotones and forests would also depend on the post-fire state of savanna groundcover vegetation. If lightning fires have occurred in savannas the same year or even the year prior to a hurricane, fires are unlikely to burn into adjacent ecotones. These conditions are illustrated in Figure 2.5B. A fire occurs in the savanna and savanna-forest ecotone in year 0 and a hurricane occurs in the same year. The biomass of post-fire fine fuels in the ecotone increases over time, but does not cross the fuel continuity threshold until a number of years post-fire. Hurricane generated fine fuels in year 0 would decompose rapidly and fall below the fuel continuity threshold before the subsequent lightning season. Even if decomposition is slowed in the ecotone, conditions will not be suitable for a hurricane-fire interaction until more dead fine fuels re-accumulate in the ecotone. Although fuel

Figure 2.5A Combined patterns of savanna fine fuel re-accumulation after a fire and fine fuel decomposition after a hurricane. Gray-shaded bars denote the natural lightning fire season which coincides with late spring/early summer lightning season. The lower, paired curves represent the regrowth of savanna fine fuels following a fire in year 0 (Figure 2.3). The upper curve represents the sum of the post-fire fine fuels plus the input and subsequent slow decomposition of savanna fine fuels following a hurricane in the same year. The sum of fine fuels increases immediately above the fuel continuity threshold during the hurricane and are maintained above the threshold for many years assuming no fire. In year 1 however, hurricane generated fuels are packed and moist and thus fuels are unlikely to produce an intense fire. In savannas we predict that hurricane-fire interactions will be delayed a year or two after hurricanes occur.

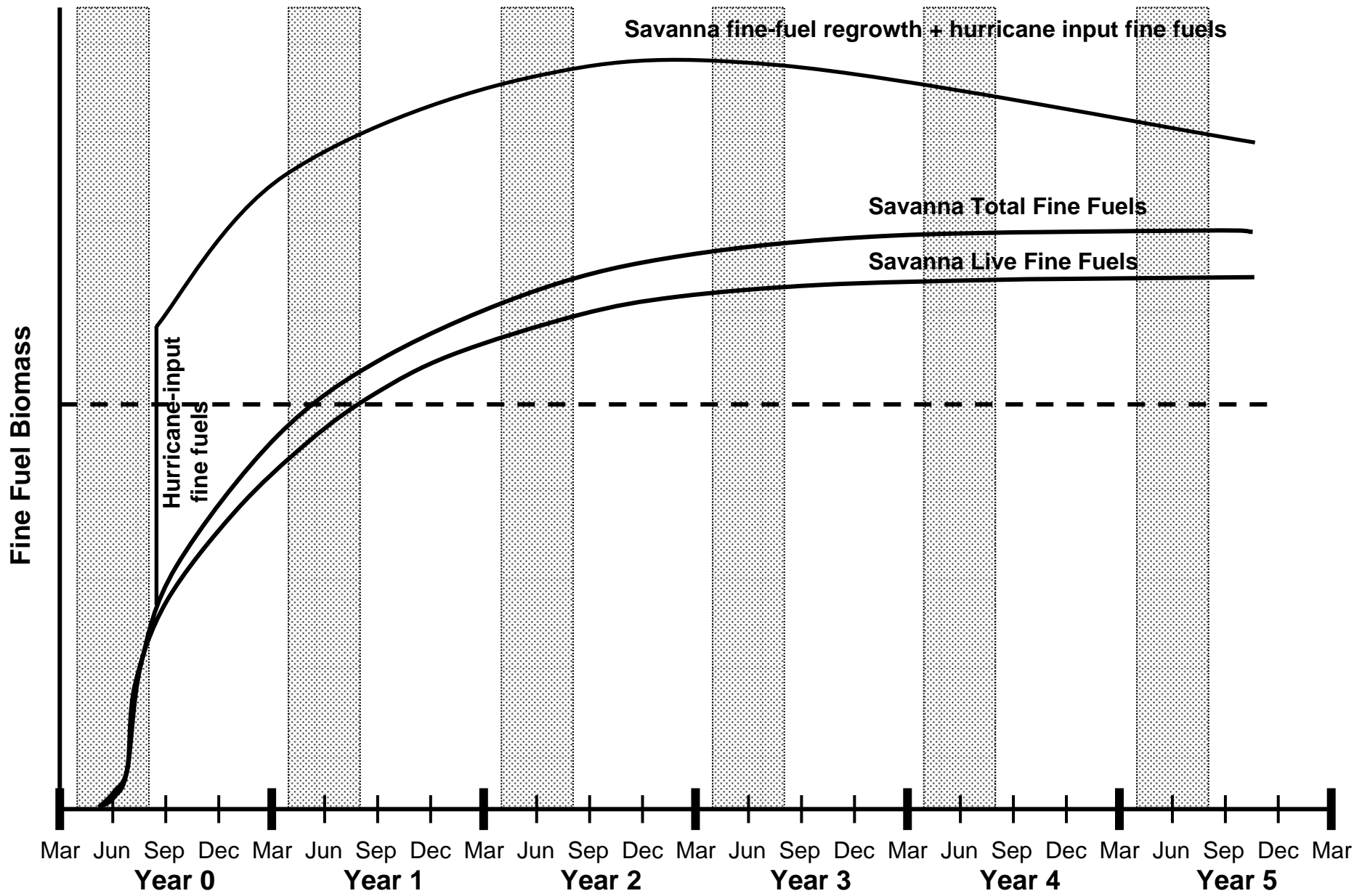
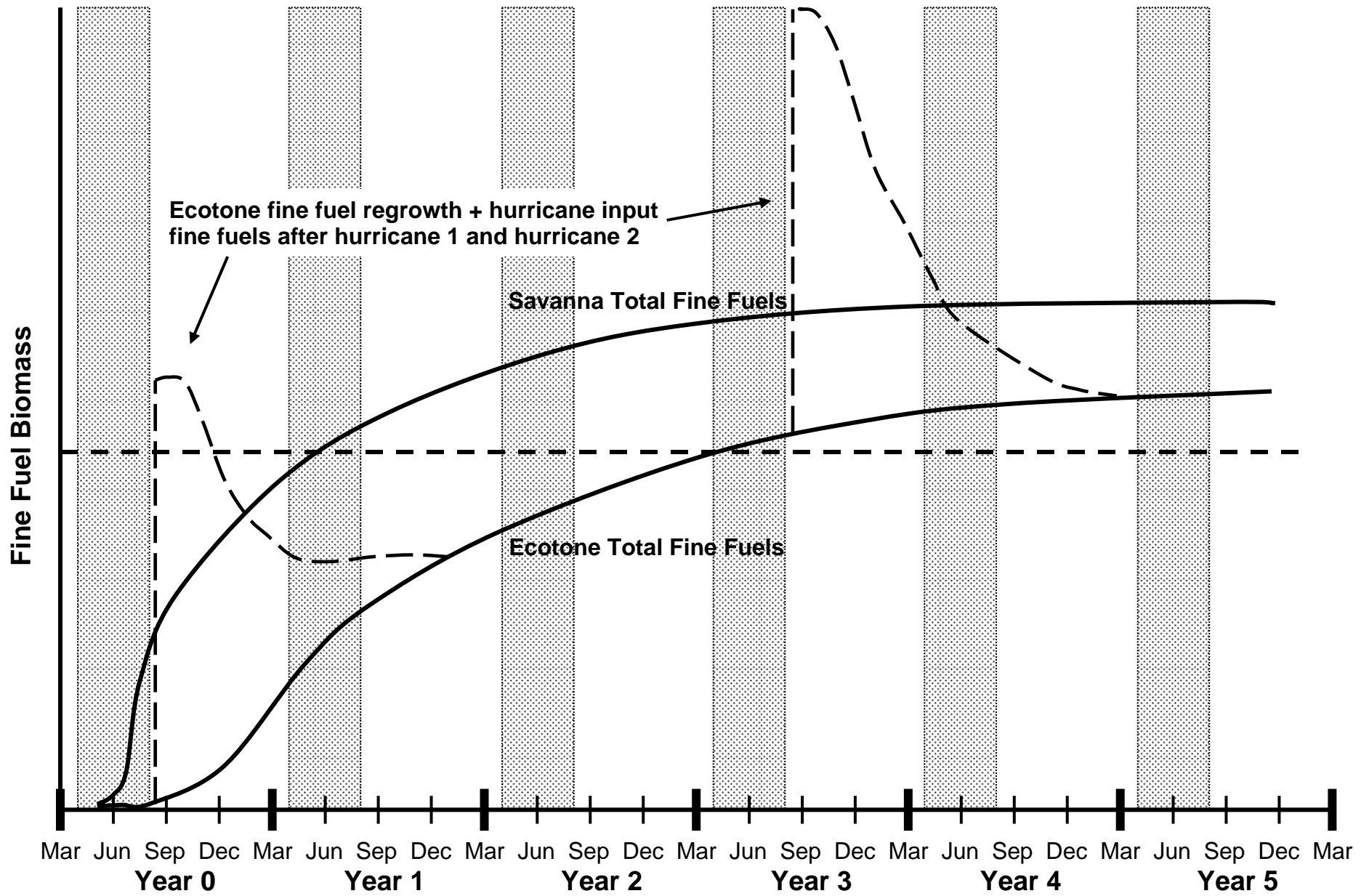


Figure 2.5B. Combined patterns of savanna-forest ecotone fine fuel re-accumulation after a fire and fine fuel decomposition after hurricanes. Gray-shaded bars denote the natural lightning fire season which coincides with late spring/early summer lightning season. The two curves (————) represent the regrowth of savanna fine fuels following a fire in year 0 (Figure 2.3). The two peaks (— — —) represents the sum of the ecotone post-fire fine fuels plus the input and subsequent rapid decomposition of ecotone fine fuels following two different hurricanes. After the hurricane in year 0, total (regrowth + hurricane) ecotone fine fuels increase above the fuel continuity threshold but decrease below the threshold before the subsequent lightning season. If the hurricane instead occurred in year 3 the sum of fine fuels could rise and stay above the fuel continuity threshold. Lightning fires could follow 6-9 months after the second hurricane. We predict that hurricane-fire interactions will occur infrequently in savanna-forest ecotones.



conditions in the ecotone increasingly favor a hurricane-fire interaction over successive years, conditions become favorable for fires more rapidly in the savannas. Thus, we predict that high fire frequencies (e.g., >2 per decade) would reduce the opportunity for hurricane-fire interactions in ecotones.

Actual hurricane-fire interactions in ecotones and forests are likely to occur only rarely. Assuming a hurricane does not follow a fire for several years, then lightning fires potentially could occur within about 6-9 months of a hurricane, since the sum of fine fuel re-accumulation and hurricane generated fine fuels may be maintained above the fuel continuity threshold (Figure 2.5B). If fire frequencies were 3 years on average in pine savannas and if those fires occurred randomly with respect to hurricanes, the opportunity for hurricane-fire interactions would be expected at most about 25% of the time. If hurricanes of a magnitude to create a uniform fuel matrix on the forest floor occurred once every 20 years (Batista and Platt 1997), then the opportunity for a hurricane-fire interaction might be expected about once every 80 years. Hurricanes of a magnitude to produce very large fuel loads (i.e., major hurricanes) occur much less often (Liu and Fearn 1993). The opportunity for hurricane-fire interactions that might cause changes in the local distribution of savannas and forests (see Myers and Van Lear 1998) should be much rarer still, at most once every several centuries.

Long-Term Implications of Hurricane-Fire Interactions. Repeated fires and hurricanes are widely hypothesized to generate long-term changes in savannas and forests (e.g., Brokaw and Grear 1991, Platt and Rathbun 1993, Peters and Platt 1996, Quigley and Platt 1996, Batista and Platt 1997, Foster et al. 1998, Batista and Platt 2003, Quigley and Platt 2003). Effects of any single fire or hurricane thus should occur within this historical context of prior fires and hurricanes. We propose that effects of prior disturbance regimes differ in pine savannas, ecotones, and forests.

Long-term hurricane-fire interactions in pine savannas may result from successive interactions involving juxtaposed fires and hurricanes within the context of frequent fires. Long-term effects of variation in fire season have been hypothesized to influence effects of hurricanes on pines in savannas, with cascading effects that also influence heterogeneity in the groundcover (Platt et al. 2002). Repeated hurricane-fire interactions over successive decades might compound that heterogeneity resulting from single interactive effects on local composition of the groundcover and overstory trees. As a result, a large number of tree and groundcover plants might be expected to persist in savannas, and among these might be species adapted for similar kinds of local disturbances generated by temporally unpredictable hurricane-fire interactions (see Platt and Connell 2003). In addition, repeated interactive disturbances might maintain open savannas that could otherwise become closed canopy woodland (Platt and Rathbun 1993, Platt et al. 2000), producing effects similar to those hypothesized to result from fire-herbivore interactions (van Langevelde et al. 2003).

Long-term synergistic effects of fires and hurricanes in savanna-forest ecotones and hardwood forests might be facilitated by local edaphic conditions or by periodic weather conditions that favor fires moving into ecotones. For example, well-drained soils or limestone substrates that dry readily might facilitate fires entering ecotones and forests (Kellman 1984, Platt and Schwartz 1990). In addition, super-annual climatic events such as the El Niño/Southern Oscillation (ENSO) may cause periodic severe droughts under La Niña conditions, resulting in increased continuity of fuels, as well as higher frequencies of lightning strikes (e.g., Brenner 1991, Beckage et al. 2003). Fires after hurricanes might be most likely under such conditions, especially if fine fuel decomposition and canopy regeneration were slowed during droughts (Myers and Van Lear 1998). Once fires intrude into ecotones and forests, the likelihood of recurrent fires may increase. For example, once burned, Amazonian forests were more fire-prone (to human fires) than unburned sites (Uhl and Kauffman 1990).

Species composition might change over time in ways that facilitate subsequent hurricane-fire interactions, especially in ecotones. Two types of species might facilitate hurricane-fire interactions: savanna species and fire-adapted species indigenous to ecotones. Fires under unusual environmental conditions, such as periodic droughts that slow recovery of a closed canopy after a hurricane, may facilitate invasion of the ecotone by savanna species. Species that are more shade-tolerant than those in open savannas also may be indigenous to ecotones. If either of these types of species is pyrogenic (sensu Mutch 1970, and see Schwilk 2003, Behm et al. 2004), fires originating in savannas should be likely to enter adjacent ecotones. Fires in ecotones could potentially produce long-term hurricane-fire effects, change the size of ecotones and produce unique plant communities along the transitions from savannas to forests. We describe such a scenario: A hardwood forest ecotone with pyrogenic species is opened by a hurricane, enabling fire to enter the forest the year after the hurricane. We predict this combination of periodic drought, hurricane, and subsequent fire to open the forest canopy, resulting in expansion of populations of more light-demanding, flammable species that generate a pyrogenic ecotone distinct from either adjacent savanna or hardwood forest. As a result, long-term fire frequency is altered and the ecotone spreads into the forest.

A number of plant species, including grasses, palms, and ferns have been noted as characteristic of savanna-forest ecotones (Myers 1985, Platt and Schwartz 1990, Kellman and Tackaberry 1993, Kellman and Meave 1997). Large-statured grasses (e.g. *Tripsacum latifolium* in Belize, *T. floridanum* in the Florida everglades, *Andropogon gerardii* in the southeastern United States), palms (*Serenoa repens* and *Sabal palmetto* in coastal and southern Florida, *Paurotis* spp. in Belize) and ferns (*Dicranopteris pectinata* in Belize, *Pteridium aquilinum* in Florida) often occur in ecotones undisturbed by human fire suppression. These species are capable of producing a large and highly flammable biomass at savanna-forest boundaries (Kellman and Tackaberry 1993, Platt 1999).

Ecotones containing pyrogenic species are widespread in the southeastern United States. Cane (*Arundinaria gigantea*) occurs in seeps of pine savannas, and in adjacent downslope hardwood forests. Once common throughout the southeastern United States, bamboo canebrakes were often tall and dense enough to cause intense fires (Hughes 1966, Platt and Brantley 1997). Canebrakes could have carried fire from savannas to forests, reaching temperatures of sufficient intensity to open the forest canopy (Hughes 1957). Once established, bamboo resprouts vigorously after fire (Hughes 1957, Hughes 1966, Platt and Brantley 1997), monopolizing burned sites and impeding forest regeneration (Penfound 1952). Other bamboos form flammable components of groundcovers in subtropical dry forests (e.g., Middleton et al. 1997). Similarly, palms such as saw palmetto (*Serenoa repens*) may influence fire regimes in savanna-forest ecotones in central and southern Florida (Huffman and Blanchard 1991, Behm et al. 2004). Such pyrogenic palms also could have been important in the extension of longleaf pine savannas from uplands downslope into seasonally flooded areas, forming savannas locally called wet pine flatwoods.

In our hypothetical model, savannas do not spread into forests. Instead, the ecotone becomes a distinct, pyrogenic association between the savanna and the forest. If flammable species spread throughout an ecotone and eliminate many hardwood trees, then a distinct community type results. Palm-dominated flatwoods and canebrakes, for example, might constitute communities in which flammable understory species become the dominant species as a result of their effects on overstory species.

Long-term effects based on our hypotheses regarding the juxtaposition of single fires and hurricanes in the context of recurrent hurricane-fire interactions over time are twofold. First, internal changes are likely, especially within savannas. Second, ecotones might expand into hardwood forests, becoming distinct associations from either pine savannas or hardwood forests. Long-term replacement of forests by savannas (e.g., Myers and Van Lear 1998) is not predicted

to occur. High natural lightning fire frequencies in savannas, with or without hurricanes, should push hardwood forests away from areas that can burn frequently and into areas with naturally lower fire frequencies. Only by adding pyrogenic species adapted for the ecotones that naturally burn less frequently is the fire frequency predicted to increase. Expansion of ecotones might be facilitated by hurricanes that open the forest canopy, increasing the likelihood of initial fires and increasing light levels, resulting in pyrogenic plants producing continuous flammable fuels (and enhancing recurrent fires).

Hurricane-Fire Interactions in Anthropogenically Altered Habitats

Increased post-hurricane fuel loads per se have been postulated to result in increased frequency and intensity of fires that potentially burn into forests from adjacent pine savannas (e.g., Myers and Van Lear 1998). Most field observations of fires occurring in forests after hurricanes, however, have been based on fires of anthropogenic origin outside the lightning season and typically during the dormant/dry season (e.g., Parsons 1955, Munro 1966, Whigham et al. 1991, Myers and Van Lear 1998). Such observations do not constitute support for the hypothesis that natural hurricane-fire interactions influenced presettlement landscapes. We consider anthropogenic fires at longer intervals or during the dormant (non-lightning) season as non-natural, especially when these fires become the predominant types of fires. Repeated non-lightning season fires result in pine savannas not resembling those present historically (Platt et al. 1988a, Frost 1993, Streng et al. 1993, Glitzenstein et al. 1995, Drewa et al. 2002, Platt et al. 2002).

Despite being followed by the dormant/dry season, hurricanes do not create a static environment of high fuel loads with low moisture content. Decomposition rates of leaves and other fine fuels, as well as rates of canopy reformation from resprouting trees, when combined with the frequency of fires in savannas, suggest that the likelihood of savanna fires burning into forests is very low, except perhaps when flammable species are present. There also is little field

evidence to support the idea that conditions produced in forests by hurricanes increase the likelihood of lightning-season fires burning into forests (also see Kellman and Tackaberry 1993). Based on personal observations of natural lightning fires following Hurricane Hattie in Belize, Wolffsohn (1967) stated that fires were neither more likely to ignite or spread following the hurricane than during "non-hurricane" years. Evidence that post-hurricane fires enter forests and cause mortality of hardwood trees is limited to anthropogenic fires occurring outside the normal lightning fire season (Parsons 1955, Munro 1966, Whigham et al. 1991).

We note that anthropogenic dormant/dry season fires potentially can create very large hurricane-fire interactions. Such effects may generate landscape-level changes, but they are likely to be very different from the effects of any hurricane-fire interactions that occurred in presettlement times when lightning-generated fires were very frequent. We argue that altering the frequency and seasonal timing of fires changes the basic nature of hurricane-fire interactions in pine savanna/hardwood forest landscapes. In savannas and the ecotones, altered fire regimes (season, frequency and intensity) result in large changes in vegetation, especially when fires no longer occur primarily within the natural lightning season (Streng et al. 1993, Glitzenstein et al. 1995, Brewer et al. 1996, Drewa et al. 2002). The same argument applies to hurricane-fire interactions. We suggest that natural and/or anthropogenic variations in fire and hurricane regimes should produce different, non-additive types of interactive effects not predictable based solely on the frequency of occurrence of the two types of disturbances.

Our model predictions are important for habitat restoration and conservation. Repeated logging and other human activities (e.g., Wahlenburg 1946, Croker and Boyer 1975, Frost 1993, McCay 2000) have resulted in severely altered fire regimes in pine savannas and hardwood forests of warm temperate and subtropical regions of North America (Hutchinson 1977, Frost 1993, Kellman and Meave 1997, Platt 1999). Moreover, during the past century, concepts based on ecological principles derived from habitats outside the region, or from altered savannas and

forests within the region, have been applied to the management of these habitats (Myers and Van Lear 1998, Platt and Peet 1998), resulting in further degradation of these systems. Pine savanna restoration efforts in fire-suppressed, mixed pine/hardwood stands should not be based on assumptions of a positive interaction between hurricane effects and subsequent fires. Myers and Van Lear (1998) have suggested that fires following hurricanes in such stands would be of high intensity, causing removal of remaining hardwood stems and promoting pine regeneration. However, hurricanes would likely occur at the end of the wet/growing season. Prescribed fires in the subsequent dry/dormant season are not likely to favor dominant savanna species, such as C4 grasses (Platt et al. 1988a, Myers 1990). Instead, fires during the dormant season, although potentially intense, appear more likely to result in resprouting of hardwoods than in recruitment of pines or herbaceous species (Doren et al. 1993, Glitzenstein et al. 1995, Platt 1999). Prescribed fires conducted during the growing season following a hurricane are not likely to be more intense on a landscape scale; canopy reformation from resprouting hardwoods and rapid decomposition of fine fuels would tend to reduce fire intensity. Instead, repeated growing season prescribed fires, regardless of hurricanes, may lead to a more continuous fine fuel layer and decreases in hardwood stem recruitment (Glitzenstein et al. 1995, Platt 1999, Drewa et al. 2002). Restoration of pine savannas based on concepts of intense dormant season prescribed fires after hurricanes may be as ill-conceived as the notion that hurricane-fire interactions have played a prominent role in the origin and maintenance of savannas (e.g., Myers and Van Lear 1998).

Summary

Our general hypotheses regarding the occurrence and effects of hurricane-fire interactions in southeastern North American coastal landscapes are based on short- and long-term characteristics of fire and hurricane regimes likely to have characterized pre-settlement savanna-forest landscapes. These disturbance regimes are predicted to have influenced both the distribution and characteristics of the different community types in southeastern North American

landscapes. We predict that hurricane-fire interactions differ in their importance among the different components of the southeastern landscapes. We predict that these interactions would be likely in savannas, affecting both the overstory and groundcover in ways that could enhance the plant species diversity and local heterogeneity in both elements of the savanna plant communities. Hurricane-fire interactions also are predicted to influence ecotones between savannas and forests by changing species composition and structure. Hurricane-fire interactions in ecotones may produce potentially unique plant communities that enter forests adjacent to savannas if pyrogenic plant species invade and alter the fire regimes in these areas. Forests appear to be least affected by hurricane-fire interactions; the nature of fire and hurricane disturbance regimes suggests that increased fine fuel loads after hurricanes do not necessarily increase the likelihoods of fires entering forests.

Our model for hurricane-fire interactions is based on concepts derived from study of pine savannas and warm-temperate/subtropical hardwood forests in southeastern North America. Although the basic model is based on specific characteristics of the most common large-scale disturbances in these habitats (fires and hurricanes), the general premises should be applicable to warm temperate and subtropical coastal regions of the world. Where multiple large-scale disturbances occur frequently, the sequence of occurrence of those disturbances relative to seasonal and post-disturbance changes in vegetation can be used to predict to what extent synergistic interactions are likely to occur. Short- and long-term effects of potential synergistic interactions can be projected based on knowledge of the effects of each disturbance on vegetation and of the longer-term responses of vegetation to the disturbances.

CHAPTER 3

EFFECTS OF SEQUENTIAL DISTURBANCES ON THE UNDERSTORY OF SAVANNA-FOREST ECOTONE

Introduction

Interactions between natural disturbances occur in a variety of habitats (e.g., Smith et al. 1994, Veblen et al. 1994, Turner et al. 1998, Santoro et al. 2001, Kulakowski and Veblen 2002). Empirically measured post-hoc effects of sequential disturbances appear highly non-additive, different from those predicted based on each disturbance in isolation (e.g., Paine et al. 1998, Robertson and Platt 2001, Platt et al. 2002). Interactive effects are possible if the same components of an ecosystem in a given landscape are influenced first by one disturbance, then by a second disturbance in ways that change with effects produced by the first disturbance. Effects of the disturbances must overlap spatially, and they must occur close enough in time for the second disturbance to modify effects of the first disturbance. Such interactive effects involving natural disturbances have rarely been tested experimentally (Fuhlendorf and Engle 2004).

Hurricanes and fires are widely recognized to influence savanna-forest landscapes in the southeastern United States. Effects of each disturbance on longleaf pine savannas and adjacent hardwood forests have been studied extensively (e.g., Platt et al. 1988b, Gresham et al. 1991, Putz and Sharitz 1991, Harcombe et al. 1993, Platt 1999 and references therein, Platt et al. 2000, Batista and Platt 2003). The theoretical basis for prediction of effects of each type of disturbance in isolation has been well developed. However, hypotheses related to interactive effects have not explicitly addressed the importance of spatial and temporal overlap in effects (e.g., Myers and Van Lear 1998).

Mechanistic hypotheses are needed to relate successive natural disturbances to populations, communities and landscapes. We have proposed that interactive effects may occur frequently in savannas, where flammable fuels generated by hurricanes persist over time and are likely to burn in frequent fires (see Chapter 2). The juxtaposition of savannas and forests in

southeastern landscapes also may result in periodic spatial and temporal overlap of effects of hurricanes and subsequent fires, potentially influencing plant community composition and structure in the ecotone between these communities. Fires ignited in savannas likely extend into savanna-forest ecotones if there are sufficient fuels dry enough to carry a fire. In addition, we proposed that flammable fuels in hardwood forests are likely to decompose before fires burn into the forests, reducing the likelihood of hurricane-fire interactions inside hardwood forests.

Spatial overlap in effects of hurricanes and fires involves two potential differences between wind-generated downed arboreal fuels and those naturally present. First, downed arboreal biomass can increase quantity and continuity of surface fuels; second, the resulting canopy openings can change fuel conditions. Hurricanes in savannas and hardwood forests produce a range of canopy openings and litter deposition (Putz and Sharitz 1991, Batista and Platt 1997, Platt et al. 2002). Fire intensity is affected by the type (e.g., Rebertus et al. 1989b), quantity (e.g., Thaxton 2003) and moisture content (e.g., Ferguson et al. 2002) of fuels naturally present and those deposited by hurricanes. Finally, both increased light availability and higher fire intensity are expected to influence understory vegetation. Thus, hurricane-fire interactions may occur in the ecotone if dry hurricane-produced fuels increase the probability, continuity, or intensity of subsequent fires.

Temporal overlap is a function of frequency and seasonality of successive disturbances. In southeastern coastal landscapes, hurricanes and natural lightning-initiated fires are frequent disturbances that historically may have occurred in the same or consecutive years. Prior to human settlement, lightning fires typically burned savannas more than once a decade (Frost 1993, Platt 1999). These lightning-season fires occur in May and June, during the transition from dry to wet seasons (Komarek 1964, Doren et al. 1993, Platt 1999, Beckage et al. 2003,

Slocum et al. 2003, Beckage et al. 2006). Hurricanes make landfall on both the Atlantic and Gulf Coasts with a return interval of 10 to 20 years (Batista and Platt 1997). North Atlantic hurricanes most often make landfall between August and October (Landsea 1993). The difference in frequency suggests that hurricanes potentially may change effects of more frequent fires, provided that there is sufficient temporal overlap in effects. In addition, natural hurricane and fire seasons are disjunct, so overlap of disturbance effects depends on the duration of individual effects in time.

We experimentally explored interactive effects of successive disturbances on vegetation in the ecotone between upland pine savannas and hardwood forests. We asked if effects of lightning-season fires differ when they are preceded by simulated hurricanes compared to when they occur alone (Figure 3.1). We used canopy disturbance and fuel deposition to mimic

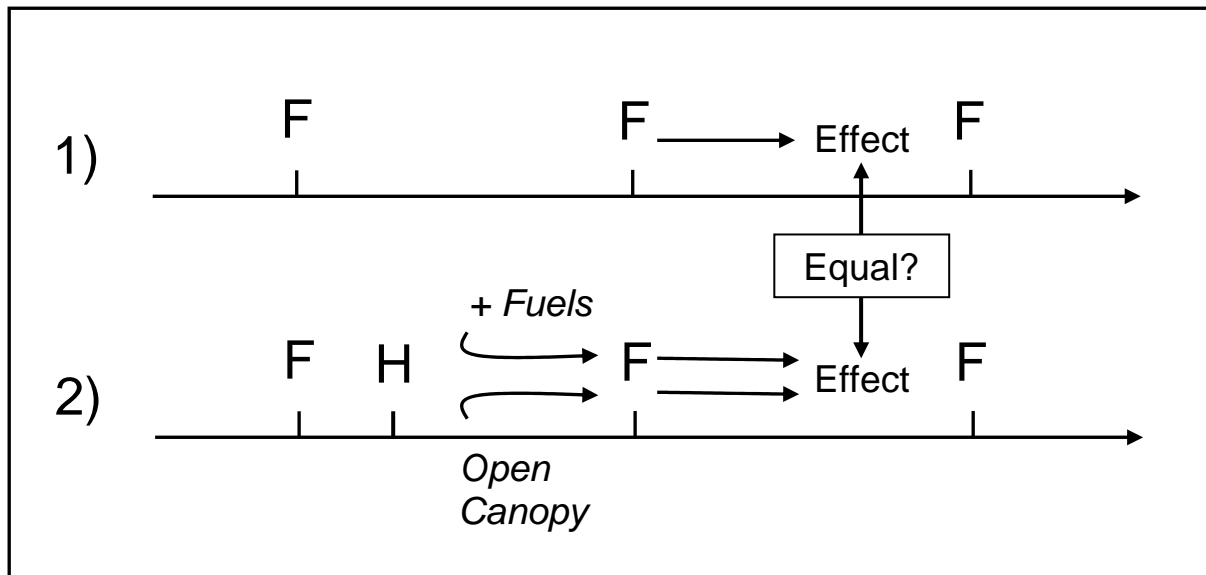


Figure 3.1. Timelines of successive fire (F) and simulated hurricane (H) treatments in savanna-forest ecotone habitat for two experimental scenarios: 1) treatment plots with at least one previous fire, then the study’s prescribed fire followed by measurement of the fire effects on vegetation, and 2) treatment plots with the same prescribed fire regime, but with a simulated hurricane disturbance after the initial fire. The hurricane treatment produced two main effects: increased fuels and canopy openness. In this study we ask if the effects of scenario 1 and 2 are different.

hurricanes, and growing-season prescribed fires to mimic natural lightning-season fires. We experimentally manipulated two aspects of the simulated hurricane disturbance, canopy cover and fine fuel loads, and we measured effects on characteristics of fires in the ecotone. We then measured responses of the vegetation over several years. We tested the following hypotheses: 1) Canopy disturbance increases fire intensity and vegetation change (compared to intact canopy), 2) Addition of fine fuels increases fire intensity and vegetation change (compared to no increase in fine fuels), and 3) Canopy disturbance and fine fuel addition interact to produce effects of fire on vegetation different from those expected from canopy disturbance or fuel additions alone.

Methods

Study Site

This study was conducted at Camp Whispering Pines (30°41'N, 90°29'W), Tangipahoa Parish, in the loess plains of eastern Louisiana. Camp Whispering Pines (hereafter CWP) is located on the western edge of the eastern Gulf Coastal Plain, 80km east of the Mississippi River. The site is underlain by well-drained Pleistocene, Tangi-Ruston-Smithdale fine sands that are mixed with and capped by thin, loess deposits on the surface and a fragipan below the surface in some places (McDaniel 1990). The moderately dissected terrain ranges between 25-50m above mean sea level across the site. CWP contains even-sized second-growth stands of longleaf pine (*Pinus palustris*) and is one of the few remaining upland pine savannas in the loess plains ecoregion of eastern Louisiana (Noel et al. 1998). Longleaf pine predominates in the canopy and the groundcover is dominated by large warm-season grasses (*Schizachyrium scoparium*, *S. tenerum*, *Panicum anceps*, *P. virgatum*, *Aristida purpurescens*, *Andropogon virginicus* var. *decipiens*, *A. gerardi*, *Sorghastrum nutans*, *Sporobolus clandestinus*), as well as smaller C3 grasses (*Dichanthelium*, including *D. acuminatum*, *D. angustifolium*, *D. ovale*, *D. strigosum*, *D.*

tenue). In addition to the grasses the understory contains a high diversity (>100 vascular plant species per 100m²) of herbaceous and shrub species typical of fertile, fine-soil pine savannas (Platt et al. 2005).

We located our study plots in the ecotone between savanna uplands and creek or river-bottom hardwood forests at CWP. The ecotone occurs on gentle slopes (<8%), descending from pinelands in level plains to the bases of ravines containing intermittent streams. Species composition of the savanna-forest ecotone at CWP is most similar to forests characterized within Louisiana as “hardwood slope forests” and “shortleaf pine/oak-hickory forest” (LNHP 1986-2004, LDWF 2005). Canopy cover increases downslope through the ecotone from pine savanna to hardwood forest. Longleaf, shortleaf (*P. echinata*), and loblolly (*P. taeda*) pines co-occur with hardwoods such as post oak (*Quercus stellata*), southern red oak (*Q. falcata*), mockernut hickory (*Carya tomentosa*) and other smaller understory hardwoods. The understory is partially open with a number of shrubs (e.g., *Ilex vomitoria*, *Vaccinium arboreum*, and *Gaylussacia dumosa*), warm season grasses, and other herbaceous species.

The site history at CWP is similar to that of other second-growth longleaf stands in the South: open-range grazing and frequent fire were followed by logging and subsequent fire suppression. The region was settled during the 1800’s resulting in large-scale fragmentation of the landscape. Initial land usage included open-range grazing and frequent dormant season fires. By the early 20th century local anthropogenic land use included extensive logging of large trees and turpentine of remnant trees (Noel et al. 1998, Platt et al. 2005). The existing even-aged stands at CWP regenerated naturally following logging of large trees in the 1930’s.

The fertile, mesic soils and high fine fuel loads suggest that natural fire frequencies at CWP and similar upland pine savannas were more than twice a decade, and biennial fires were

likely common in presettlement times. Thus a biennial prescribed fire frequency, although perhaps higher than natural frequencies were in many xeric savannas, are within the frequencies that we and others (e.g., Frost 1993) have postulated for productive pine savannas. Camp Whispering Pines is privately owned and managed by the Southeast Louisiana Girl Scout Council. Purchased in the late 1960's, fires were actively suppressed for several decades. Since the early 1990s, CWP has been managed as an educational and recreational facility and as a site for restoration of native longleaf pine savanna. An adaptive forest management plan developed for CWP in 1994 instituted an aggressive prescribed fire program involving biennial spring (April-May) fires designed to mimic lightning fires. Head fires are ignited along roads and fire lanes in the upland pine savanna. These fires burn unimpeded across the landscape, burning up and down slopes and into local drainages as fuel conditions allow.

Field Study

We implemented a repeated measures split-plot experimental design to decouple hurricane effects from those of fire alone. Canopy disturbance treatments (whole plot factor) were randomly applied to plots within blocks. Fine fuel addition treatments (split-plot factor) were randomly applied to subplots within plots. We followed canopy disturbance and fuel addition treatments with prescribed fires in all plots. After the 2002 prescribed fires we measured three non-repeated environmental variables, percent subplot area burned, maximum fire temperatures and percent transmitted light. We measured three repeated vegetation variables, percent vegetation cover, stem density, and species richness, within subplots over three years (2002-2004, repeated factor). A second prescribed fire was applied prior to the 2004 vegetation census. Fuel treatments were not reapplied in the second fire, thus prescribed fires in 2004 were less intense than the 2002 prescribed fires.

We began the experiment in early 2001. We established 12 plots, each 400m², in three blocks containing four plots each. Each block was a continuous area of savanna-forest ecotone habitat on slopes within different creek drainages. Adjacent plots were separated by at least 20m. We collected pre-treatment data on canopy tree and understory plant composition and abundance in the fall of 2001. We tagged, measured, and identified to species all woody stems \geq 2cm dbh within experimental plots (Appendix 3.1). Within plots we randomly placed five 1m² pretreatment subplots during the fall of 2001. In each subplot, we visually estimated the total percent cover of vegetation. We also identified all woody and herbaceous ramets to species, and recorded total stem density of each species. Following canopy disturbance treatments we added subplots for three fuel addition treatments, each with 5 replicates, and the pretreatment subplots became unaltered controls. The design includes a total of 240 subplots; 20 per plot.

Canopy Disturbance Treatment: The canopy disturbance treatment was designed to decrease canopy tree density within the range expected based on effects of prior category 3 and 4 hurricanes in southeastern savanna-forest landscapes. In pine savannas direct mortality of trees following two hurricanes (Kate in 1985 and Andrew in 1992) ranged from 10% to 30% (Platt et al. 1988b, Platt and Rathbun 1993, Platt et al. 2000). Mortality from the same two hurricanes affecting hardwood forests ranged from 7% to 12% (Slater et al. 1995, Batista and Platt 1997). At CWP we randomly selected two plots per block for the canopy disturbance treatment. Within canopy-removed plots we marked 10-12 canopy trees (20-45cm dbh) for removal including both pines and hardwoods. In the fall of 2001, loggers entered plots on the upslope side with skidders and felled and removed selected trees. Soil disturbance by machinery was minimized by removing individual trees along a single path within each plot. On average 20% of subplot area was affected by logging activity. Loggers removed boles of cut pines and hardwoods, but left

crowns with leaves and branches intact to simulate hurricane-produced fine fuels. Total tree mortality included smaller stems snapped or broken by fallen canopy trees or by machinery. On average the canopy disturbance treatment resulted in mortality of 25% (n=6) trees per plot, or $0.44 \pm 0.07 \text{ m}^2$ (mean \pm SE, n=6) basal area removed.

Following the canopy disturbance treatment, during full leaf-out, we measured percent transmitted light in canopy-removed and canopy intact plots. Percent transmitted light was recorded in 5 (control) subplots per plot in August 2002 after canopy disturbance treatments. We measured transmitted light in the understory on overcast days or before sunset. We used a Nikon Coolpix 4500 digital camera with the Nikon FC-E8 Fisheye Converter lens attachment to take 180° canopy photos. Camera user settings were programmed to: “programmed auto”; self-timer mode; no flash; image size 1600x1200; image quality “fine”; and converter lens setting “F1” (zoom fixed at widest angle, focus fixed at infinity, and metering fixed at center weighted). The top of the fisheye lens was always oriented north and the camera was leveled using a bubble level and adjustable tripod. At the top right corner of all control subplots (5 per plot) we took one photo at 0.65m high. We analyzed fisheye digital images using the Gap Light Analyzer (GLA V2) program (Frazer et al. 1999). Specific configuration settings for regional climatic patterns, growing season length, and geographic location used to calculate percent direct transmitted light were programmed into GLA (Appendix 3.2).

Fuel Load Treatment: To simulate post-hurricane fine fuel loads, we applied three types of fine fuels to subplots. The three fine fuel types controlled for variation in fuels expected from the mixed species overstory of savanna-forest ecotone. Fuel treatments were composed of 1) deciduous hardwood leaves and branches, 2) longleaf pine needles, cones, and branches, and 3) mixed pine (shortleaf and loblolly) needles, cones, and branches. Control plots consisted of un-

manipulated fuels loads. Fuel loads were designed to mimic amounts produced by category 3-4 hurricanes. Fuels were distributed by weight (3.4 ± 0.29 kg per subplot, mean \pm SE, n=24) and each type was added to five subplots per plot. We modified some random subplot locations to reduce effects of logging tracks. We thus sampled areas of minimum soil disturbance and areas containing fallen tree crowns, but not areas with ruts and tracks caused by logging equipment.

Prescribed Fire Characteristics: Prescribed fires entered study plots from upslope longleaf pine stands during the lightning fire season. We ignited fires in burn units containing blocks 2 and 3 on April 22, and block 1 on April 30, 2002. Fires were low intensity creeping fires with backing fires down slope. In plots where burns were incomplete, we ignited vegetation in the vicinity of subplots to ensure that fires entered all subplots.

We measured two fire characteristics. We used percent subplot area burned to estimate patchiness of fires and maximum fire temperatures to estimate local fire intensity in every subplot. Percent area burned of subplots and maximum fire temperatures were measured in all 20 fuel addition subplots per plot after prescribed fires in 2002. The percent subplot area burned was visually estimated immediately following fires. To measure maximum fire temperature we used a series of 12 Tempil temperature indicating tablets (Big Three Industries, Inc. Tempil^o Division, South Plainfield, New Jersey, USA). Individual tablets were wrapped in heavy-duty aluminum foil prior to fires and assembled into sets of 12, one per temperature. Each set included a tablet designed to melt at 48°C, 132°C, 212°C, 302°C, 371°C, 454°C, 538°C, 621°C, 732°C, 843°C, 954°C, and 1038°C. On the morning of the prescribed fire we placed one set of tablets at ground level in the center of each of the 240 fine fuel subplots. Tablets were collected immediately following fires and used to determine the maximum melting temperature. Melting temperatures were adjusted for the effect of aluminum foil using the regression equation of

Drewa et al. (2002). The adjusted temperatures are as follows: 85°C, 189°C, 289°C, 400°C, 486°C, 589°C, 693°C, 796°C, 933°C, 1071°C, 1209°C, and 1313°C.

Vegetation Response Measurements: We measured responses of vegetation to treatment combinations for three growing seasons following the initial prescribed fires. Understory vegetation characteristics were measured in the 20 fine fuel treatment subplots in each plot. Beginning 6 weeks after prescribed fires in the first growing season (2002) we recorded 1) percent vegetation cover, 2) stem density, and 3) species present to calculate species richness. We repeated the census during the second growing season (2003) when research plots were not burned. An additional census in 2004 followed the second biennial growing season burn to determine whether treatment effects continued. For the 2004 fires fine fuel treatments were not re-applied and we did not measure maximum fire temperatures. To reduce the order bias during each census we randomized the sampling order of blocks, randomized the order of plots within blocks and then randomly selected 3 of the five subplots per fuel treatment to census on the first round each summer. As soon as we completed measurements on 3/5 of all fuel treatment subplots we began again and sampled the remaining 2/5 of subplots using the same order of blocks and plots. During both the second and third growing seasons we re-randomized the subplot order but followed the same order for blocks, and plots within blocks.

Statistical Analyses

Analysis of variance (ANOVA) was used to compare the effects of canopy disturbance and fuel addition on fire characteristics and response of vegetation. The experimental design was a fully factorial split plot with repeated measures. Linear models for repeated measures analyses were constructed with canopy treatment (whole plot), fuel treatment (split plot), and census year (repeated factor) as fixed effects. Block, plot, and subplot were treated as random

effects in PROC MIXED of SAS Version 8.2 (SAS Institute 2001). We used PROC UNIVARIATE to examine each dataset for normality and homoscedasticity (using residuals and residuals vs. predicted values). Appropriate transformations were used for each response variable as necessary.

Individual degree of freedom orthogonal contrasts were developed to test *a priori* hypotheses about the main and interaction effects of canopy disturbance, fuel addition and year (Table 3.1). We constructed two contrasts to test whether response variables changed linearly or quadratically over time. Three contrasts tested the effects of fuel treatment combinations. First, we hypothesized that response variables for the three fine fuel additions (deciduous + longleaf + mixed pine) differed from unaltered controls. Second, we tested whether effects of the deciduous hardwood treatment differed from the two pine treatments. Third, we examined whether there were differences among two pine treatments. Year by canopy contrasts tested the hypothesis that canopy-removed and canopy-intact effects changed in different linear or quadratic ways over time. Likewise, the year by fuel contrasts tested that the effects of fuel treatments changed in different linear or quadratic ways over time. Finally, we constructed three contrasts for the fuel addition by canopy disturbance treatment interaction. First, we hypothesized that responses to canopy-removed and canopy-intact treatments change differently for unaltered control subplots compared to fuel addition treatments. Second, we tested that effects of deciduous fuel and pine fuel additions differ between canopy-removed and canopy-intact treatments. Third, we hypothesized responses to canopy-removed and canopy-intact treatments would change differently for longleaf fuel addition compared to mixed pine fuel addition treatments. These contrasts were incorporated into analyses of the vegetation responses

Table 3.1. Orthogonal contrasts for hypotheses examined using ANOVA of replicated data, based on a total of 240 subplots.

Source of Variation	DF	Questions addressed
Year	2	Do response variables change over time?
Linear	1	Do response variables change linearly over time?
Quadratic	1	Do response variables change quadratically over time?
Canopy	1	Do response variables differ between canopy-removed and canopy-intact treatments?
Fuels	3	Do response variables differ among fuel addition treatments?
Control X (Deciduous + Longleaf + Mixed Pine)	1	Do response variables differ between fine fuel addition treatments and unaltered controls?
Deciduous X (Longleaf + Mixed Pine)	1	Do response variables differ between hardwood and pine fine fuel addition treatments?
Longleaf X Mixed Pine	1	Do response variables differ between longleaf and mixed pine fine fuel addition treatments?
Year X Canopy	2	Do response variables of canopy-removed and canopy-intact treatments change differently over time?
Linear X (Removed X Intact)	1	Do response variables of canopy-removed and canopy-intact treatments change in different linear ways over time?
Quadratic X (Removed X Intact)]	1	Do response variables of canopy-removed and canopy-intact treatments change in different quadratic ways over time?
Year X Fuel	6	Do response variables of fuel addition treatments change differently over time?
Linear X [(Control) X (Deciduous + Longleaf + Mixed Pine)]	1	Do response variables of fuel addition treatments and unaltered fuels (controls) change in different linear ways over time?
Linear X [(Deciduous) X (Longleaf + Mixed Pine)]	1	Do response variables of hardwood and pine fine fuel addition treatments change in different linear ways over time?
Linear X (Longleaf + Mixed Pine)	1	Do response variables of longleaf and mixed pine fine fuel addition treatments change in different linear ways over time?
Quadratic X [(Control) X (Deciduous + Longleaf + Mixed Pine)]	1	Do response variables of fuel addition treatments and unaltered fuels (controls) change in different quadratic ways over time?
Quadratic X [(Deciduous) X (Longleaf + Mixed Pine)]	1	Do response variables of hardwood and pine fine fuel addition treatments change in different quadratic ways over time?
Quadratic X (Longleaf + Mixed Pine)	1	Do response variables of longleaf and mixed pine fine fuel addition treatments change in different quadratic ways over time?

(Table 3.1. continued)

Canopy X Fuel	3	Do response variables of canopy-removed and canopy-intact treatments change differently with different fuel addition treatments?
(Removed X Intact) X [(Control) X (Deciduous + Longleaf + Mixed Pine)]	1	Do response variables of canopy-removed and canopy-intact treatments change differently for unaltered control subplots compared to fuel addition treatments?
(Removed X Intact) X [(Deciduous) X (Longleaf + Mixed Pine)]	1	Do response variables of canopy-removed and canopy-intact treatments change differently for deciduous fine fuel addition compared to pine fine fuel addition treatments?
(Removed X Intact) X (Longleaf + Mixed Pine)	1	Do response variables of canopy-removed and canopy-intact treatments change differently for longleaf pine fine fuel addition compared to mixed pine fine fuel addition treatments?
Year X Canopy X Fuel	6	Do response variables of canopy-removed and canopy-intact treatments change differently over time with different fuel addition treatments?

measured over three years. For analysis of the non-repeated variables maximum fire temperature and percent area burned we incorporated contrasts for the fuel treatment main effects and fuel addition by canopy disturbance interaction.

Pretreatment Understory Vegetation: We compared understory vegetation characteristics between plots and blocks prior to canopy disturbance and fuel addition to detect pre-treatment differences in percent cover, stem density and species richness. Analysis of variance in PROC MIXED was used to determine differences between blocks and plots within blocks (SAS Institute 2001).

Disturbance Treatment Effects: The three non-repeated dependent variables were analyzed to test effects of canopy disturbance and fuel addition treatments. Each response variable was analyzed using ANOVA in PROC MIXED (SAS Institute 2001). Percent fuel consumption was arcsin-square root transformed, maximum fire temperatures were square root transformed, and percent transmitted light was logit transformed to meet model assumptions.

Response of Vegetation: We conducted repeated measures ANOVA on the vegetation response variables using PROC MIXED to test for disturbance treatment effects and interactions (SAS Institute 2001). In addition to percent vegetation cover, total stem density, and species richness we also analyzed woody stem density, herbaceous stem density, woody species richness and herbaceous species richness. We logit transformed percent cover of vegetation, log transformed all measures of stem density (natural log of $n + 1$), and square-root transformed all measures of species richness to meet model assumptions. Covariance structures were modeled with random subjects and heterogeneous variance with time. We used the Kenward-Roger approximation to the degrees of freedom for the reference distribution. For all statistical tests we used $\alpha = 0.05$ as the level of significance. Graphical depictions of data are least square means

and asymmetrical confidence intervals, back transformed appropriately for each response variable.

Results

Pretreatment Conditions

Prior to experimental treatments, understory vegetation was similar among plots within blocks. Mean percent cover of vegetation for plots within blocks ranged from 4% to 36%; differences were not significant ($p=0.3088$). Mean total stem densities ranged from 11 to 47 stems/m² and did not differ significantly ($p=0.4104$). Vegetation characteristics were different between blocks. Mean percent cover of vegetation was 11% for the block in one drainage and 28% for both blocks in adjacent drainages ($p=0.009$). Mean stem densities among the blocks (18, 29 and 33 stems/m²) varied significantly among the three blocks at the onset of the experiment ($p=0.0258$).

Effects of Canopy Disturbance on Understory Light Availability

Canopy disturbance increased light in the understory of canopy-removed plots compared to canopy-intact plots. Estimated mean percent transmitted light levels for canopy-removed and canopy-intact treatments were 32% and 25%, respectively (Figure 3.2). Mean percent transmitted light in canopy-removed plots ranged from 26-42 percent. In canopy-intact plots means ranged from 20-31% transmitted light. These differences were significant ($p=0.0192$). Removal of canopy trees in this study resulted in gaps open from the tree canopy to the ground as well as overstory gaps with shrubs and subcanopy trees in the understory.

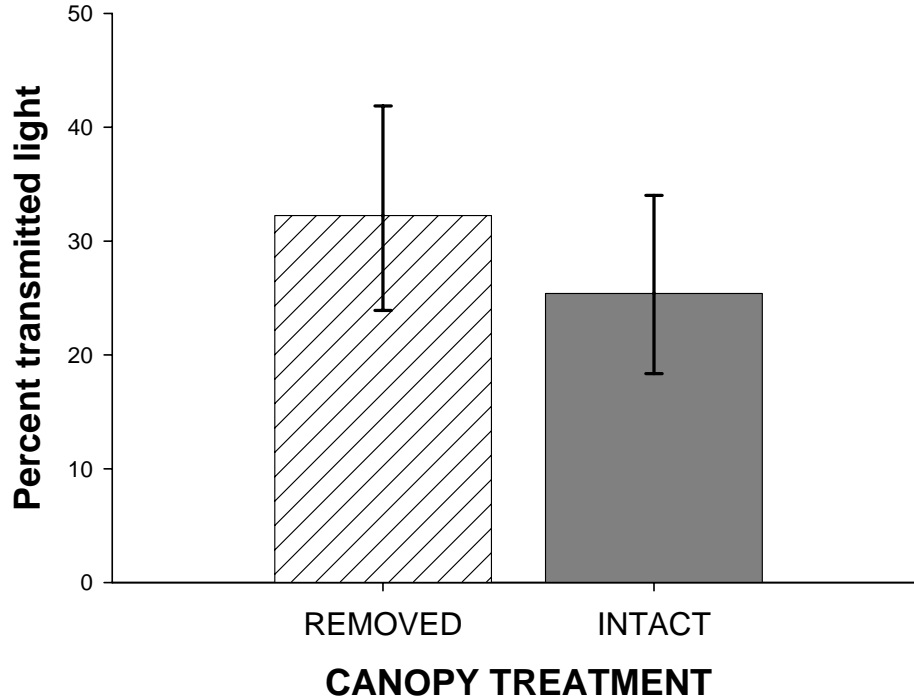


Figure 3.2. Mean percent transmitted direct light per plot for canopy treatment. Light availability was measured during the 2002 growing season. Mean values for each plot are back-transformed least square means. Error bars are back transformed 95% confidence intervals for estimated means.

Effects of Canopy Disturbance and Fuel Additions on Local Fire Characteristics

Maximum Fire Temperatures: Both canopy disturbance and fuel addition affected maximum fire temperatures in fuel treatment subplots. Canopy disturbance significantly increased maximum fire temperatures; mean maximum fire temperatures were 625°C in canopy-removed plots and 512°C in canopy-intact plots ($p=0.0014$, Table 3.2). Maximum fire temperatures also increased significantly with fuel addition treatments ($p<0.0001$, Table 3.2). Linear contrasts indicated highly significant differences ($p<0.0001$) between the unaltered control and the three fuel addition treatments, as well as between the deciduous fuel addition treatment and the two pine fuel treatments. Generally, mean fire temperatures were higher in pine fuel addition subplots and lower in control and deciduous subplots, regardless of canopy

treatment. Effects of the two types of pine fuels were similar ($p=0.3353$). Low flammability of deciduous hardwood fuels resulted in similar maximum temperatures in deciduous fuel subplots and control subplots within canopy treatments (Figure 3.3A).

Canopy disturbance interacted with fuel addition treatments to affect maximum fire temperatures. Mean maximum fire temperatures were similar for both pine fuel types in canopy-removed and canopy intact plots (Figure 3.3A). In contrast, canopy disturbance increased fire temperatures in control and deciduous subplots, resulting in a significant fuel by canopy treatment interaction ($p=0.0022$, Table 3.2). These differences also resulted in significant canopy by fuel interactions for linear contrasts of controls compared to all fuels (contrast $p=0.0426$) and deciduous fuels compared to pine fuels (contrast $p=0.0011$) within canopy-removed and canopy-intact plots (Table 3.2).

Table 3.2. Result of mixed model ANOVA of maximum fire temperature with orthogonal individual degree of freedom contrasts. Error term for canopy disturbance = Block x Plot(Canopy). Error term for fuel and interactions = residual. NDF = numerator degrees of freedom; DDF = denominator degrees of freedom based on Kenward-Roger approximation. Covariance structure = heterogeneous variance.

Source of Variation	NDF	DDF	F	<i>p</i>
Fixed Effects:				
Canopy	1	232	10.39	0.0014
Fuel	3	232	110.37	<0.0001
Canopy x Fuel	3	232	5.02	0.0022
Individual Degree of Freedom Contrasts:				
FUEL:				
Control x (Deciduous + Longleaf + Mixed Pine)	1	232	131.60	<0.0001
Deciduous x (Longleaf + Mixed Pine Fuels)	1	232	198.59	<0.0001
Longleaf Pine Fuel x Mixed Pine Fuel	1	232	0.93	0.3353
CANOPY X FUEL				
(Removed X Intact) X [(Control) X (Deciduous + Longleaf + Mixed Pine)]	1	232	4.16	0.0426
(Removed X Intact) X [(Deciduous) X (Longleaf + Mixed Pine)]	1	232	10.88	0.0011
(Removed X Intact) X (Longleaf + Mixed Pine)	1	232	0.02	0.8871

Percent Area Burned: Percent area of subplots burned was influenced by canopy disturbance and fuel addition treatments. The mean percent area burned of subplots was 96% in canopy-removed plots and 92% in canopy-intact plots; these differences in percent area burned were significant ($p=0.0196$). Overall, fuel addition treatments significantly affected percent area burned ($p<0.0001$, Table 3.3). Differences in percent area burned were greatest within control and deciduous fuel additions, with less area burned in canopy-intact plots (Figure 3.3B). Among control and deciduous fuel treatment subplots percent area burned ranged from 0% to 100%. In contrast, at least 75% of the area of all longleaf and mixed pine fuel subplots was burned, and the majority of subplots burned completely. Pine fuel treatments (longleaf and mixed pine) burned nearly completely (94-100% plot averages), but deciduous fuel addition subplots and control subplots ranged from 28% to 96% mean area burned for plots. Linear contrasts indicated highly significant differences ($p<0.0001$) between the unaltered control and the three fuel addition treatments and between the deciduous fuel addition treatment and the two pine fuel treatments. The two pine treatments had similar effects on percent area burned ($p=0.6775$, Table 3.3).

Canopy disturbance also influenced effects of fuel addition treatments on percent area of subplots burned. Area burned was greater for deciduous fuel addition subplots and control subplots within the canopy removed treatment plots (Figure 3.3B, effect slices $p=0.0008$). This difference also results in a significant linear contrast for the canopy by fuel interaction of deciduous compared to pine fuels (contrast $p=0.0134$, Table 3.3). Effects of control and deciduous fuel additions were similar, but the least mean area burned occurred in deciduous fuel subplots under intact canopy. Mean percent area burned for the two pine fuels were similar, which may have resulted in the non-significant canopy by fuel interaction for percent area burned ($p=0.0846$, Table 3.3).

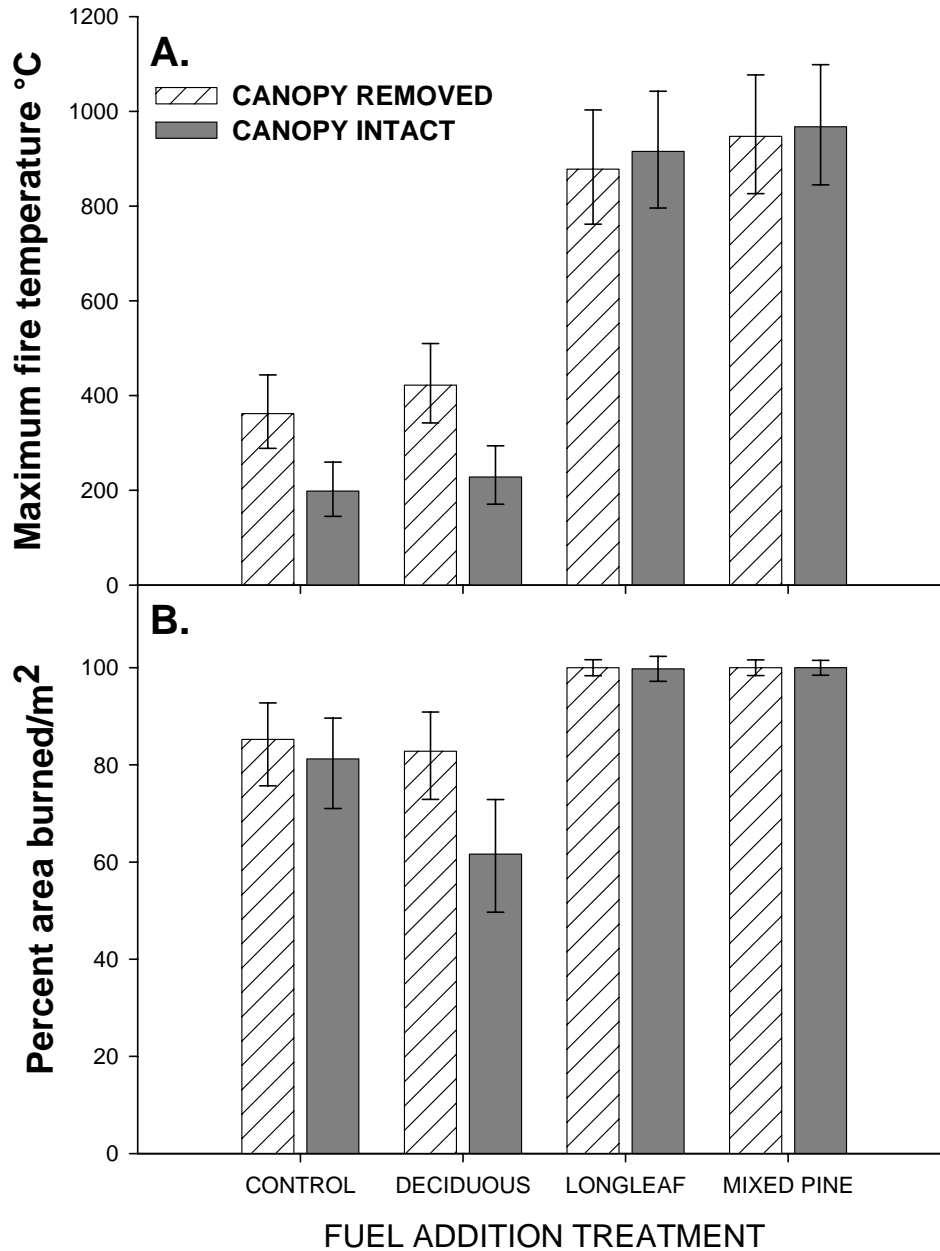


Figure 3.3. **A)** Mean maximum fire temperature for canopy disturbance and fuel addition treatments. Maximum temperature was square-root transformed to meet model assumptions. **B)** Mean percent area burned per subplot for canopy disturbance and fuel treatments. Percent area burned was arcsin transformed to meet model assumptions. Mean values for each treatment combination are back-transformed least square means. Error bars are back transformed 95% confidence intervals for estimated means.

Table 3.3. Result of mixed model ANOVA of percent area burned of subplots with orthogonal individual degree of freedom contrasts. Error term for canopy disturbance = Block x Plot(Canopy). Error term for fuel and interactions = residual. NDF = numerator degrees of freedom; DDF = denominator degrees of freedom based on Kenward-Roger approximation. Covariance structure = heterogeneous variance.

Source of Variation	NDF	DDF	F	<i>p</i>
Fixed Effects:				
Canopy	1	223	5.53	0.0196
Fuel	3	223	58.99	<0.0001
Canopy x Fuel	3	223	2.24	0.0846
Individual Degree of Freedom Contrasts:				
FUEL:				
Control x (Deciduous + Longleaf + Mixed Pine)	1	223	30.53	<0.0001
Deciduous x (Longleaf + Mixed Pine Fuels)	1	223	147.79	<0.0001
Longleaf Pine Fuel x Mixed Pine Fuel	1	223	0.17	0.6775
CANOPY X FUEL				
(Removed X Intact) X [(Control) X (Deciduous + Longleaf + Mixed Pine)]	1	223	0.24	0.6212
(Removed X Intact) X [(Deciduous) X (Longleaf + Mixed Pine)]	1	223	6.22	0.0134
(Removed X Intact) X (Longleaf + Mixed Pine)	1	223	0.19	0.6611

Effects of Canopy Disturbance and Fuel Additions on Vegetation

Vegetation in all plots changed over time. Means for three responses of vegetation increased from the first post-treatment census to the second census (Figure 3.4). Mean percent cover of vegetation increased from 4% in the first year following the prescribed fire to 23% in the second year, then decreased to 16% following the second fire (Figure 3.4A). Average stem density for all sampling plots increased from 19 to 40 in the second year, then to 44 stems/m² in the third year (Figure 3.4B) Species richness per subplot increased between the first and second years following the initial prescribed fire but not in the final census (Figure 3.4C). The effect of time was significant for each response variable ($p < 0.0001$, Tables 3.4, 3.5, 3.6). Orthogonal contrasts with time were significant for percent vegetation cover, total stem density, and species counts ($p < 0.0001$, Tables 3.4, 3.5, 3.6). Contrasts indicated that models of linear increases in

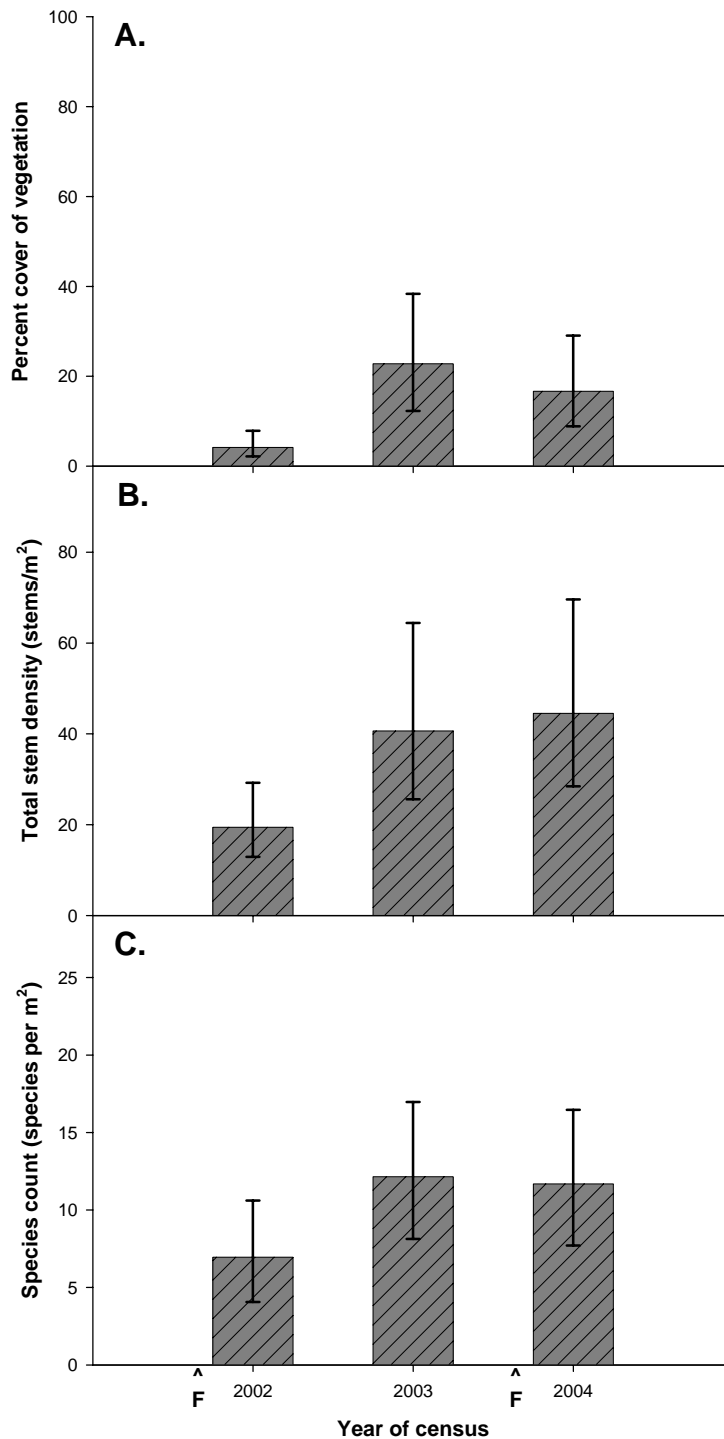


Figure 3.4. Changes in vegetation responses over three census years. **A)** Mean percent cover of vegetation per 1m². **B)** Mean total stem density. **C)** Mean species richness per subplot. “F” on x-axis represents date of prescribed fire. Values for each treatment combination are back-transformed least square means. Error bars are back transformed 95% confidence intervals for estimated means.

Table 3.4. Result of mixed model ANOVA of percent vegetation cover repeated measures with significant orthogonal individual degree of freedom contrasts. Error term for canopy disturbance = Block x Plot(Canopy). Error term for fuel and interactions = Subplot(Fuel x Block x Plot x Canopy). Error term for Year and interactions = residual. NDF = numerator degrees of freedom; DDF = denominator degrees of freedom based on Kenward-Roger approximation. Covariance structure = heterogeneous variance.

Source of Variation	NDF	DDF	F	<i>p</i>
Fixed Effects:				
Year	2	273	366.73	<0.0001
Canopy	1	8.20	4.31	0.0707
Fuel	3	223	2.06	0.1063
Year x Canopy	2	273	16.21	<0.0001
Year x Fuel	6	342	2.06	0.0572
Canopy x Fuel	3	223	1.05	0.3709
Year x Canopy x Fuel	6	342	0.74	0.6165
Individual Degree of Freedom Contrasts:				
YEAR:				
Linear	1	327	397.19	<0.0001
Quadratic	1	304	471.08	<0.0001
YEAR X CANOPY				
Linear X (Removed X Intact)	1	327	32.10	<0.0001
YEAR X FUEL				
Linear X [(Control) X (Deciduous + Longleaf + Mixed Pine)]	1	327	8.21	0.0044

Table 3.5. Result of mixed model ANOVA of stem density repeated measures with significant orthogonal individual degree of freedom contrasts. Error term for canopy disturbance = Block x Plot(Canopy). Error term for fuel and interactions = Subplot(Fuel x Block x Plot x Canopy). Error term for Year and interactions = residual. NDF = numerator degrees of freedom; DDF = denominator degrees of freedom based on Kenward-Roger approximation. Covariance structure = heterogeneous variance.

Source of Variation	NDF	DDF	F	<i>p</i>
Fixed Effects:				
Year	2	266	162.21	<0.0001
Canopy	1	8.18	3.72	0.0890
Fuel	3	244	0.52	0.6719
Year x Canopy	2	266	34.36	<0.0001
Year x Fuel	6	336	2.65	0.0160
Canopy x Fuel	3	244	2.32	0.2698
Year x Canopy x Fuel	6	336	1.89	0.0817
Individual Degree of Freedom Contrasts:				
YEAR:				
Linear	1	272	304.24	<0.0001
Quadratic	1	318	118.51	<0.0001
YEAR X CANOPY				
Linear X (Removed X Intact)	1	272	65.19	<0.0001
Quadratic X (Removed X Intact)]	1	318	23.61	<0.0001
YEAR X FUEL				
Linear X [(Control) X (Deciduous + Longleaf + Mixed Pine)]	1	272	8.37	0.0041
Quadratic X [(Control) X (Deciduous + Longleaf + Mixed Pine)]	1	318	4.60	0.0327

Table 3.6. Result of mixed model ANOVA of number of species repeated measures with significant orthogonal individual degree of freedom contrasts. Error term for canopy disturbance = Block x Plot(Canopy). Error term for fuel and interactions = Subplot(Fuel x Block x Plot x Canopy). Error term for Year and interactions = residual. NDF = numerator degrees of freedom; DDF = denominator degrees of freedom based on Kenward-Roger approximation. Covariance structure = heterogeneous variance.

Source of Variation	NDF	DDF	F	<i>p</i>
Fixed Effects:				
Year	2	265	234.92	<0.0001
Canopy	1	8.00	4.48	0.0671
Fuel	3	223	0.93	0.4291
Year x Canopy	2	265	56.72	<0.0001
Year x Fuel	6	335	2.91	0.0089
Canopy x Fuel	3	223	0.89	0.4458
Year x Canopy x Fuel	6	335	1.10	0.3630
Individual Degree of Freedom Contrasts:				
YEAR:				
Linear	1	269	373.42	<0.0001
Quadratic	1	286	190.73	<0.0001
YEAR X CANOPY				
Linear X (Removed X Intact)	1	269	91.88	<0.0001
Quadratic X (Removed X Intact)	1	286	43.93	<0.0001
YEAR X FUEL				
Linear X [(Control) X (Deciduous + Longleaf + Mixed Pine)]	1	269	10.05	0.0017
Quadratic X [(Deciduous) X (Longleaf + Mixed Pine)]	1	286	4.37	0.0374

time fit for each of the vegetation responses. In addition, there also were significant quadratic components to the responses.

Canopy disturbance affected responses of vegetation over the duration of the study. Canopy treatments influenced percent cover, stem densities, and numbers of species differently over time, resulting in significant interactions between canopy treatment and time ($p < 0.0001$, Tables 3.4, 3.5, 3.6).

Patterns of responses over time to canopy treatments were similar for three response variables. Little response of vegetation to canopy treatment was noted in the first year following treatments. Mean percent cover of vegetation was below 5%, stem densities averaged 18 and 21 stems/m² respectively, and there were seven species on average per subplot for canopy-removed and canopy-intact plots (Figure 3.5). For the 2002 census year interactions with canopy disturbance were not significantly different for any of the response variables (effect slices $p > 0.53$). In the second and third years means were consistently greater in canopy-removed treatment plots than in canopy-intact treatment plots. By the second census mean percent cover had increased to 31% in canopy-removed plots, but only 16% in canopy-intact plots. Following the second biennial fire in 2004, means for canopy-removed and canopy-intact plots declined, but differently, to 25 and 10 percent cover of vegetation respectively (Figure 3.5A). Mean total stem density in canopy-removed plots increased to 53 and 61 stems/m² in the subsequent two years, while canopy-intact plot means leveled off at 31 and 32 stems per subplot (Figure 3.5B). Species richness doubled from 7 to 14 species/m² after the first year in canopy-removed plots and then stayed the same. In contrast, canopy-intact plots species count means only increased from 7 to 9 species on average in 2003 and remained the same in 2004 (Figure 3.5C). Means response variables for interactions between canopy disturbance and time are significantly

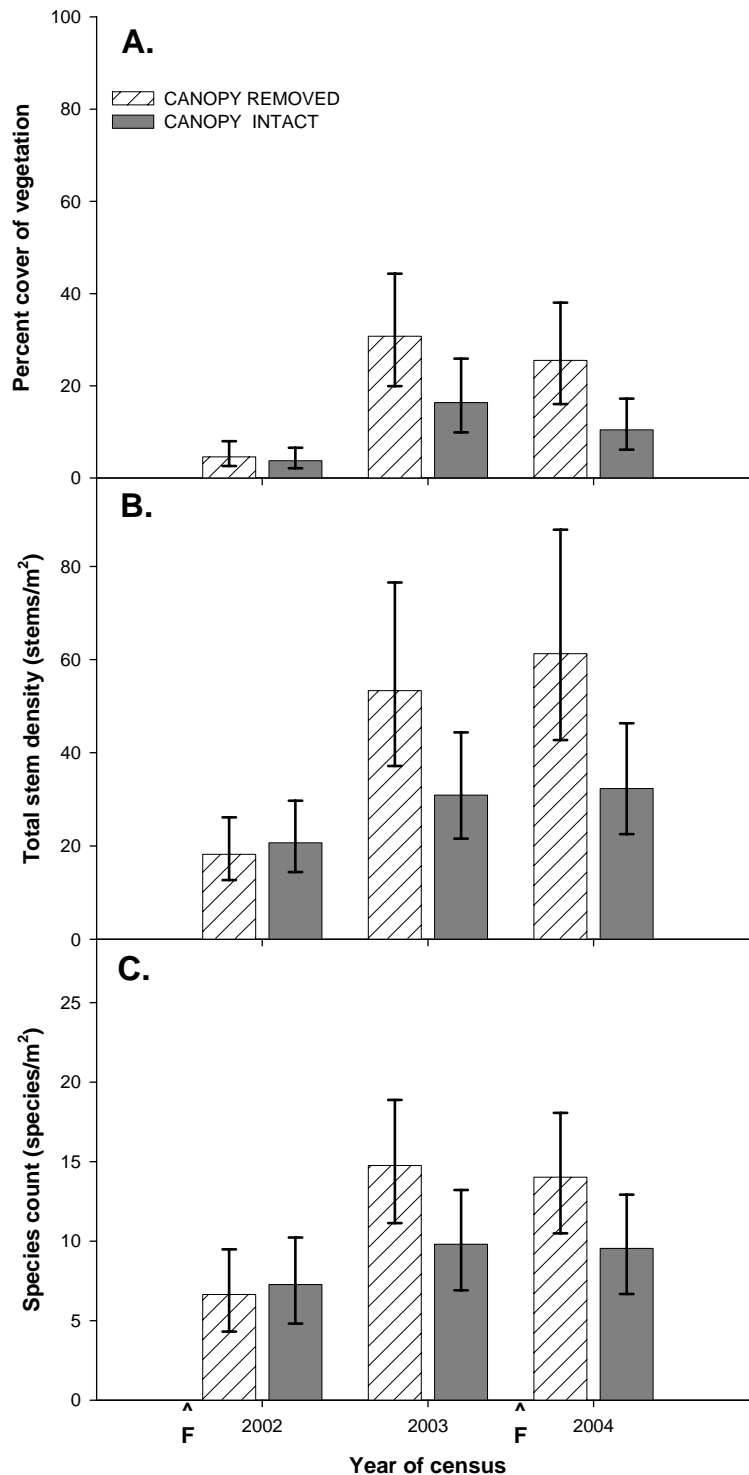


Figure 3.5. Changes in responses for canopy-removed vs. canopy-intact treatment subplots over three census years. **A)** Mean percent cover of vegetation. **B)** Total stem density. **C)** Mean of species count. F=fire. Mean values for each treatment combination are back-transformed least square means. Error bars are back transformed 95% confidence intervals for estimated means.

different for the second and third years (effect slices $p < 0.04$). Overall, the main effect of canopy disturbance resulted in responses of vegetation that were greater in canopy-removed plots than in canopy intact plots, but the effects were marginal on mean percent cover ($p = 0.07$), stem density ($p = 0.09$) and species count (0.07).

Planned contrasts of year by canopy disturbance effects also indicated a long-term effect of opening the canopy. Percent cover of vegetation changed in different linear ways over time for canopy-removed compared to canopy-intact treatments ($p < 0.0001$, Table 3.4). Opening the canopy resulted in greater increases in percent cover in the second and third years compared to plots with undisturbed overstory (Figure 3.5A). Stem densities changed in different linear and quadratic ways over time in the two canopy treatment plots ($p < 0.0001$, Table 3.5). Mean stem densities continually increased in canopy-removed plots over the course of the study, while canopy-intact means stayed the same in years 2 and 3 (Figure 3.5B). Total number of species also changed in different linear and quadratic ways over time with different canopy treatments ($p < 0.0001$, Table 3.6). Species counts were similar in the initial post-fire census, but counts increased and were greater within canopy removed plots in the subsequent years (Figure 3.5C).

Effects of fuel manipulations on vegetation were transient. The three fuel treatments influenced vegetation differently than unaltered controls in the first year, but differences disappeared in the second and third years after the initial fire. Average percent cover in the first year was 5% in control subplots and 2% for the three fuel treatments (effect slices $p = 0.004$). In year two, percent cover was 25% and 22% in control and fuel addition subplots, respectively. By the third year mean percent cover was 17% in both control and fuel addition subplots. Mean total stem density in year one was 25 and 18 stems/m² in control and fuel addition subplots, respectively, but means were identical for control and fuel addition subplots in the next two

years. Numbers of species for controls and fuel addition subplots in year one were 8 and 6 species/m², respectively, and 12 species/m² in both treatment subplots in the following years. Significant differences only occurred in the first year for species richness (effects slices $p=0.02$). Overall, the fuel addition treatments did not differently influence any of the three original vegetation responses in the repeated measures analysis ($p>0.1$). Interactive effects of canopy disturbance and fine fuels also were not significant ($p>0.26$).

Orthogonal linear contrasts also indicated a transient effect of fuel additions. Contrasts testing hypotheses of different linear changes in time for controls compared to fuel additions were significant for three vegetation response variables. The effect of the three combined fuel treatments was reduced percent cover of vegetation (Figure 3.6A) after the initial prescribed fire (contrast $p=0.0044$, Table 3.4). This difference in mean percent cover continued in the second census year (no fire) but disappeared in the third year. Fuel additions also resulted in reduced mean total stem density (Figure 3.6B) after the initial prescribed fires (contrast $p=0.0041$, Table 3.5). Effects of added fuels on stem densities disappeared in the second and third years. Contrasts indicated that stem densities for fuel addition compared to controls (Figure 3.6B) differed in significant linear (contrast= 0.0041) and quadratic ways (contrast= 0.0327). The number of species present in sampling plots (Figure 3.6C) differed in response to fuel effects in the first year, but the difference also disappeared in the subsequent censuses (contrast $p=0.0017$, Table 3.6). Species numbers in deciduous fuel vs. pine (longleaf + mixed pine) also changed in different quadratic ways over time (contrast= 0.0374).

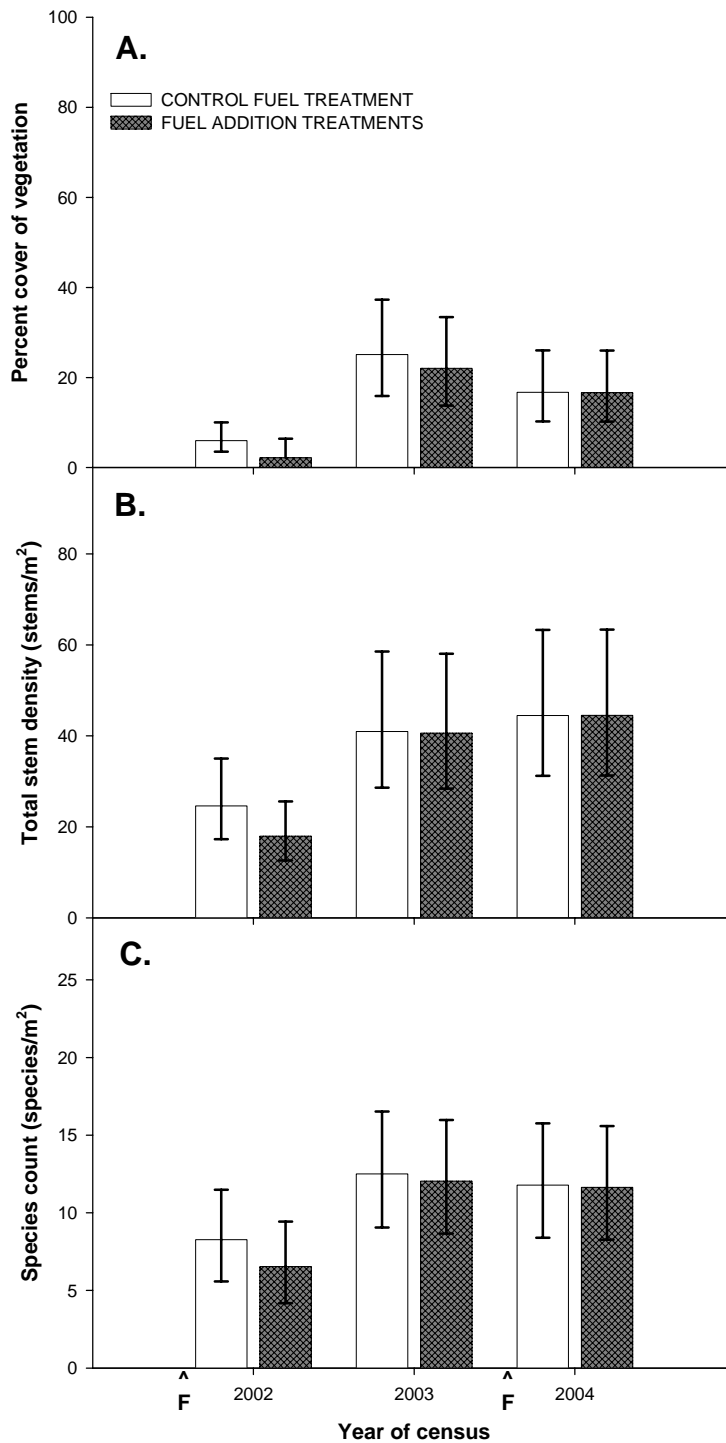


Figure 3.6. Changes in responses of vegetation variables for control vs. fuel addition treatment subplots over three census years. **A)** Mean percent cover of vegetation. **B)** Total stem density. **C)** Mean of species count. F=fire. Mean values for each treatment combination are back-transformed least square means. Error bars are back transformed 95% confidence intervals for estimated means.

Responses of Woody and Herbaceous Vegetation Components

Changes in woody (shrubs and trees) stem density over time were similar to changes in herb (grasses and forbs) stem density. Both vegetation components increased over time but density of woody species was much lower than herbs in all three years. Mean density of woody species increased from 5 to 9 stems/m² over the course of the study while mean herb density increased from 15 to 36 stems/m² (Figure 3.7). Means differed significantly for both understory components ($p < 0.0001$, Tables 3.7 and 3.8) and stem densities changed in different linear and quadratic ways over time ($p < 0.0001$, Tables 3.7 and 3.8). Patterns of change in mean richness of woody and herbaceous species over time were similar to changes in stem densities.

Woody stem density and species richness were the only vegetation responses significantly affected by one of the disturbance treatments. Canopy disturbance did not strongly influence stem densities or species richness of woody or herbaceous plants in this study. However, fuel additions significantly reduced woody stem densities ($p < 0.0105$, Table 3.7). Mean stem density of woody species was highest within control fuel treatment subplots (6 stems/m²), the same for deciduous hardwood and longleaf treatments (5 stems/m²) and lowest in mixed pine fuel treatment subplots (4 stems/m²) (Figure 3.8A). Linear contrast of controls and the three fuel treatments indicated that woody stem density was significantly greater in control subplots (Figure 3.8B, contrasts $p = 0.0024$, Table 3.7). Like stem density, woody species richness was reduced in fuel addition plots relative to controls. Woody species counts were significantly reduced by fuel treatments ($p = 0.0039$), and control by fuel contrasts were significant (0.0026).

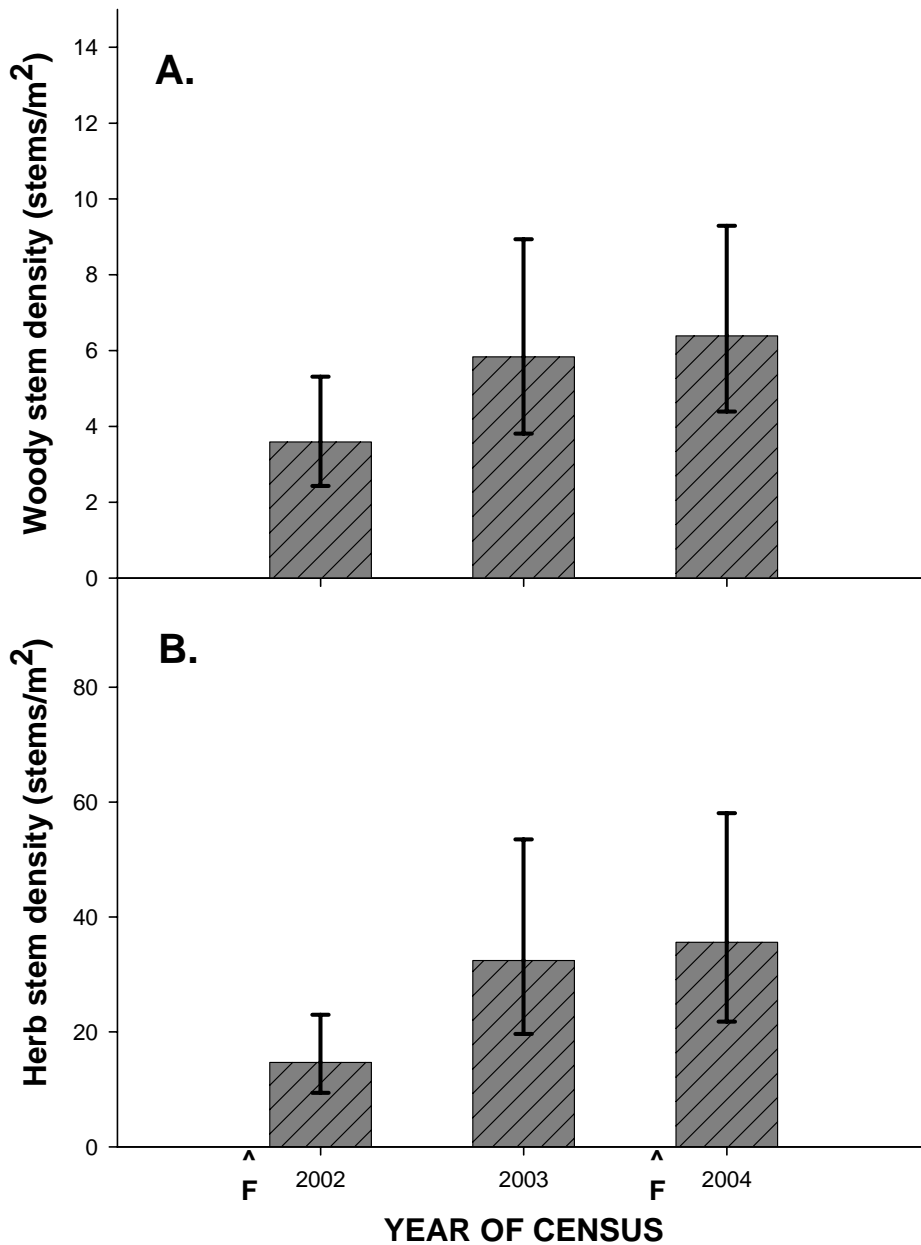


Figure 3.7. Changes in mean stems/m² for **A)** woody species and **B)** herb species over three census years. F=Fire. Mean values for each treatment combination are back-transformed least square means. Error bars are back transformed 95% confidence intervals for estimated means.

Table 3.7. Result of mixed model ANOVA of woody stem density repeated measures with significant orthogonal individual degree of freedom contrasts. Error term for canopy disturbance = Block x Plot(Canopy). Error term for fuel and interactions = Subplot(Fuel x Block x Plot x Canopy). Error term for Year and interactions = residual. NDF = numerator degrees of freedom; DDF = denominator degrees of freedom based on Kenward-Roger approximation. Covariance structure = heterogeneous variance.

Source of Variation	NDF	DDF	F	<i>p</i>
Fixed Effects:				
Year	2	269	71.85	<0.0001
Canopy	1	8.29	1.04	0.3374
Fuel	3	232	3.83	0.0105
Year x Canopy	2	269	4.47	0.0123
Year x Fuel	6	338	2.29	0.0353
Canopy x Fuel	3	232	0.12	0.9454
Year x Canopy x Fuel	6	338	0.55	0.7687
Individual Degree of Freedom Contrasts:				
YEAR:				
Linear	1	317	99.33	<0.0001
Quadratic	1	318	118.51	<0.0001
FUELS:				
Control x (Deciduous + Longleaf + Mixed Pine)	1	232	9.39	0.0024
YEAR X CANOPY				
Linear X (Removed X Intact)	1	317	8.61	0.0036
YEAR X FUEL				
Linear X [(Control) X (Deciduous + Longleaf + Mixed Pine)]	1	317	12.04	0.0006

Table 3.8. Result of mixed model ANOVA of herb stem density repeated measures with significant orthogonal individual degree of freedom contrasts. Error term for canopy disturbance = Block x Plot(Canopy). Error term for fuel and interactions = Subplot(Fuel x Block x Plot x Canopy). Error term for Year and interactions = residual. NDF = numerator degrees of freedom; DDF = denominator degrees of freedom based on Kenward-Roger approximation. Covariance structure = heterogeneous variance.

Source of Variation	NDF	DDF	F	<i>p</i>
Fixed Effects:				
Year	2	261	163.40	<0.0001
Canopy	1	8.12	2.74	0.1359
Fuel	3	239	0.44	0.7243
Year x Canopy	2	261	46.40	<0.0001
Year x Fuel	6	332	2.29	0.0351
Canopy x Fuel	3	239	1.56	0.1993
Year x Canopy x Fuel	6	332	2.25	0.0383
Individual Degree of Freedom Contrasts:				
YEAR:				
Linear	1	263	307.84	<0.0001
Quadratic	1	302	114.96	<0.0001
YEAR X CANOPY				
Linear X (Removed X Intact)	1	263	87.02	<0.0001
Quadratic X (Removed X Intact)]	1	302	33.43	<0.0001
YEAR X FUEL				
Quadratic X [(Control) X (Deciduous + Longleaf + Mixed Pine)]	1	302	4.58	0.0331

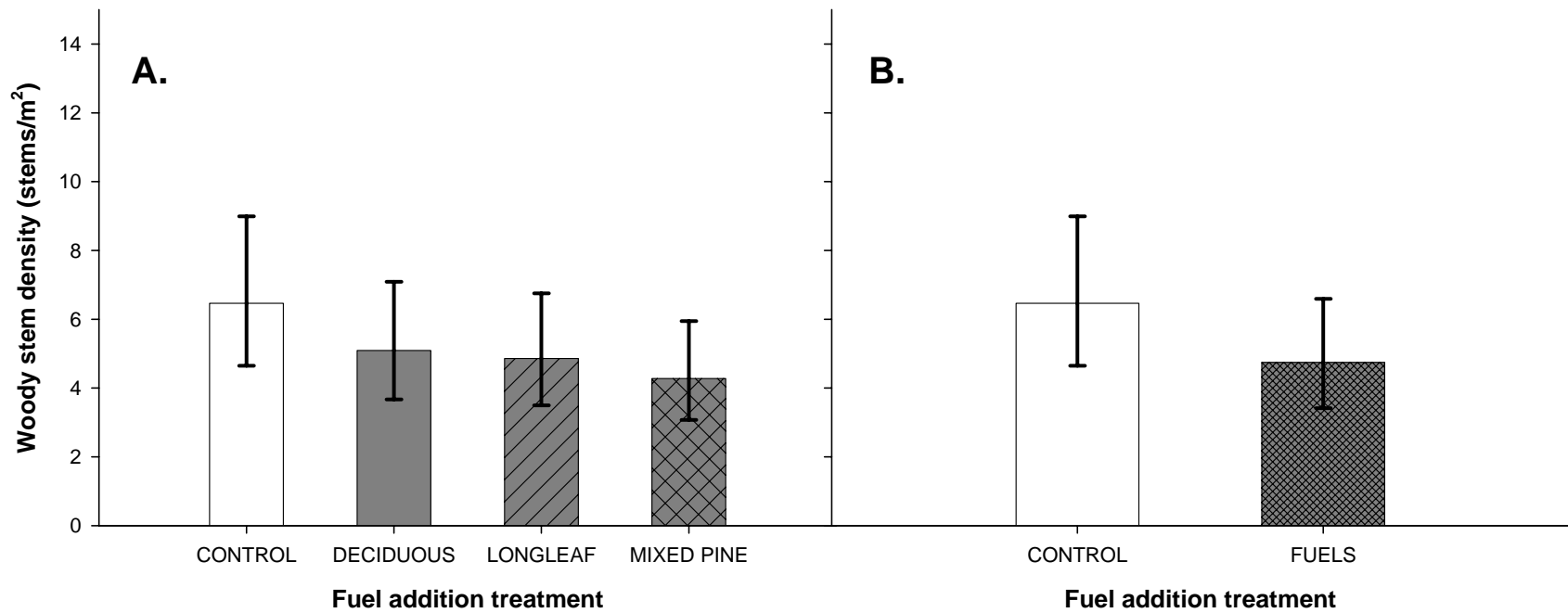


Figure 3.8. **A)** Mean number of woody stems/m² within four fuel addition treatments. **B)** Grouped mean of woody stem density for three fuel additions compared to unaltered control. Mean values for each treatment combination are back-transformed least square means. Error bars are back transformed 95% confidence intervals for estimated means.

The effect of canopy disturbance on woody and herbaceous stem densities changed over time. The number of woody stems in canopy-removed plots increased from 4 to 6 and then to 8 stems/m² over three years while woody stems in canopy-intact plots increased from 4 to 6 stems/m² and then remained the same (Figure 3.9A). Mean herb stem density also continued to increase in canopy-removed plots over time while densities in canopy-intact plots were the same in the second and third years (Figure 3.9B). Differences between canopy-removed and canopy intact plots resulted in a significant interaction of canopy disturbance over time for both woody stems ($p=0.0123$, Table 3.7) and herb stems ($p<0.0001$, Table 3.8). Woody stem density changed in different linear ways over time for canopy-removed compared to canopy-intact treatments ($p<0.0036$, Table 3.7). Density of herbs changed in different linear and quadratic ways over time in the two canopy treatment plots ($p<0.0001$, Table 3.8).

The suppressive effects of fuel addition on woody stem densities and species richness were longer-lasting than on any other measure of vegetation. Fuels significantly reduced woody stem densities and species richness for two census years (effect slices $p<0.0002$ and $p<0.03$). In the first year the highest mean woody stem density was in control subplots (5 stems/m²) and the lowest density was in mixed pine fuel addition subplots (3 stems/m²). Effects were strongest for stem densities. Relative differences for fuel addition treatments were similar in year 2 and all means increased. In the third study year mean woody stem densities were 7 stems/m² in control, deciduous hardwood, and longleaf plots and 6 stems/m² in mixed pine fuel addition plots. These differences resulted in a significant interaction of fuel addition and time ($p=0.0353$, Table 3.7). Additionally, differences in mean woody stem densities in control subplots and three fuels combined changed over time. Mean woody stem density in control fuel treatment subplots were greater than mean woody density in fuel addition subplots in all three years (Figure 3.10A). The

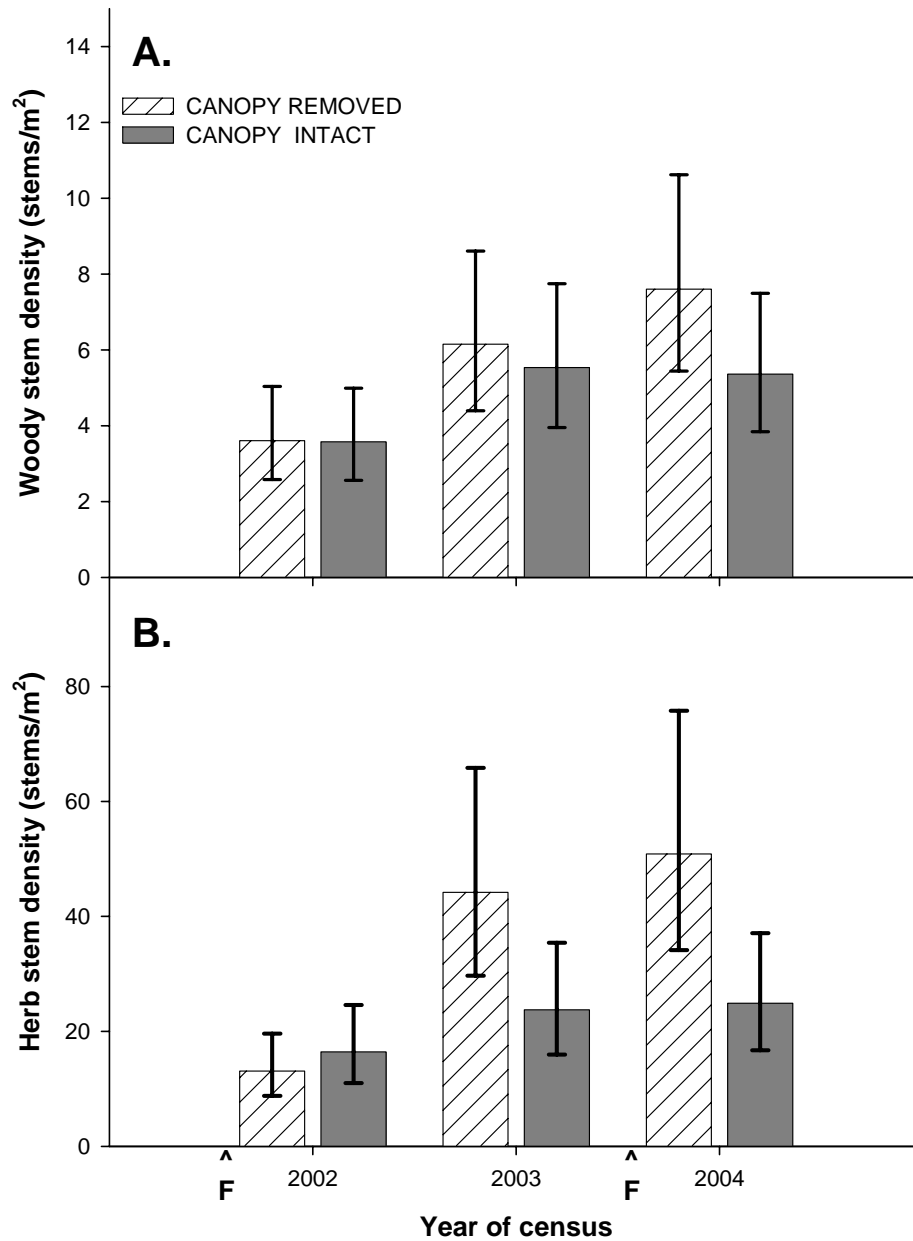


Figure 3.9. Changes in woody (A) and herb (B) stem density for canopy-removed vs. canopy-intact treatment subplots over three census years. F=fire. Mean values for each treatment combination are back-transformed least square means. Error bars are back transformed 95% confidence intervals for estimated means.

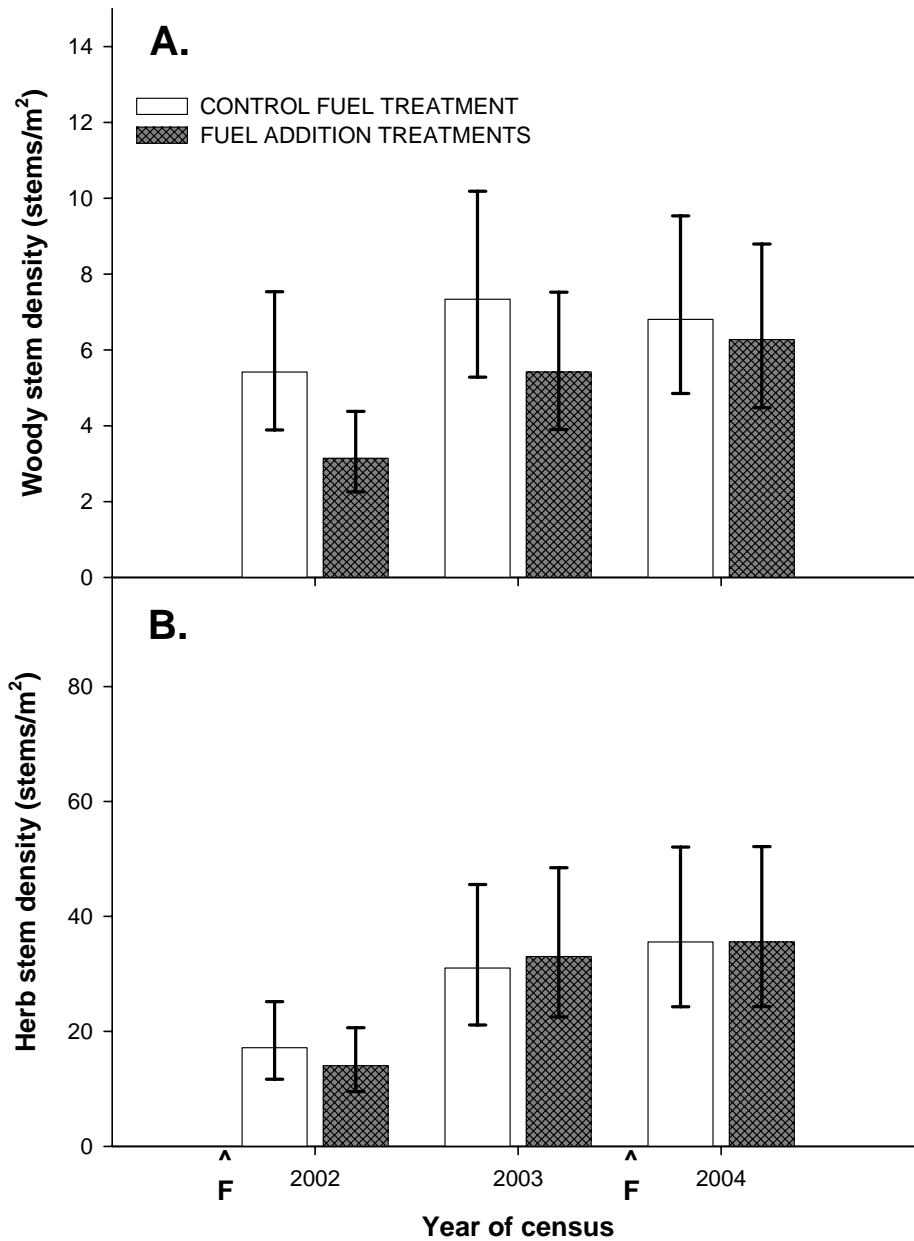


Figure 3.10. Changes in woody (A) and herb (B) stem density for controls and grouped fuel addition subplots over three census years. F=fire. Mean values for each treatment combination are back-transformed least square means. Error bars are back transformed 95% confidence intervals for estimated means.

orthogonal contrast testing hypotheses of different linear changes in time for controls compared to fuel additions was significant for woody stems (contrast $p=0.0006$, Table 3.7).

For herb densities the effect of fuel addition was not even transient. Like total stem counts, herb stem densities were not differently affected by fuel additions over time. Fuels did not significantly influence herb densities in any single year (effects slices $p>0.23$). Mean herb densities did increase in all subplots over time and these changes resulted in a significant time by fuel treatment interaction ($p=0.0331$, Table 3.8). Differences in mean herb stem densities in control subplots and three fuels combined changed over time. However, in contrast to woody stems, mean herb stem density was higher in control plots in 2002, lower in control plots in 2003, and equal in control and fuel addition subplots in 2004 (Figure 3.10B). For mean herb density the orthogonal contrast testing hypotheses of different quadratic changes in time for controls compared to fuel additions was significant ($p=0.0331$, Table 3.8). Patterns and significant effects are generally similar for changes in herbaceous species richness.

Discussion

Responses of Vegetation to Canopy Disturbance

Canopy disturbance resulted in small but significant increases in understory light availability. Differences in transmitted light levels between canopy-removed and canopy-intact plots were not large because numerous understory trees were still present. Similar patterns have been noted in other studies (e.g., Canham et al. 1990). Transmitted light levels in the disturbed savanna-forest ecotone understory ranged from 26-42%. These levels overlap with the 38-80% range found in a 60-80 year-old second growth longleaf pine savanna understory (Battaglia et al. 2003). Hurricane disturbance can be expected to increase understory light availability, but

increases may not be large because understory trees often survive hurricane winds (Batista and Platt 2003, Kwit and Platt 2003).

The overall influence of opening the canopy on understory vegetation was weak. This weak effect may have resulted from the small but significant difference in transmitted light levels. Despite weak overall responses of groundcover vegetation, canopy disturbance effects were significant during individual years, and effects persisted through time. All measures of vegetation response to canopy disturbance, with the exception of woody stem density and woody species richness, were significantly higher in canopy-removed plots in the second and third years of the study. Annual and overall differences might have been larger had hurricane disturbance directly affected understory trees. Canopy gaps that open all the way to the ground are expected to result in greater changes in light levels and larger responses of groundcover vegetation, even in already open longleaf pine savanna (McGuire et al. 2001). Our results indicate that the response of vegetation to canopy disturbance is primarily driven by increases in herbaceous groundcover species. Similar responses of herbaceous vegetation were found following selective removal of densely occurring, mature, invasive pines in Florida sandhills (Provencher et al. 2000).

In the absence of subsequent disturbance, responses of understory shrubs and trees to the open canopy may result in rapid canopy closure. Warm temperate and subtropical forests have well-developed shrub layers that include both small- and large-stature species (Quigley and Platt 2003). After hurricanes, understory trees and shrubs respond to new environmental conditions by growing in size, flowering, and setting seed (Pascarella and Horvitz 1998). Generally, post-hurricane ingrowth and growth rates of advance recruit, understory trees are highest in recent hurricane gaps (Harcombe et al. 2002, Kwit and Platt 2003). Thus, without additional

disturbances such as fires, shrubs and understory trees are expected to block light transmission to the groundcover soon after hurricane disturbance.

Response of Vegetation to Fire Following Canopy Disturbance and Fuel Addition

Recurring growing season fires may prevent closure of gaps by understory trees and shrubs in the savanna-forest ecotone. Canopy disturbance by tornado in the Big Thicket region of southeastern Texas caused changes in species composition and density over three years so that former pine savanna stands became mixed pine-hardwood stands (Liu et al. 1997). The trend towards more shade-tolerant and less fire-tolerant canopy species was reversed only by reintroduction of prescribed understory fires. If subsequent fires increase mortality or delay resprouting of canopy tree seedlings, saplings and root sprouts, canopy closure in ecotones may be delayed. These effects are predicted, especially if open canopy and abundant fuels increase fire intensity.

Modified fire effects where fuels were added only temporarily influenced vegetation response, but duration of effects differed for woody and herbaceous vegetation components. Fuel addition treatments in our study reduced percent cover of vegetation and species richness in the first census year. Reductions of total stem density were only marginally significant. Woody stem densities and species richness were significantly reduced by fuel addition in both the first and second years. In contrast there was no effect of fuel treatments on herbaceous stem density or species richness. Low mortality from fire and high rates of resprouting and reseedling is expected for savanna groundcover species that are adapted to frequent fire (Walker and Peet 1983, Abrahamson 1984b). Thus, temporary effects in savanna-forest ecotone may reflect slow regrowth of biomass and delayed resprouting during the initial postfire growing season. High fuel loads increased damage, reduced size and numbers of shrub resprouts in frequently burned

longleaf pine savanna (Thaxton 2003). Therefore, transient effects of fuel addition treatments are predictable, especially in savanna-forest ecotone where at least some proportion of the groundcover community includes fire-adapted species from adjacent savannas.

Effects of Hurricane-Fire Interactions on Intensity of Fires

Two common effects of hurricanes, removal of the canopy and deposition of fine fuels, affected the behavior of subsequent fires in the ecotone between pine savannas and forests. Maximum fire temperatures increased, and more area burned, both when the canopy was removed and when fine fuels were added. Thus, increased intensity and decreased patchiness might be expected to characterize natural, lightning fires that follow hurricanes.

Lightning-season prescribed fires in our study were hotter where canopy was disturbed. Few other studies have directly tested for differences in fire intensity between gaps and closed-canopy forest. Furthermore, no previous studies have examined effects of lightning season fires in gaps and closed-canopy forest. Low fire temperatures were qualitatively associated with greater shading in long-unburned Florida sandhills (Rebertus et al. 1989a). Flammability, and thus fire probability, decreased with greater canopy cover (Streng and Harcombe 1982, Biddulph and Kellman 1998). We expect natural lightning fires that follow canopy disturbance in savanna-forest ecotone to be hotter and more extensive.

Our study and others show that fuel type and quantity directly influence fire behavior. In our study, pine fuel additions generated much higher maximum fire temperatures and consistently burned more area than either deciduous hardwood fuel additions or controls. Higher and less variable maximum fire temperatures were recorded in areas of xeric sandhills and flatwoods containing more and larger pines (Platt et al. 1991). In mixed oak-pine forest Williamson and Black (1981) measured higher maximum fire temperatures under pines than

under oaks. We observed that pyrogenic pine fuels burned readily and completely when ignited, whereas deciduous fuels did not ignite easily, often smoldered, and did not burn completely. These differences between pine and deciduous hardwood fuels resulted from leaves of the latter being more compacted and less aerated than needles in pine fuels. Thus, intense fires following hurricanes are most likely to occur where downed fuels are predominantly pyrogenic fuels from pines. If fuels within a landscape are a mixture of overstory hardwoods and pines then fire intensities are likely to be patchy, with higher intensity “hot spots” where large branches or crowns of downed pines have fallen. Therefore fire intensity following hurricane disturbance should directly depend on the types of canopy trees damaged by hurricane winds.

The two hurricane effects interacted to produce even greater increases in maximum fire temperatures under open canopies with added fine fuels. Higher maximum fire temperatures have been predicted under open canopy based on increased drying of fuels from high insolation and low relative humidity compared to fuels under closed canopy (Loope et al. 1994, Myers and Van Lear 1998). Anecdotal evidence following hurricanes has been used to suggest that open canopy, along with increased fuels, results in intense and extensive dry season fires (e.g., Furley and Newey 1979, Whigham et al. 1991). We experimentally demonstrated that deciduous fuels were the least likely to result in intense fires under closed canopy, but were most likely to be influenced by the warmer, drier conditions below open canopy. Although canopy disturbance did increase maximum fire temperatures of deciduous fuels, it did not influence fire temperatures of more pyrogenic fuels. Rather, the effects of the interaction between hurricane disturbance treatments on fire temperatures in this study were mostly driven by the effect of canopy disturbance on deciduous hardwood fuels. Hurricanes tend to damage hardwood species more than pines (see Chapter 2 and references therein), and thus can be expected to produce

proportionally more hardwood litter than pine litter in a savanna-forest ecotone. Therefore, fuel loads and thus, interacting hurricane effects will depend not only on the overstory species composition, but on the relative damage to pines and hardwoods.

Different Effects of Hurricane-Fire Interactions on Woody and Herbaceous Vegetation

Both removal of the canopy and deposition of fine fuels affected the groundcover vegetation in the ecotone between pine savannas and downslope forests. Fewer interacting effects influenced vegetation, however, than the interactions that affected the behavior of fires. The increased intensity and decreased patchiness expected to characterize natural, lightning fires that follow hurricanes appears to have limited effects on groundcover vegetation.

The most pronounced interactive effect on savanna-forest ecotone vegetation involved woody species. A hurricane-fire interaction occurred when hot fires from increased pine needle loads reduced stem densities and species richness of woody plants. This interactive effect was independent of canopy removal, indicating that increases in pine needles from fallen branches or tree crowns need not be located in open areas to have an effect on woody species. In Thaxton (2003), experimentally generated local high fuel loads in frequently burned longleaf pine savanna decreased shrub resprouting. Drewa et al. (2002) found that stem densities of root-crown shrubs decreased as fire temperatures increased from growing season fires. Less frequent fires result in increased shrub sizes and abundance compared to frequently burned longleaf pine savanna (Platt and Schwartz 1990, Glitzenstein et al. 1995, Drewa 1999, Gilliam and Platt 1999). Increased intensity of fires may be important in reduction of shrubs. Maximum temperatures and fire intensities associated with growing-season fires in pine savannas did not significantly reduce shrub sizes and densities (Olson and Platt 1995, Drewa et al. 2002). Nonetheless, increases in

pyrogenic fuel loads following hurricanes could reduce hardwood stem densities in the ecotone on scales that vary with occurrences of pines and effects of hurricanes.

Intense fires that reduce hardwood stem densities create post-fire recruitment opportunities for herbaceous species. Open spaces in the groundcover produced by locally intense fires in longleaf pine savanna have been predicted to increase heterogeneity and diversity in the groundcover community by reducing competition and promoting establishment of herbaceous species (Thaxton 2003). In our study, increased fuel loads and resulting more intense fires did not reduce stem densities of herbaceous species. Moreover, numbers and cover of herbaceous species increased over time, suggesting more opportunities for recruitment, at least transiently, after fires. Increased abundance of herbaceous species, coupled with decreases in shrubs, could promote the occurrence and spread of more fires. The result could be increased likelihood of establishment by fire-resistant species, both pines (e.g., longleaf or shortleaf pine) and herbs.

Predicted Long-Term Effects of Interactions in Savanna-Forest Landscapes

Hurricane-fire interactions will vary across the savanna-forest landscape as a function of overstory tree composition. We predict high fire temperatures following hurricane disturbance in pine savanna where downed fuels would predominantly consist of pyrogenic pine needles. In hardwood forests, we predict hurricane-fire interactions will be rare because fires there are extremely infrequent and forest fuels are not pyrogenic. Within mixed species ecotones we predict that fire behavior would be more variable, because hurricane-generated fuels are a heterogeneous mix of mostly hardwood fuels or mostly pine fuels. We expect interacting hurricane effects to increase fire temperatures in the ecotone because of the strong influence of open canopy on hardwood deciduous fuels. If the extent of hurricane damage is greater for

hardwoods compared to pines, then we expect more interactions in mixed species savanna-forest ecotones than in adjacent pine savannas. Following hurricanes, fire intensity will be high but variable across savanna-forest landscapes.

Interacting hurricane and fire effects could lead to further changes in understory vegetation with repeated fires. Increased fire intensity associated with pine fuels will influence savanna and ecotone vegetation, especially if herbaceous species provide continuous fuels among pines. In Florida sandhills, hotter fires under adult pines increased mortality of oak seedlings compared to pines (Williamson and Black 1981). If reduction of woody stems involved differential mortality of hardwood species over pines, then long-term effects could include increased pine fuels and more intense fires. Further, if pines and other pyrogenic species invade the ecotone after hot fires and become established they would eventually change the fine fuel composition and promote hotter, more complete fires (Platt et al. 1991). Invasion by species from adjacent savannas or fire-adapted species indigenous to ecotones might produce unique ecotone community, distinct from either adjacent savanna or hardwood forest. Such changes in groundcover species composition could lead to long-term changes in community composition and vegetation structure across the savanna-forest landscape. Furthermore, invasions by pyrogenic species in the ecotone may facilitate subsequent hurricane-fire interactions.

CHAPTER 4

CONCLUSIONS

In this dissertation, I developed general hypotheses regarding the occurrence and effects of hurricane-fire interactions in southeastern coastal landscapes. My hypotheses were based on short- and long-term characteristics of natural fire and hurricane regimes likely to have characterized pre-settlement savanna-forest landscapes. My models incorporate hurricanes that occur during the Atlantic hurricane season (June to November) and fires that occur during the spring lightning season (March to June). These conceptual models explicitly address the importance of spatial and temporal overlap in hurricane and fire effects for interactions to occur. These models were based on rates of re-accumulation of fine fuels following fires and rates of decomposition of hurricane-generated fuels after hurricanes.

I predicted that hurricane-fire interactions differ in their importance in savanna, ecotone and hardwood forest landscape components. The models indicated that interactions would be likely in savannas, affecting both the overstory and groundcover in ways that could enhance plant species diversity and local heterogeneity. I also predicted that hurricane-fire interactions would influence ecotones between savannas and forests by changing species composition and structure. In ecotones, hurricane-fire interactions may produce potentially unique plant communities if pyrogenic species invade and alter the fire regimes in these areas. In my models, forests were least likely to be affected by hurricane-fire interactions. Because of the timing of fire and hurricane disturbance regimes and rapid post-hurricane litter decomposition, hurricane-generated fine fuels do not necessarily increase the likelihood of fires entering forests.

I tested hypotheses of hurricane-fire interactions in savanna-forest ecotones in an experimental study. I asked whether effects of fires were different if they were preceded by hurricane effects compared to when fires occurred alone. I used canopy disturbance and fuel addition treatments to simulate two common hurricane effects. In my study hurricane effects individually and synergistically altered the behavior of subsequent fires. Hurricane effects that

produced the hottest fires reduced stem densities and species richness of woody species in the savanna-ecotone understory. Canopy disturbance and fuel addition did not strongly influence stem densities of herbaceous species, but herb densities did increase over time. I predicted that increased abundances of herbs, coupled with decreased density of shrubs and trees, might enhance the probability and extent of future fires.

I predict that the nature of hurricane-fire interaction effects is directly related to the species composition and vertical structure of ecotones. First, interactions involved variable effects of different types of fuels. Canopy tree species present in savanna-forest ecotone include a mixture of numerous species of deciduous hardwoods and several species of pines. Deciduous fuels were affected by canopy openings more than pine fuels, resulting in interactions of open canopy and added fuel effects that increased fire temperatures. Therefore the number of interacting effects in ecotones depends in part on the overstory composition and the types of downed fuels expected from hurricanes. Second, savanna-forest ecotone vegetation is characterized by abundant shrubs and small trees in the groundcover layer. High fuel loads and fire reduced stem densities and species richness of woody plants. Thus, interacting hurricane and fire effects impacted an important component of the ecotone plant community. Interactions, if they occur, would be inherently different in either savanna or hardwood forests. The nature hurricane-fire interactions may be strongest in savanna-forest ecotone where hurricane-generated fuels include both deciduous hardwood and pine species, and where shrubs and trees susceptible to high intensity fires are abundant.

Based on my results, I predicted that hurricane-fire interactions may alter the species composition of the ecotone. High fire intensity opens space in the groundcover and may increase the likelihood of establishment of new species. If open spaces are invaded by savanna pines and

other pyrogenic species they would eventually change the fine fuel composition, resulting in more intense and more extensive fires in the ecotone. Invasion by savanna species or fire-adapted species indigenous to ecotones may produce a unique ecotone community, distinct from either adjacent savanna or hardwood forest. Such changes in the groundcover species composition may lead to long-term changes in community composition within the ecotone and across the savanna-forest landscape.

I extended my models' predictions to incorporate alternate disturbance regimes. Natural climate-driven fire regimes generated predictions different from those involving anthropogenic fire regimes. I proposed that restoration and management efforts in southeastern North American landscapes be based on presettlement, not anthropogenic patterns of disturbances.

The results of my experimental study may be used to improve restoration methods in second-growth longleaf pine savanna and other fire-dependant systems. Because natural disturbance is fundamental to the development of forest structure and function (Denslow 1980), restoration methods that are based on an ecological understanding of the process of natural disturbances will better approach restoration goals (Attiwill 1994, Beckage et al. 2005). Management techniques based on natural disturbances should result in plant communities that more closely approximate pre-settlement plant communities. An understanding of the effects of hurricane-fire interactions on savanna-forest ecotone vegetation could provide valuable insights for developing new techniques of longleaf pine savanna restoration, as well as in other frequently disturbed systems.

The occurrence and effects of hurricane-fire interactions may change over time. Climate driven changes in disturbance regimes are expected to alter the frequency and intensity of both hurricanes and fires, and thus the likelihood of hurricane-fire interactions. Human activities have

directly affected fire regimes in North America through fire suppression and alteration of fire-dependent systems (Malamud et al. 2005). In addition, through anthropogenic climate change humans have indirectly altered both hurricane and fire regimes. Intensity of hurricanes is predicted to increase over the next century with increasing global mean temperatures (Knutson and Tuleya 2004, Emanuel 2005). In contrast, as a result of predicted semi-permanent El Nino conditions associated with global warming, fire frequency is expected to decrease in the southeast (Timmermann et al. 1999, Beckage et al. 2003). These altered disturbance regimes suggest stronger hurricane-fire interaction effects. Intense hurricanes that produce extensive canopy gaps and extremely high fuel loads, coupled with longer fire return-intervals could result in more intense fires and greater effects on understory vegetation than currently predicted.

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APPENDIX A

TREE SPECIES LIST

Tree species present within 12 400m² savanna-forest ecotone plots at Camp Whispering Pines, Tangipahoa Parish, LA. Individuals marked and recorded had stems >2cm at dbh.

Species	Family
<i>Acer rubrum</i> L.	Aceraceae
<i>Carpinus caroliniana</i> Walt.	Betulaceae
<i>Carya tomentosa</i>	Juglandaceae
<i>Cornus florida</i> L.	Cornaceae
<i>Crataegus marshallii</i> Eggl.	Rosaceae
<i>Fagus grandifolia</i> Ehrh.	Fagaceae
<i>Hamamelis virginiana</i> L.	Hamamelidaceae
<i>Ilex opaca</i> Aiton	Aquifoliaceae
<i>Ilex vomitoria</i> Aiton	Aquifoliaceae
<i>Liquidambar styraciflua</i> L.	Hamamelidaceae
<i>Liriodendron tulipifera</i> L.	Magnoliaceae
<i>Magnolia grandiflora</i> L.	Magnoliaceae
<i>Magnolia virginiana</i> L.	Magnoliaceae
<i>Myrica cerifera</i> L.	Myricaceae
<i>Nyssa sylvatica</i> Marsh.	Nyssaceae
<i>Oxydendrum arboreum</i> (L.)DC.	Ericaceae
<i>Pinus echinata</i> Mill.	Pinaceae
<i>Pinus palustris</i> Mill.	Pinaceae
<i>Pinus taeda</i> L.	Pinaceae
<i>Prunus mexicana</i> S. Wats.	Rosaceae
<i>Prunus serotina</i> Ehrh.	Rosaceae
<i>Quercus alba</i> L.	Fagaceae
<i>Quercus marilandica</i> Muench.	Fagaceae
<i>Quercus nigra</i> L.	Fagaceae
<i>Quercus stellata</i> Wangenh.	Fagaceae
<i>Rhododendron canescens</i> (Michx.) Sweet	Ericaceae
<i>Sassafras albidum</i> (Nutt.) Nees	Lauraceae
<i>Symplocos tinctoria</i> (L.) L'Her.	Symplocaceae
<i>Ulmus alata</i> Michaux	Ulmaceae
<i>Vaccinium arboreum</i> Marshall	Ericaceae

APPENDIX B

CANOPY PHOTO ANALYSIS SETTINGS

Configuration settings used to process
fisheye photos taken at Camp Whispering
Pines for Gap Light Analyzer (V2)

GLA Configuration Summary

Image

Initial Cursor Point: 1.15 degrees
Projection Distortion: Polar

Site

Latitude: 30°41'0 North
Longitude: 90°29'0 East
Elevation: 35m
Slope: 0
Aspect: 0
Topographic Mask: Yes

Resolution

Solar Time Step: 2 mins
Growing Season Start: Feb. 28
Growing Season End: Dec. 15
Azimuth Regions: 36
Zenith Regions: 9

Radiation

Data Source: Modeled
Solar Constant: 1367
Output Units: Mols m-2 d-1
Cloudiness Index (kt): 0.5
BeamFraction: 0.5
SpectralFraction: 0.5
Sky Brightness Dist.: UOC Model
Clear-Sky Trans.: 0.65

VITA

Heather Alicia Passmore was born in Boulder, Colorado, on June 25, 1974, to Carol Ann and John Robert Passmore. She and Paul R. Gagnon were married in Baton Rouge, Louisiana, in November 2004. Heather grew up in Durham, North Carolina, and graduated from the Carolina Friends School in 1992. Her interest in and love for biology started in high school and was greatly inspired by her teacher Dr. Norm Budnitz. She pursued her dual interests in biology and Spanish at Earlham College, Richmond, Indiana, where she earned her Bachelor of Arts in biology with a minor in Spanish in June 1996. After college she returned to Durham to work in the community ecology laboratory of Dr. James S. Clark at Duke University. This experience inspired her to pursue her doctoral studies in plant ecology. She performed her dissertation research under the supervision of Dr. William J. Platt at Louisiana State University. In Louisiana she developed a love for the diverse and beautiful longleaf pine savanna and a passion for the study of fire effects on plant communities. After defending her dissertation she will begin a postdoctoral research position with Dr. Kyle E. Harms.