IMPACT OF INTERACTING DISTURBANCES ON LONGLEAF PINE COMMUNITIES

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IMPACT OF INTERACTING DISTURBANCES ON LONGLEAF PINE COMMUNITIES

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IMPACT OF INTERACTING DISTURBANCES ON LONGLEAF PINE COMMUNITIES

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Becky Lynne Estes, daughter of Robert and Ruth (Halfman) Estes, was born April 25, 1975, in Oxford, Alabama. She graduated from John Carroll High School in 1993. She attended University of the South and graduated with a Bachelor of Science degree in Natural Resources in May, 1997. After working for the Bureau of Land Management in Ely, Nevada as a Range Technician, she entered Graduate School at Auburn University in September, 1998. In May of 2000, she was awarded the James Floyd Goggans Forest Biology Fellowship during her duration at Auburn University. Upon completion of her Masters of Science in 2001, she worked as a Research Technician for the USDA Forest Service Southern Research Station in Auburn, AL. After two years service, she entered the PhD program in the School of Forestry and Wildlife Sciences at Auburn University under the supervision of Dr. Dean Gjerstad.

DISSERTATION ABSTRACT

IMPACT OF INTERACTING DISTURBANCES ON LONGLEAF PINE COMMUNITIES

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Doctor of Philosophy, Auburn University, December 15, 2006
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Disturbance in longleaf pine (*Pinus palustris* P. Mill.) communities alters the structure, function, and composition of the forest. Species heterogeneity and diversity were investigated at the Escambia Experimental Forest located in Brewton, AL in an attempt to document spatial effects of past disturbance. To identify the short term effects of present disturbance, the interactions of harvesting, hurricane, and salvaging on the fuel complex were examined and fire intensity was determined during prescribed fires. Finally, understory community composition was related to post-disturbance variables. The heterogeneity and diversity indices were similarly affected by fire regime in the Escambia Experimental Forest over the past 55 years. Species diversity and heterogeneity increased with a longer fire return interval and decreased with a greater number of fires, indicating that more frequent fires could result in a homogeneous landscape. Fire intensity was a major determinant of post-fire effects and was influenced by variation in the fuel complex. The prescribed burns had maximum fire temperatures at a low range of 121-148°C and a high range of 288-315°C. Variance occurred at small block sizes along transects sampled in no harvest compartments and at moderate to high block sizes along transects in harvested compartments. Variance peaks were observed at several block sizes, indicating non-stationary patterns of gaps and patches. Along transects located in the “no harvest” compartments, litter depth explained 20% of the variability in maximum fire temperature, while variability along transects located in harvested compartments were explained by 10 and 100-hr fuels (28-33%). Community composition, following the multiple disturbances, was assessed using ordination techniques. Species covers, including *Pityopsis graminifolia*, *Lespedeza procumbens*, *Solidago odora, Sasafrass albidum*, *Cornus florida, Andropogon* spp., *Aristida* spp., *Ilex glabra*, *Gaylussacia dumosa*, *Prunus serotina*, *Nyssa sylvatica*, and *Quercus falcata,* were correlated with maximum fire temperature. Other species covers, such as *Dichanthelium* spp., *Smilax* spp., *Ceanothus americanus, Carphephorus odoratissimus, Rubus* spp., and *Panicum* spp., required bare soil to re-colonize. Species heterogeneity and diversity in longleaf pine forests are influenced by numerous factors modified by decades of natural and human-caused disturbance.

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Style manual or journals used: Fire Ecology, Natural Areas Journal, Forest Ecology and Management

Computer software used: S-PLUS, S+SPATIALSTATS, SAS System for Windows 9.1, PASSAGE 1.1, PCORD 4.0, Microsoft Word 2003, Microsoft Excel 2003, and Endnote 8

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

1. GENERAL INTRODUCTION

1.1 Introduction

Disturbance impacts ecological systems on varying scales of frequency and intensity. Interaction of multiple disturbances can alter the trajectory of post-disturbance communities (Turner and Dale, 1998; Platt et al., 2002). Human-caused disturbance also affects natural communities, interacting with natural disturbance and resulting in more extreme shifts in composition, structure and function. Evaluation of disturbance is an important part of ecological research.

Overstory removal via harvesting, hurricanes, and fire are three major disturbances that alter the structure and composition of upland longleaf pine communities in the Coastal Plain. The primary goal of the Escambia Experimental Forest, located in Brewton, AL, is to manage longleaf pine (*Pinus palustris* P. Mill.) as the dominant canopy species and maintain intact native groundcover. Three experimental treatments (selection, shelterwood, and no harvest) were applied across part of the forest in a collaborative study to assess ecological impacts of the short and long term management of longleaf pine forests.

Approximately one month following the harvest, Hurricane Ivan made landfall (September 16, 2004) and was a major factor in further shaping forest structure.

Hurricanes in the Southeast are natural storm disturbances that originate in the Atlantic Ocean and travel into the Gulf of Mexico at intervals of 1 to 20 years (Batista and Platt, 2003). Hurricanes cause two major changes to forest structure: reduction of overstory cover and an increase in the fuel complex. High amounts of fuel present a unique challenge to managers who use prescribed fires to maintain longleaf pine forests. Understanding post-hurricane changes in fuel loading and fire intensity are important in planning fuelbed reduction fires.

Frequent low intensity burns are important in maintaining variable horizontal structure in fire-dependent communities such as the longleaf pine forests (Landers et al., 1995; Palik and Pederson, 1996; Carter and Foster, 2004). Fire intensity is a measure of the heat that is released during a fire expressed as the amount of fuel, the specific fuel's heat of combustion and the rate of spread (Whelan, 1995). Fire intensity is influenced by characteristics such as fuel load, type, arrangement, and moisture, as well as climate and topography (Hobbs and Atkins, 1988; Whelan, 1995; Franklin et al., 1997; Archibold et al., 1998). Variations in fire intensity influence fire severity, which alters the response of vegetation by creating structural variability and influencing succession patterns, competition, and species stability (Whelan, 1995).

Disturbance-mediated communities harbor species that are resilient to effects of multiple disturbances and in some cases depend on them to maintain populations. Hurricane-fire interactions have historically shaped longleaf pine forests and maintained the habitat necessary to foster these unique communities. This interaction coupled with human-caused disturbance may dually affect the trajectory of the post-community structure. The goal of the research in this dissertation was to explore the patterns of structure and composition that result from the multiple disturbances.

Primary objectives of this study were:

1. Quantify the heterogeneity in the understory layer of a second-growth naturally-regenerated longleaf pine forest and determine influence of past disturbance and management regimes,
2. Determine changes in spatial patterns of fuels following multiple disturbances and quantify the effects on fire intensity in prescribed fires,
3. Assess post-disturbance vegetation patterns and relate observations to disturbance and fire intensity and,
4. Document post-hurricane changes in the longleaf pine canopy.

1.2 General Outline

This dissertation explores spatial variation in longleaf pine forests and is divided into three sections (Chapters 3, 4, and 5) that address the alteration of understory and overstory structure following human-caused and natural disturbances. The spatial structure as a function of site location and scale was assessed using techniques associated with statistical spatial ecology. Results were quantifications of the heterogeneity in the second-growth, naturally-regenerated longleaf pine forest and alterations in spatial patterns following disturbance (i.e., logging, hurricane, prescribed fire and salvage operations).

The second chapter serves as an extensive literature review covering the topics in Chapters 3-5. In addition, Chapter 2 reviews the history of hurricanes in the region of the study site over the past 150 years.

Chapter 3 documents baseline species heterogeneity in the longleaf pine understory communities using the Shannon-Weiner Diversity Index (H') and the Heterogeneity Index (HI) (Collins, 1992). The HI was based on the percent dissimilarity between all combinations of species cover along the transects and indicates within-site heterogeneity (Collins, 1992). Determination of past process influence on present species heterogeneity was based on indication of disturbance history based on present environmental variables (i.e., fire return interval, fire frequency, canopy cover, and litter depth). Elucidation of present species heterogeneity based on past disturbance may provide better insight for predictive modeling.

Variations in fire intensity alter the response of vegetation creating structural variability and influencing succession patterns, competition, and species stability (Whelan, 1995). Spatial analysis may increase the understanding of small-scale impacts of fire intensity on plant communities. Chapter 4 analyzes the spatial scale of pre-burn fuel characteristics and fire intensity. Maximum fire temperature was used as a surrogate for fire intensity. Patterns were determined using spatial variance techniques, specifically Three-Term Local Block Quadrat Variance (3TTLQV), to ascertain similarities in variance (Ludwig and Reynolds, 1988; Dale, 1999). Models predicting fire temperature were developed using stepwise regression techniques to isolate predictive fuel characteristics.

Non-randomness in natural communities is more common than the occurrence of truly random distributions because the environment is made up of patchy space (Levin et al., 1993; Perry et al., 2002). To understand post-disturbance plant composition, community composition was assessed using multivariate techniques. Chapter 5 explores patterns in a post-disturbance longleaf pine understory. Canonical Correspondence Analysis (CCA) was performed to detect community structure and relate it to the post-fire environment.

Chapter 6 synthesizes the results presented in the three main chapters of the dissertation. Suggestions for future research and management implications are discussed in order to address the effects of multiple disturbances on managed longleaf pine forests.

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2. DISTURBANCE IN LONGLEAF PINE COMMUNITIES

2.1 The significance of longleaf pine communities

Longleaf pine (*Pinus palustris* P. Mill.) was historically one of the most common species encountered across the Southeast, because of its well-known ability to tolerate and even require frequent disturbance. It has an extensive natural range, encompassing areas from Southeastern Virginia to Central Florida and west into Texas, and covered approximately 25 million hectares prior to European settlement (Schwarz, 1907; Frost, 1993). Longleaf pine habitat consists of dry sandhills, fall line uplands, wet flatwoods, and savannas as well as ridgetop areas in Alabama and Georgia (Frost and Musselman, 1987; Boyer, 1990; Harcombe et al., 1993; Peet and Allard, 1993; Stout and Marion, 1993; Maceina et al., 2000; Varner et al., 2003).

The longleaf pine communities that once dominated the southeastern United States are now reduced to about 3% their original area (Frost, 1993; Peet and Allard, 1993). This decline resulted from impacts of logging, turpentining, fire suppression and exclusion, conversion to agriculture and, more recently, urban development (Frost and Musselman, 1987; Frost, 1993). The history of longleaf pine exploitation began with the extraction of resinous products to seal naval ships, often referred to as naval stores, following European settlement (Outcalt, 2000). Around the same time, removal of longleaf pine for timber increased and continued into the 1920s until most of the old-growth longleaf pine had been harvested (Wahlenberg, 1946).

The common belief at the time was that such a ubiquitous species would be successful at re-establishing itself (Wahlenberg, 1946). Unfortunately, this turned out to be incorrect since longleaf pine was unable to fully regenerate cutover sites because of its erratic seed production (Boyer, 1990; Outcalt, 2000). Longleaf pine was also slow to regenerate on many cutover areas and those seedlings that did establish were uprooted and eaten by free-ranging feral hogs (Schwarz, 1907; Campbell, 1955; Frost, 1993). Where poor quality seed trees were left, some longleaf pine stands did re-establish successfully after the first harvest, but in the mid 1940s cutting resumed in many of these areas (Campbell, 1955). Replacement of many forests with plantations of more rapid growing pines such as loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm.) was also quite prevalent (Ware et al., 1993; Means, 1997; Gilliam and Platt, 2006). Fire suppression policies that began in the 1950s also resulted in a loss of longleaf pine habitat as hardwood trees gradually replaced them (Campbell, 1955; Frost, 1993; Brockway and Lewis, 1997; Platt, 1999). Today, only 3% of the historical longleaf pine range remains and of this amount 2% has the intact understory, sparse overstory and negligible midstory that are characteristic of typical virgin old-growth longleaf pine communities (Frost, 1993).

The historic longleaf pine forests have been described as open and park-like with a unique structure dominated primarily by longleaf pine and a diverse understory (Schwarz, 1907; Wahlenberg, 1946; Gilliam and Platt, 2006). Longleaf pine communities have high biodiversity in the temperate United States containing 140 species in 1000 m^2, including a diverse array of grasses, asters, legumes, insectivorous and endemic plant species (Peet and Allard, 1993). Grasses, such as wiregrass (*Aristida* spp.) and bluestems (*Andropogon* spp.), are key to the composition of the longleaf pine understory as they provide standing fuel for regular fires (Frost et al., 1986; Haywood and Harris, 1999). Scattered hardwood trees that escape fire also occur throughout the midstory of the longleaf community (Rebertus et al., 1989a). This stratified community type reacts in different manners to the dominant modes of disturbance (fire and hurricanes), with fire occurring frequently and driving the trajectory of the understory and hurricanes occurring infrequently and impacting the overstory directly and the understory indirectly (Gilliam and Platt, 2006).

The remaining longleaf pine forests contribute significantly to the ecological integrity of the Southeast. They harbor species adapted to the presence of fire and whose populations may decline in its absence (Outcalt, 2000). Longleaf pines also contribute to the forest products industry due to its resistance to disease and its usefulness in producing a variety of products, such as pulp, saw logs, poles, and pine straw mulch to name a few (Croker, 1987). The ecological, economic, and social values of longleaf pine ecosystems have established a need for restoration and maintenance and an understanding of the community components and processes that are important for effective management (Gilliam and Platt, 2006).

2.2 Heterogeneity and species diversity

Ecological heterogeneity is effectively defined by Webster's dictionary as anything "consisting of diverse ingredients" tending towards homogeneity in its absence. Ecological heterogeneity is a consequence of minor variations in environmental characteristics, community structure and species composition (Désilets and Houle, 2005). Environmental, structural, and compositional heterogeneity are scale dependent, revealing widely different results on hierarchical levels of scale (Chaneton and Facelli, 1991; Whittaker et al., 2001). In addition to spatial heterogeneity, resources also fluctuate over time and significantly impact diversity (Farley and Fitter, 1999; Guo et al., 2004).

Environmental heterogeneity consists of different levels of resources being available at different locations (Williams et al., 1994). Structural heterogeneity is the composition of layers in a community which is apparent in the varying horizontal variation of understory plant species in the longleaf pine forest. Compositional heterogeneity is a measure of the dissimilarity in species composition from one point to another (Collins, 1992). This measurement provides a value of species heterogeneity that can be attributed to environmental variation. Compositional heterogeneity bears similarities to measurements of beta diversity that assess changes in species assemblages across landscapes. The relationship between species diversity and compositional heterogeneity is not cause and affect as heterogeneity cannot directly facilitate increased species diversity, rather it creates the necessary conditions conducive to high species diversity (Désilets and Houle, 2005). Plant species diversity fluctuates as a result of either environmental heterogeneity or resource productivity (Bakker et al., 2003). In some cases, resource productivity is more effective at determining rates of plant species diversity and therefore studies attempting to explain diversity solely as a consequence of environmental heterogeneity have seen inconclusive results (Baer et al., 2003; Désilets and Houle, 2005).

Structural heterogeneity in longleaf pine communities is evident in the understory that is composed of numerous plant populations; the longleaf pine overstory is often the only common species the sites (Neyland et al., 1998). Studies in longleaf pine forests explain the structural and compositional heterogeneity as a result of environmental heterogeneity in soil moisture and texture, topographical variation, fire frequency, canopy closure and ground disturbance (Rome, 1988; Gilliam et al., 1993; Peet and Allard, 1993; Kirkman et al., 1996; Drew et al., 1998; Rodgers and Provencher, 1999; Smith et al., 1999; Kirkman et al., 2001; Drewa et al., 2002b). These environmental factors are strongly structured by disturbance and stress and play a role in maintaining species assemblages (Collins, 1992; Collins et al., 1995; Guo et al., 2004). Ecological heterogeneity plays an important role in the longleaf pine ecosystem and focusing on its maintenance is one approach whereby managers can effectively restore and conserve this rare habitat.

2.3 Determining patterns of heterogeneity: Spatial statistics

Spatial statistics is a topic of increased interest in the field of ecology because of its ability to analyze the distribution of the environmental features (Hill, 1973). Spatial pattern explains the arrangement of organisms in space described as patch size, spacing, and density varying according to scale and intensity (Dale and MacIssac, 1989; Dale, 1999). Spatial pattern in organisms depends on factors involving morphological, environmental, and phytosociological gradients (Dale, 1999). Disturbance also plays a large role in molding spatial structure, exhibiting a circular relationship in which ecological heterogeneity facilitates disturbance and disturbance modifies the spatial structure (Dale, 1999).

Spatial heterogeneity is the norm in natural communities and forms as the result of structured and non-random events (Dale, 1999). Patches and gaps in forest canopies and shrub cover have been well documented as determining the pattern of understory recruitment (Brockway and Outcalt, 1998; Dale, 1999; McGuire et al., 2001). Fuel arrangement determines fire intensity and subsequent vegetation patterns (Franklin et al., 1997). Natural disturbance plays an important role in shaping spatial patterns. These disturbance events are a primary source of both temporal and spatial variability (Sousa, 1984). Natural disturbance regimes are becoming more heavily influenced by human activities altering the duration and intensity of disturbance (Turner and Dale, 1998). Management practices are inherently based on modifying spatial structures of vegetation to meet varying objectives. Therefore, it is important to document changes in the composition and structure of natural and managed communities to better understand spatial heterogeneity.

2.4 Disturbance in a longleaf pine forest

Disturbance is defined as any event that occurs at irregular intervals and causes structural changes with variable frequency, intensity, severity and extent (Sousa, 1984; White and Pickett, 1985; Chaneton and Facelli, 1991; Williams et al., 1994). Heterogeneity in systems determines future disturbance severity while disturbance alters the successional trajectory of communities influencing composition and structure (Risser, 1987). It is not plausible to interpret these disturbances individually as they have an interactive effect on future community outcomes (Platt et al., 2002).

The structural and compositional heterogeneity of longleaf pine communities are disturbance-mediated, with frequent low intensity surface fires and less frequent wind disturbance in the form of hurricanes. These dominant disturbances have different impacts on stand physiognomy and composition (Gilliam et al., 2006). Species composition of longleaf pine communities vary with response to the disturbance regime. Typically, shrubs and trees are less sensitive to disturbance intensity and frequency than herbaceous species, which tend to respond to changes on a smaller scale (Drewa et al., 2002b).

Various hypotheses have been proposed to explain the relationship between species diversity and disturbance. The premise behind these hypotheses may be expanded to explain the role of disturbance on patterns of community heterogeneity. In longleaf pine management, the techniques of the Most Frequent Fire Hypothesis (MFFH) were widely practiced, burning the understory as frequently as fuel allowed in an attempt to maintain species richness and composition as well as longleaf pine regeneration

(Glitzenstein et al., 2003). This fire regime created an environment that favored rhizomatous grasses over clonal shrubs and hardwood trees (Glitzenstien et al., 1995). The increased burning regime also increases mortality of juvenile longleaf pines that are not capable of growing taller than maximum flame height to escape terminal bud damage. Following the MFFH, species diversity would increase with disturbance frequency. A threshold effect may exist where additional disturbance results in little additive effect on diversity and is termed the Saturation Hypothesis (SH) (Mehlman, 1992; Beckage and Stout, 2000; Glitzenstein et al., 2003).

The Intermediate Disturbance Hypothesis (IDH) is composed of two predictions extremely relevant to fire regime: 1) high levels of diversity occur at intermediate levels of disturbance and 2) an intermediate length of time following disturbance maximizes diversity (Connell, 1978). This challenges the initial floristic composition model of succession which predicts high species diversity immediately after a disturbance as pioneer species take hold and species diversity decreases throughout seral development (Egler, 1954). At an intermediate level of disturbance, early and late successional species (r and K strategists, respectively) are able to coexist as well as species that are unable to persist at either low or high rates of disturbance (Connell, 1978). Schwilk et al. (1997) tested the IDH in South African fynbos and found it may not be applicable where fire is the main form of disturbance. Species diversity and heterogeneity in this instance were both maximized in areas that experienced a 40 year fire return interval and were lowest at high (4-6) and intermediate (15-26) fire return intervals (Schwilk et al., 1997). One challenge in validating the IDH is defining “intermediate” rate of disturbance, as the frequency of disturbance varies between community types (Glitzenstein et al., 2003).

The Frequent Fire Species Loss Hypothesis (FFSLH) has been observed in grassland habitats and contradicts other disturbance hypotheses (Collins, 1992). More frequent fire increases dominant grasses that minimize growing space for forb species, resulting in a linear decrease in plant species diversity (Collins, 1992). This hypothesis may only be applicable in systems where rhizomatous grasses are dominant. Bunch grasses, such as wiregrass and bluestems, in some longleaf pine forests do not spread as readily following fire, perhaps minimizing their impact on other plant species (Kirkman et al., 2001). Establishing the role of disturbance in shaping longleaf pine communities may be helpful in maintaining and restoring native species composition.

2.5 Frequent fire as a disturbance in the longleaf pine community

Frequent low intensity fires, occurring every 1-3 years, are important in maintaining variable horizontal structure in fire-dependent communities such as longleaf pine ecosystems (Heyward, 1939; Landers et al., 1995; Palik and Pederson, 1996; Carter and Foster, 2004). Historically, more than 90 percent of longleaf pine forests were burned over a 4 year interval by a number of sources: 1) naturally occurring lightning ignited fires, 2) fires set by Native Americans to improve hunting, 3) controlled fire used to protect resources in the naval industry and 4) controlled fires used by settlers to reduce fire hazard (Wahlenberg, 1946; Campbell, 1955; Komarek, 1977). A decrease in the spread of natural fires due to the wildland-urban interface, landscape features acting as firebreaks and region wide habitat fragmentation has prompted a reliance on prescribed fires (Simberloff, 1993; Stanturf et al., 2002).

Some have hypothesized that longleaf pines are self-perpetuating by producing large pyrogenic needles that facilitate fire (Grace and Platt, 1995). Longleaf pine and associated forb and grass species (i.e., *Aristida* spp., wiregrass, and *Andropogon* spp., bunchgrasses) are extremely resilient to the historically occurring surface fires (Abrahamson and Hartnett, 1990). Fires allow these species to persist and flourish in this disturbance prone environment (Landers et al., 1995). Longleaf pines have adapted to frequent fire in a number of ways: 1) regenerating in relatively open patches characteristically low in adult tree density, 2) remaining in the grass stage to protect the terminal bud, 3) bolting several feet to escape the flame lengths common in surface fires, 4) natural pruning of bottom limbs to reduce ladder fuels and 5) thick bark to protect vascular cambium from lethal heat (Chapman, 1932; Grace and Platt, 1995; Abrahamson and Abrahamson, 1996). Fire suppression was a common practice between 1920 and 1980 and had negative consequences for maintenance of longleaf pine forests (Brockway and Lewis, 1997). Unburned longleaf pine stands appear healthy as overstory trees tend to survive for decades, but changes in the understory occur quickly. As time since fire lengthens, litter layer and shrub cover increase reducing access to mineral soil and increasing light competition: both important factors for newly regenerated seedlings (Means and Grow, 1985; Barnett, 1999).

Fire intensity is a measure of the heat that is released during a fire expressed as the amount of fuel, the specific fuel’s heat of combustion and the rate of spread (Whelan, 1995). Fire intensity is influenced by characteristics such as fuel load, type, arrangement, and moisture, as well as climate, and topography (Hobbs and Atkins, 1988; Whelan, 1995; Franklin et al., 1997; Archibold et al., 1998). Fire behavior becomes more consistent as fuel loads increase resulting in a more intense and homogeneous fire. The post-burn landscape supports decreased heterogeneity and may be unsuitable for certain species (Hobbs and Atkins, 1988; Franklin et al., 1997). Natural and imposed disturbance regimes impact the accumulation and arrangement of fuel across landscapes. Natural disturbances such as hurricanes distribute heavy fuel loads (Myers and van Lear, 1998). Timber harvesting can also increase fuel loads, as well as impact fuel continuity at different spatial scales. Past management practices play an important role in determining fire intensity (Franklin et al., 1997). Spatial patterning of fuel components could provide useful information to managers, helping them to understand the impacts on fire intensity and subsequent recovery.

Vegetation composition impacts fire intensity and understanding the spatial arrangement is important to maintain suitable habitats (Breininger et al., 2002). Fire does not burn continuously across the landscape, rather it creates patches due to variation in fuel loadings, moisture, weather conditions, slope, and residence time (Williams et al., 1994). These patches vary spatially and create microsites suitable for vegetation recovery (Brewer et al., 1996). The patchiness of a fire is often a goal of managers and spatial analysis provides a method whereby adequate variation can be predicted and utilized (Williams et al., 1994; Kennard and Outcalt, 2006). Vegetation types vary in flammability and impact fire continuity (Williams et al., 1994). Following a fire, resource distribution is patchy influencing vegetation patterns as a result in variation in ash depth, nutrition, soil heating, and soil micro-flora (Williams et al., 1994; Whelan, 1995). Fire severity alters the response of vegetation creating variable structure and influencing succession patterns, competition, and species stability (Whelan, 1995; Kennard et al., 2002). Response of vegetation to fire depends on the intensity of the fire as well as species structure and characteristics. Post-fire survival of an organism depends on the morphological and structural traits of the specific species, resulting in variable spatial patterns (Whelan, 1995).

Fire temperature is used as an indicator of fire intensity and allows researchers to identify the impacts at a specific location. Variable fire temperature can have dramatic effects on communities, influencing growth and survival (Rebertus et al., 1989b). Heterogeneous fire temperature influences patterns of germination, seed-release, and sprouting (Hobbs and Atkins, 1988; Franklin et al., 1997). Some species rely on fire to scarify their seeds, while others re-sprout prolifically (Olson and Platt, 1995; Menges and Hawkes, 1998; Drewa et al., 2002a). Fire also stimulates flowering of some plants, increasing recruitment (Brewer and Platt, 1994; Brewer et al., 1996; Kirkman et al., 1998).

The effects of fire on vegetation are patchy, creating increased light, nutrients and decreased litter as well as causing shoot dieback (McConnell and Menges, 2002). Various plants react differently to these changes in the microenvironment. Low severity fires increase nutrition and herbaceous growth while subsurface mortality occurs in high severity fires (Neary et al., 1999). Other species have developed serotinous cones, maintaining the seed bank in the cone, protecting them from high-intensity fires (Ne'eman et al., 1999). Seedling growth in some species is affected by the location of coarse woody debris that increases fire residence time creating access to mineral soil

(Ne'eman et al., 1992). Fuel addition in frequently burned longleaf pine communities increases fire intensity and potentially damages shrubs, particularly sprouting capability and regeneration (Thaxton, 2003; Thaxton and Platt, 2006).

Patterns of fire spread are very important to determine post-fire vegetation composition and structure (Rebertus et al., 1989b). Prescribed burns need to be conducted on contiguous natural units including wetland areas to mimic a naturally ignited fire and maintain ecotones and community heterogeneity (Frost et al., 1986). Longleaf pine communities are fire dependent, and not only does longleaf pine regeneration depend on frequent fires, but the vast majority of understory species do as well. Longleaf pine seeds cannot adequately establish unless a fire has provided access to the mineral soil and reduced competition from shrubs (Kush and Meldahl, 2000). Fire exclusion in longleaf pines increases the structural heterogeneity and the litter layer depth and changes species composition, eventually succeeding to a hardwood dominated forest, culminating in crown closure and a decrease in understory species richness (Frost et al., 1986; Bridges and Orzell, 1989; Kush and Meldahl, 2000).

Despite knowing fire is essential in longleaf pine forests, the optimal frequency and season of burning is still debated (White et al., 1990; Boyer, 1994; Haywood et al., 1995; Haywood et al., 2001; Beckage et al., 2005). In some cases, fire season and frequency as well as intensity were found not to substantially affect the population dynamics of longleaf pines (Glitzenstein et al., 1995). However, understory species have variable responses to fire frequency and intensity (Plocher, 1999; Glitzenstein et al., 2003). Most scientists agree that varying the fire regime is beneficial for a number of species, as this maximizes landscape heterogeneity (Gilliam and Christensen, 1986; Hermann et al., 1998; Hiers et al., 2000).

2.6 Overstory disturbance in longleaf pine forests

Disturbance in the form of forest fires and hurricanes is common throughout the landscape. Longleaf pine forests have adapted to disturbance making them both fire-resistant and hurricane-resilient (Platt et al., 2002; Batista and Platt, 2003). The last hurricane to affect the Escambia Experimental Forest was Hurricane Opal in 1995 (NOAA, 2006) (Figure 2.1). However, the 2004 and 2005 hurricane seasons were active in the Gulf of Mexico, producing a number of storms that made landfall in the Southeast, altering the spatial patterns of the longleaf pine forests. Understanding the frequency and intensity of Atlantic hurricanes is important to predicting future impacts on longleaf pine communities.

Hurricanes have been important in shaping the Gulf coastal region over several thousand years, although our recorded knowledge of hurricane occurrence is limited to the past 150 years (Liu and Fearn, 1993; Liu and Fearn, 2000). According to Liu and Fearn (1993; 2000), the Gulf Florida and Alabama coast has a 0.34 – 0.36 % annual probability of being struck by a Category 4 or 5 hurricane in the next century.

Considering records through the 2006 hurricane season, only one Category 4 hurricane (Frederic) made landfall in close proximity to the Escambia Experimental Forest (Liu and Fearn, 1993) (Figure 2.1, Table 2.1). Other significant storms have impacted the region (1852, 1860, 1882, 1894, 1926, 1975, and 1995), all rated category 3 at landfall on the Saffir-Simpson scale (NOAA, 2006) (Table 2.1). Another Category 3 storm, occurring in 1916, (Notnamed 5) passed directly over the Escambia Experimental Forest (NOAA, 2006) (Figure 2.1). A number of other Atlantic hurricanes made landfall in the Southeast in the past two seasons (i.e., Charley, Frances, Ivan, Jeanne, Dennis), causing over a billion dollars in timber losses and millions more in personal property loss (NOAA, 2006). Ivan and Dennis had the most significant impact on the longleaf pine communities in the Escambia Experimental Forest. Both were rated a Category 3 upon approaching Brewton, AL with winds gusting up to 80 kph and rainfall totaling 18 cm during Ivan and winds reaching 61 kph and rainfall totaling 8 cm during Dennis (Table 2.1). In 2005, other devastating storms (Katrina and Rita) made landfall to the west of Alabama in Mississippi and Louisiana causing significant damage across other forested landscapes. Other hurricanes that have had severe consequences for the forestry industry occurred on the Atlantic coast. Hurricane Hugo, a Category 4 hurricane, struck the South Carolina coast in 1989 causing the greatest blowdown in US history and resulting in timber losses totaling billions of dollars (Saveland and Wade, 1991).

Hurricanes are complex occurrences that form as a result of meteorological and physiographic interactions (Boose et al., 1994). Hurricanes form over the ocean when water temperatures are at least 26°C, but trajectory and intensity depends on a host of factors (Lugo, 2000). Hurricane intensity and frequency are determined by the North Atlantic Oscillation (NAO) while the El Niño Southern Oscillation (ENSO) guides the dominant ocean currents and therefore the trajectory of the hurricane (Beckage et al., 2006). The ENSO is composed of two well known seasons: El Niño and La Niña, which occur at warm and cool ocean temperatures, respectively. These oscillations have occurred in the past at 3-7 year intervals (Tudhope et al., 2001; Beckage et al., 2003). The ENSO determines the frequency and intensity of Atlantic hurricanes with more frequent and intense hurricanes occurring during cooler ocean temperatures in La Niña (Webster et al., 2005; Beckage et al., 2006; Hoyos et al., 2006). The North Atlantic Oscillation (NAO) influences the trajectory of developed hurricanes with a negative oscillation increasing the westerly track and a positive increasing the northerly track (Beckage et al., 2006). In years when La Niña is dominant and the NAO is negative, the probability of frequent high intensity storms that track into the west (Gulf Coast regions) and make landfall are significant (Beckage et al., 2006).

Movement of hurricanes across land masses is non-uniform due to interactions with topography and local climate, resulting in post-disturbance landscape heterogeneity (Boose et al., 1994). Major hurricane effects are associated with high winds and storm surge after landfall as well as substantial inland flooding as a result of heavy precipitation and tornadoes associated with the storm front (Lugo, 2000).

The complex effects of hurricanes produce variable impact on structure and composition of forested communities. There is often an immediate impact on the carbon balance as live woody components become coarse woody debris (Lugo, 2000; Beckage et al., 2006). Tree growth is slowed and regeneration is initially reduced but increases quickly after disturbance when nutrient cycling is accelerated (Lugo et al., 1983; Batista and Platt, 2003). Canopy gaps form as a result of windfall following hurricanes. These gaps are characterized with large quantities of biomass with intact trees surrounding them (Mascaro et al., 2005). Some tree species persist in disturbance prone climates, providing them an advantage over more sensitive species (Batista and Platt, 2003; Platt and Connell, 2003). Longleaf pines are resilient to hurricane disturbance as adult trees are typically resistant to wind damage and there is a flush of recruitment, growth, and survival (Batista and Platt, 2003).

Fire and hurricanes have obvious interacting effects as hurricanes contribute to fuel loads, thereby increasing fire intensity and altering forest structure (Myers et al., 1993; Myers and van Lear, 1998; Passmore, 2005). As an example, Hurricane Hugo (1989) drastically increased fuel loads along the South Carolina coast (Saveland and Wade, 1991). This storm occurred during a La Niña season that is also characterized by less annual rainfall creating drought like conditions (Beckage et al., 2006). The drought coupled with the increase in fuel loads predisposed the landscape to a high probability of fire ignition and intensity (Beckage et al., 2003).

The interaction between hurricanes and fire has been well established but little has been done to determine the impact of fire regime on the effects of hurricanes across the landscape. This is an important consideration as the majority of disturbance in forest stands is anthropogenic (i.e., prescribed fire, overstory removal, artificial regeneration and more). Changes to fire regime such as shifting prescribed burns to the dormant season instead of the naturally occurring growing season may influence overstory mortality following hurricanes (Platt et al., 2002). Maintaining the natural fire regime may help to maintain healthy trees more adjusted to their growing space (Platt et al., 2002).

Before 2004, no recorded Category 4 or 5 hurricanes had made landfall directly south of Brewton, AL and a handful of hurricanes rated Category 3 had come close to the

Escambia Experimental Forest (Liu and Fearn, 2000). It is probable that a higher magnitude storm could do greater damage to this area and to other communities where longleaf pines are dominant. Hurricanes potentially threaten the health and integrity of longleaf pine forests by increasing fuel loads leading to excessive fire hazard (Jose, 2005). Salvage logging operations often a necessity, following a large-scale disturbance, to remove dangerously, high fuel loads could potentially impact the understory causing excessive ground disturbance (Cooper-Ellis et al., 1999; Jose, 2005). Salvage logging could have lasting negative consequences, since downed trees play a critical role as ecological legacies in forest recovery (Cooper-Ellis et al., 1999; Mitchell et al., 2002). Reduction in tree density following a high-intensity hurricane may eliminate the longleaf pine seed source, resulting in a need for costly artificial regeneration. Insect damage is another concern, in the months following a hurricane, as attack on weakened trees increases mortality (Leininger et al., 1997). The landowner benefits in the short term following a hurricane, but is hard hit financially in the long term due to decreases in volume production (Sheffield and Thompson, 1996).

Anthropogenic changes to climate may alter disturbance regimes including hurricane frequency and intensity (Dale et al., 2001). It has been surmised that a gradual increase in sea surface temperature will impact the intensity of hurricanes, primarily resulting in a greater occurrence of those rated Category 4 and 5 (Hoyos et al., 2006). Contradicting anecdotal evidence indicates a decrease in hurricane frequency as the climate temperature increases and hurricanes are isolated to areas north of the Gulf (Platt et al., 2002). This has two potentially negative consequences for longleaf pines, increased frequency and intensity of disturbance will result in less available longleaf pine seed source and a decrease in disturbances may result in an increase in tree density and a shift towards a closed forest (Grace and Platt, 1995; Platt et al., 2002; Platt and Connell, 2003). All of these changes will influence longleaf pine distribution and species abundance, inherently changing the composition of present day communities (Beckage et al., 2006).

Hurricane disturbance is often difficult to study due to its unpredictable nature (Myers and van Lear, 1998). However, understanding disturbance-mediated systems requires a full knowledge of hurricane impacts. Access to this type of data may aid in future prediction of forest response to multiple natural disturbances (Boose et al., 1994).

2.7 Overstory removal in longleaf pine forests

The overstory structure of longleaf pine forests significantly affects understory community composition. Increased light availability following decreased canopy closure in the overstory, as well as a reduction in oak and shrub midstory results in a more diverse herbaceous community (Harrington and Edwards, 1999). The pros and cons of maintaining the overstory as an even- or uneven-aged stand are still debated, although there appears to be little difference in the production of longleaf pine volume (Croker and Boyer, 1975; Farrar and Boyer, 1991). Understanding the impact of canopy cover removal is important in management of a stand for multiple benefits.

Uneven-aged management focuses on gap-based regeneration emphasizing small- to large-scale tree-fall disturbance. Gaps have increased regeneration because they have reduced aboveground and belowground competition and provide increased access to resources such as water, nutrients and light (Palik et al., 1997; Brockway and Outcalt, 1998). This is beneficial in longleaf pine forests where adequate recruitment can be maximized in these openings. Often recruitment in gaps is extremely variable with successful regeneration clumping in the center of small gaps, because the periphery is inhospitable for growth (Coates and Burton, 1997; Palik et al., 1997). Research has established a minimum gap size of between 0.10 - 0.14 ha for successful longleaf pine regeneration (McGuire et al., 2001).

High forest cover retention and limited disruption from harvest in selection systems (uneven-aged) allows for a continuity of regeneration and maintenance of habitat for rare species such as red-cockaded woodpecker, gopher tortoise, and indigo snake (Farrar and Boyer, 1991). Selection systems, however, may not benefit all species and often lengthen longleaf pine growing time due to upper canopy competition (Farrar and Boyer, 1991). Focusing on silviculture treatments, such as group selection that creates adequate gap sizes and reduces competition by allowing sufficient light to reach the forest floor, may be essential to adequate management (Palik and Pregitzer, 1995; Palik et al., 1997; Brockway and Outcalt, 1998; Gagnon et al., 2003).

Even-aged management focuses on maintaining one age class through time. The principal method used in longleaf pine management is the shelterwood that creates large gaps for longleaf pine regeneration. Shelterwood has been touted as a reliable and low cost method to manage regeneration (Boyer, 1979). Two modifications are employed in the shelterwood method: irregular retains residual trees until the next harvest and uniform shelterwood removes the residual trees following successful establishment. The shelterwood method with its wide spacing may benefit rare wildlife such as red cockaded woodpecker (Hedrick et al., 1998). Major disadvantages of even-aged silviculture are the lack of continuous overstory cover that decreases structural diversity and an increase ground disturbance that is often harmful to native understory species.

Overstory mortality in longleaf pine forests, resulting from lightning strikes, fire injury, suppression, windthrow, and harvesting, maintains structurally diverse stands creating habitat for understory plants and animals (Palik and Pederson 1996). Fire injury rarely causes overstory tree mortality except in high intensity burns that can cause extensive crown scorch (Boyer, 1987; Waldrop et al., 1987). Lightning-strike mortality is most common on xeric sandhill longleaf pine sites and targets mature longleaf pine trees acting as a "thin from above" (Palik and Pederson, 1996). Suppression mortality is observed at high tree density and is more readily found on fertile mesic longleaf pine sites (Palik and Pederson, 1996). Windthrow mortality, primarily resulting from hurricanes or tornadoes, can cause extreme canopy structure shifts, often removing large areas of dominant trees (Glitzenstein et al., 1986; Platt et al., 1988).

Mortality of mature longleaf pines has a significant impact on gap sizes that can limit longleaf pine regeneration (Palik et al., 1997). Small scale (1-2 trees) gaps as a result of natural disturbance occur frequently, resulting in slow rates of canopy turnover (>263 years) while infrequent large-scale disturbance can cause complete canopy turnover (Platt et al., 1988; Palik and Pederson, 1996). Understanding the natural mortality in longleaf pine forests can provide a better understanding of stand dynamics and provide a guide for silviculture management.

Silviculture that mimics natural disturbance creates variation in pattern and process necessary to maintain the complexity of the forest (Mitchell et al., 2002). Longleaf pine forests are adapted to natural disturbance such as hurricanes that create a variable canopy suitable to successful regeneration (Palik and Pederson, 1996). Silvicultural techniques can mimic natural disturbance and create gaps surrounded by cone producing trees to facilitate adequate seed catch and establishment (Palik and Pederson, 1996). Sustaining a continuous overstory also allows the buildup of pine needles necessary to fuel the frequent surface fires needed to maintain community structure.

A number of silviculture methods attempt to mimic natural disturbance regimes while others maximize tree growing space: all of them have advantages and disadvantages dependent on stand goals (Farrar and Boyer, 1991). The Stoddard/Neel approach is a variation of the single-tree selection method of regeneration. It retains high quality trees on a site thereby a continuous canopy cover and heterogeneous understory are maintained (Moser et al., 2002). This method relies on frequent prescribed fire to reduce competition and maintain a native groundcover. The group selection method (with BDq volume regulation) focuses on creating gaps suitable for longleaf pine regeneration (Farrar, 1996). This approach also maintains adequate overstory cover throughout the stand life cycle. The BDq technique is often difficult to implement because it requires an extensive pre-harvest inventory and presents few guidelines for actual tree marking. Similar to the Stoddard/Neel Method the understory is maintained by frequent surface fire.

Differences between natural disturbance and regeneration methods are the degree of ground disturbance, amount of residual fuels left on site, and partiality to the commercial species. Of these, site preparation is used frequently by industrial forestry and is applied as either herbicides, mechanical, prescribed fire, or a combination of the methods (Abrahamson and Hartnett, 1990). Mechanical site preparation (i.e., chopping, disking, and bedding) used to reduce hardwood and shrubby competition can displace certain understory species and cause regeneration mortality (Noss, 1989; Abrahamson and Hartnett, 1990; Hedman et al., 2000; Carter and Foster, 2004). Mechanical site preparation decreases wiregrass composition due to root disturbance, while increases in other grasses such as *Panicum* spp. and *Andropogon* spp. are noted (Campbell, 1955; Moore et al., 1982; Swindel et al., 1983; Outcalt, 1992). Timber harvesting also creates variable conditions across a site due to skid trails, landings, and roads for site access. The intensity of the harvest is a function of the number of trees removed and weather conditions that can impact the amount of disturbance on a site. Harvesting causes changes in the fuel complex: 1) fuel loads are altered and often increased as logging slash remains behind following a harvest, 2) litter is reduced or scattered causing discontinuity and 3) bare soil is exposed (Wood et al., 1989; Robichaud and Miller, 1999). These changes in the fuel complex impact fire spread and intensity during a prescribed burn.

The use of fire in silviculture has been well documented to reduce competition prior to regeneration and to maintain native species diversity (Outcalt, 1992). Site preparation fires and slash fires can be more intense than the ground fires common in longleaf forests and therefore can have a greater impact on species diversity (Vose and Allen, 1988; Carter and Foster, 2004).

The observation of pattern in the field of forestry is very important as overstory tree arrangement impacts recruitment and competition in the understory (Matern, 1986). Determining spatial pattern in forest management decisions is critical when meeting objectives (i.e., single tree selection, group selection, and shelterwood) (Kimmins, 1997).

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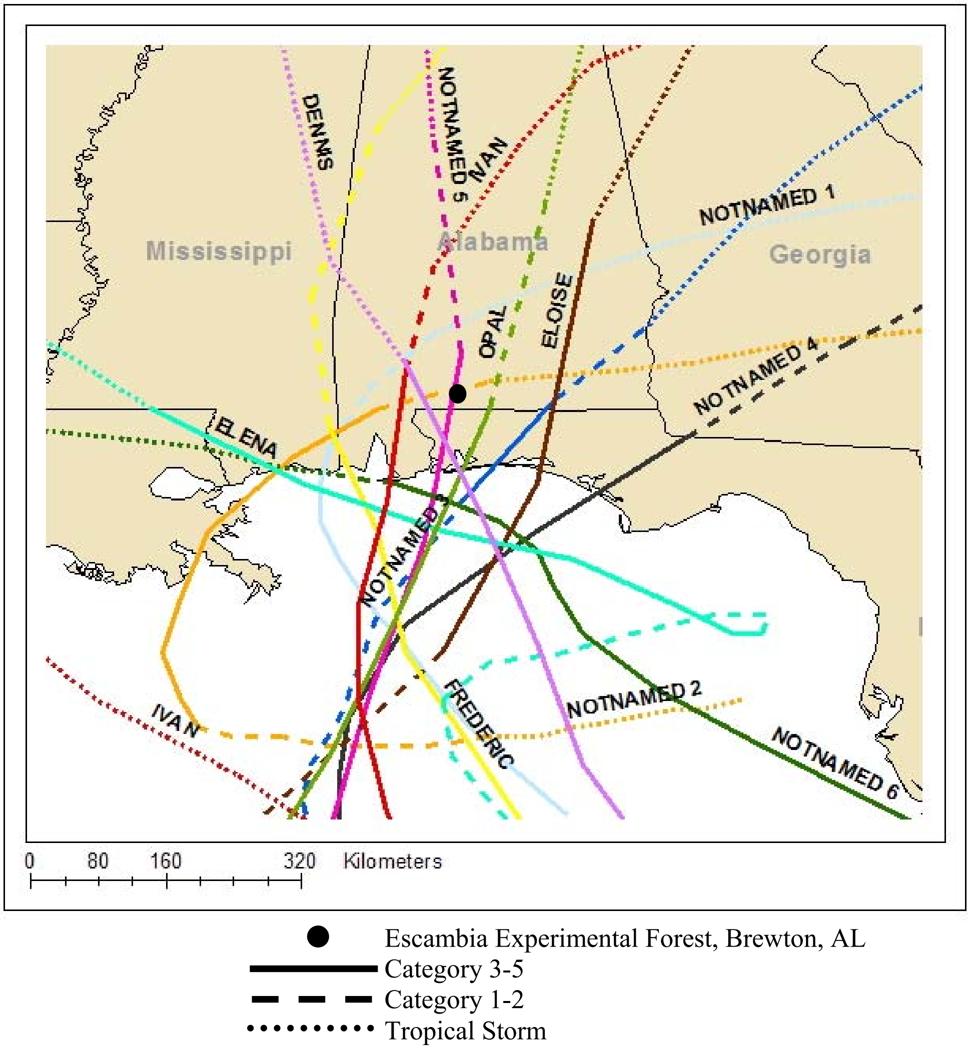
Table 2.1 Records of hurricanes in a 100 km radius of the Escambia Experimental Forest that exceeded a Category 2 at landfall on the Saffir-Simpson scale (NOAA, 2006).

Year	**Month**	**Day**	**Name**	**Windspeed at Landfall (KPH)**	**Pressure at Landfall (MB)**	**Category at Landfall**
1852	8	26	NOTNAMED 1	184	n/a	3
1860	8	12	NOTNAMED 2	184	n/a	3
1882	9	10	NOTNAMED 3	184	n/a	3
1894	10	8	NOTNAMED 4	193	n/a	3
1916	10	18	NOTNAMED 5	193	n/a	3
1926	9	20	NOTNAMED 6	202	n/a	3
1975	9	23	ELOISE	193	958	3
1979	9	13	FREDERIC	212	946	4
1985	9	2	ELENA	202	953	3
1995	10	4	OPAL	202	938	3
2004	9	16	IVAN	202	931	3
2005	7	10	DENNIS	202	942	3

Figure 2.1 Occurrence of hurricanes in a 100 km radius of the Escambia Experimental Forest, Brewton, AL, USA. Additional environmental information is available in Table 2.1 (NOAA, 2006).



3 ASSESSING HETEROGENEITY AND DIVERSITY IN THE UNDERSTORY OF A LONGLEAF PINE FOREST

3.1 Abstract

The longleaf pine (*Pinus palustris* P. Mill.) canopy structure and function, maintained by natural disturbance maintains the heterogeneous understory that harbors a variety of plant species. Species composition and heterogeneity were investigated at the Escambia Experimental Forest located in Brewton, AL to explore spatial effects of past disturbance. Canopy cover, community composition, and litter depth were determined the summer of 2004 and fire frequency data were calculated over the past 55 years. Community composition data were used to compute the Heterogeneity Index (HI) that was calculated as a Percent Dissimilarity (PD) by comparing species composition along a 200-m transect. Species diversity was also calculated with the Shannon-Weiner Diversity Index. The objective was to determine if the environmental predictors had any relationship with the heterogeneity or the diversity index. The HI was lowest in stands with low canopy cover, basal area, and litter depth and higher with increased canopy cover, indicating that a spatially variable overstory enriched habitat heterogeneity. There was a canopy cover threshold where HI decreased possibly due to low light availability. Diversity was maximized at intermediate levels of canopy cover, possibly supporting the Intermediate Disturbance Hypothesis. Increased litter depth resulted in higher rates of HI but lower rates of diversity. Based on other studies and the results here, heterogeneity may decrease as litter becomes deeper and the forest floor becomes less variable. The heterogeneity and diversity indices were similarly affected by the fire regime in the Escambia Experimental Forest in the past 55 years. The HI increased with a longer FRI and decreased with a greater number of fires indicating that more frequent fires could result in a homogeneous landscape. Species diversity also increased as FRI lengthened with the exception of T14 where high levels of diversity were observed at the highest FRI. Heterogeneity and species diversity in longleaf pine communities are influenced by a number of environmental variables and determining these predictors may assist in future management decisions.

Index terms: longleaf pine, *Pinus palustris* P. Mill., heterogeneity, species diversity, fire return interval, prescribed fire

3.2 Introduction

Longleaf pine forests have been described as one of the most diverse ecosystems in the temperate United States, consisting of an overstory dominated by longleaf pine (*Pinus palustris* P. Mill.) and a co-dominant scrub oak (*Quercus* spp.) midstory (Wahlenberg, 1946; Hardin and White, 1989). The structure and function of longleaf pine forests maintains high diversity and heterogeneity in the understory (Brockway and Outcalt, 1998). Species counts in mesic and mountain longleaf pine forests document up to 140 species in 1000 m^2, consisting of a diverse array of grasses, asters, legumes, insectivorous and endemic plant species (Peet and Allard, 1993; Varner III et al., 2003). Grasses, such as wiregrass (*Aristida* spp.) and bluestems (*Andropogon* spp.), are key to the composition of the longleaf pine understory as they provide standing fuel for regular fires (Frost et al., 1986; Haywood and Harris, 1999). The diversity and heterogeneity of the herbaceous understory support a variety of habitats suitable for animal species, some of which rely solely on the unique longleaf pine community (Hedrick et al., 1998; Hermann et al., 1998). Recent loss due to land conversion, fire suppression, and fragmentation has reduced acreage to 3% of its original area (Means and Grow, 1985; Hardin and White, 1989; Brockway and Lewis, 1997).

In ecological terms, heterogeneity is an uneven distribution of the biotic and abiotic components of an ecosystem (Wijesinghe and Hutchings, 1997). Environmental, structural, and compositional heterogeneity are three types of heterogeneity present in the longleaf pine forests. Heterogeneity is scale dependent, revealing widely different results on hierarchical levels of scale (Chaneton and Facelli, 1991; Whittaker et al., 2001). In addition to spatial heterogeneity, resources also fluctuate over time and significantly impact diversity (Farley and Fitter, 1999; Guo et al., 2004).

Heterogeneity consists of both contrast, defined as the degree of dissimilarity in species composition from one point to another, and scale, referring to the actual size of the varying patches that make up a landscape (Collins, 1992; Wijesinghe and Hutchings, 1997). Heterogeneity is common in natural communities and is a result of structured and non-random disturbance events (Sousa, 1984). It can also be attributed to variation in the abiotic environment, such as soil characteristics or light availability, but is also a consequence of multi-species interactions (Galiano, 1983; Wijesinghe and Hutchings, 1997). In turn, heterogeneity impacts succession, stability, and competition (Dale, 1999).

The relationship between species diversity and heterogeneity has only been partially explored in the longleaf pine habitat. Species diversity and heterogeneity increased in mesic flatwood sites that were also high in productivity (Legendre, 1993; Kirkman et al., 2001). These conclusions insinuate that compositional homogeneity reduces diversity making sites of regeneration no different from another decreasing the accessibility for specialized species to compete (Legendre and Legendre, 1998). Increased heterogeneity may also be an artifact of the infrequent occurrence of rare species that inflate the dissimilarity index (Kirkman et al., 2001).

The longleaf pine forest have been described as heterogeneous and composed of several understory plant communities, with longleaf pines often being the only species the sites have in common (Neyland et al., 1998). Studies explain this heterogeneity as a result of minor variations in soil moisture and texture, topographical gradations, fire frequency and intensity, canopy closure and soil alteration (Rome, 1988; Gilliam et al., 1993; Peet and Allard, 1993; Kirkman et al., 1996; Drew et al., 1998; Rodgers and Provencher, 1999; Smith et al., 1999; Drewa et al., 2002).

Disturbance is defined as an event varying in frequency, intensity, severity and extent that occurs at irregular intervals resulting in community change (Sousa, 1984; Williams et al., 1994). Heterogeneity in systems determines future disturbance severity while disturbance alters the successional trajectory of communities influencing compositional and structural heterogeneity (Risser, 1987).

The structural and compositional heterogeneity of longleaf pine ecosystems is mediated by disturbance, characterized by frequent low intensity surface fires, isolated wind-throw events, as well as infrequent wind disturbance in the form of hurricanes. These dominant disturbances have different impacts on stand physiognomy and composition (Gilliam et al., 2006). Plant species composition in longleaf pine communities varies with response to the disturbance regime. Typically, shrubs and trees are less sensitive to disturbance intensity and frequency than herbaceous species, which tend to respond to changes on a smaller scale (Drewa et al., 2002). The variable community facilitates increased species diversity by creating suitable habitat (Collins, 1992; Collins et al., 1995).

Some studies have attempted to quantify the effects of disturbance on spatial and temporal heterogeneity (Collins, 1992; Kirkman et al., 2001). Various hypotheses have been proposed to explain the relationship between species diversity and disturbance (Figure 3.1). The ideas behind these hypotheses may be expanded to explain the influence of disturbance on heterogeneity and vice versa. In longleaf pine management, the techniques of the Most Frequent Fire Hypothesis (MFFH) were widely practiced, burning the understory as frequently as fuel allowed in an attempt to maintain species richness and composition as well as longleaf pine regeneration (Glitzenstein et al., 2003). This fire regime favored the presence of rhizomatous grasses over clonal shrubs and hardwood trees (Glitzenstien et al., 1995). This burning regime can also increase mortality of juvenile longleaf pines that are not capable of growing taller than the maximum flame height to escape terminal bud damage. Following the MFFH, species diversity would increase with disturbance frequency. A threshold effect may exist where additional disturbance results in little additive effect on diversity and is termed the Saturation Hypothesis (SH) (Mehlman, 1992; Beckage and Stout, 2000; Glitzenstein et al., 2003).

The Intermediate Disturbance Hypothesis (IDH) is composed of two predictions extremely relevant to fire regime: 1) high levels of diversity occur at intermediate levels of disturbance and 2) an intermediate length of time following disturbance maximizes diversity (Connell, 1978). This challenges the initial floristic composition model of succession which predicts high species diversity immediately after a disturbance as pioneer species take hold and species diversity decreases throughout seral development (Egler, 1954). At an intermediate level of disturbance, early and late successional species (r and K strategists, respectively) are able to coexist as well as species that are unable to persist at either low or high rates of disturbance (Connell, 1978). Schwilk et al. (1997) tested the IDH in South African fynbos and found it may not be applicable where fire is the main form of disturbance. Species diversity and heterogeneity in this instance were both maximized in areas that experienced a 40 year fire return interval and were lowest at high (4-6) and intermediate (15-26) fire return intervals (Schwilk et al., 1997). One challenge in validating the IDH is defining “intermediate” rate of disturbance, as the frequency of disturbance varies between community types (Glitzenstein et al., 2003).

The Frequent Fire Species Loss Hypothesis (FFSLH) has been observed in grassland habitats and contradicts other disturbance hypotheses (Collins, 1992). More frequent fire increases dominant grasses that minimize growing space for forb species, resulting in a linear decrease in plant species diversity (Collins, 1992). This hypothesis may only be applicable in systems where rhizomatous grasses are dominant. Bunch grasses, such as wiregrass and bluestems, in some longleaf pine forests do not spread as readily following fire, perhaps minimizing their impact on other plant species (Kirkman et al., 2001). Establishing the role of disturbance in shaping longleaf pine communities may be helpful in maintaining and restoring native species composition.

In order to observe patterns of heterogeneity and diversity across the Escambia Experimental Forest, species composition and environmental variables were measured. This study observed patterns of diversity and heterogeneity in response to disturbance, both natural and past management practices. Specific questions were: (1) Do disturbance hypotheses that predict patterns of species diversity also explain heterogeneity? (2) How are species diversity and heterogeneity affected by past fire frequency and overstory disturbance? and (3) Does composition based on growth form impact species diversity and heterogeneity?

3.3 Study Area

The Escambia Experimental Forest (EEF) (31° 01’ N, 87° 04’ W) is located ten kilometers south of Brewton, Alabama and consists of 1,214 hectares of second-growth longleaf pine (Figure 3.2). The EEF was established in 1947 and is managed by the USDA Forest Service Southern Research Station through a 99-year lease with the T.R. Miller Company of Brewton, AL. The EEF was established to research the management of longleaf pine from regeneration to maturity.

The EEF is located within the upper coastal plain in south central Escambia County. The climate is subtropical with abundant annual precipitation arriving primarily during the long growing season occurring from April to October. Mean average temperatures range from 16 to 33°C in spring and summer with the warmest months in July and August and the coldest ranging from 5 to 20° C (Alabama Cooperative Extension Agency, 2006). Predominant soils are in the Troup series which are typically coarse sands, silts and clays that are low in organic matter and nutrients and have average water holding capacity. Surface slopes range from 5-15% with numerous drainages across the landscape (Mattox, 1975).

The dominant tree species on 80% of the EEF is second-growth longleaf pine that was naturally established from the 1958 seed crop (Boyer and Miller, 1994). The remaining 20% of the site is in pine-hardwood bottoms. In the longleaf pine stands, all stages of growth are represented from seedlings to saplings to mature trees ranging from 9 to 88 years of age. The midstory is occupied by a variety of scrub oaks and the understory consists of grasses, forbs, shrubs, and vines.

3.4 Methods

This research is a part of a larger study conducted by the USDA Forest Service, Southern Research Station. The Comparative Analysis of Forest Reproduction Treatments (CART) study's primary objective is to evaluate the short- and long-term management and ecological consequences of forest regeneration methods on the overstory, midstory, and understory across three longleaf pine sites in the Southeast (Brockway and Outcalt, 2004).

For this study, vegetation and environmental sampling was conducted on fourteen

200-m transects located across the EEF that were surrounded by 9 ha compartments of high quality second growth longleaf pine forest (Figure 3.2). The area surrounding each transect consisted of compartments utilized by the CART study and represented various degrees of past fire and overstory management. Each transect was located in the center of the fourteen compartments and was laid out at a random azimuth. Metal stakes were located at the center and the ends of each transect and each location was mapped with a Global Positioning System (GPS) for ease of relocation.

3.4.1 Vegetation and Environmental Sampling

Vegetation data were collected along each of the 14 transects at every meter so that each set had 200 point-referenced data. This resulted in an extensive data set documenting vegetation patterns along the transects. Trees, shrubs, vines, grasses, and forbs were recorded using a line-transect method along the 200 meters recording a total percent cover by species at every 1-m increment. Every time a plant crossed the sampling plane in each 10 cm section a hit was recorded for a total of up to 10 hits per 1 meter segment. The 1-10 tally was transformed into species cover based on the following cover class midpoints: 1-0.5%, 2-2.5%, 3-7.5%, 4-15%, 5-25%, 6-38%, 7-53%, 8-68%, 9-83%, and 10-95% (Mueller-Dombois and Ellenberg, 1974). Species and genus were recorded when possible for all plant species encountered following the specific taxonomic authorities (Radford et al., 1968; Clewell, 1990).

Overstory trees were documented in a 10 x 200 meter belt transect recording the distance (x coordinate) along the transect and from the center (y coordinate) of the transect. Species name and diameter at breast height (DBH) were recorded for every tree greater than 10 cm DBH. Diameter data were used to estimate basal area per hectare.

Canopy cover was determined along the transect at 8-m intervals using a convex spherical densitometer. At every interval, 4 samples, one in each cardinal direction, and a transect average was computed using standard densitometer calculations. Litter depth, defined as the depth of identifiable needle or leaf debris, was measured at 1-m increments along the transects and recorded to the nearest centimeter.

Annual fire history, from 1949-2003, for the EEF was available in a GIS database containing digitized fire compartment maps. The number of fires that occurred in each compartment over the 55 year period was recorded and expressed as a Fire Return Interval (FRI) that denoted the mean number of years that occurred between subsequent fires. All of the compartments had been burned within the past 2 or 3 years prior to sampling and all compartments were burned in February 2005 following completion of data collection. The prescribed burns were conducted to reduce competition for successful longleaf pine regeneration, control brown spot disease and reduce fuel loads.

3.4.2 Data Analysis

Herbaceous data were compiled to assess a Heterogeneity Index (HI) and the Shannon-Weiner Diversity Index (Collins, 1992). Each combination of 1-m linear pairs was considered along each transect to calculate HI.

Percent Similarity (PS) was determined using p_a as the percent cover of species p in linear pair a and p_b as the percent cover of species p in linear pair b and s is total number of species (Whittaker, 1975) (Equation 3.1). In this way, cover of species in linear pair, p_a, were compared to the same species cover in linear pair, p_b. Averages were taken of these combinations of PS for a total of n = 14 to indicate a within-site Percent Dissimilarity (PD) that was 1 – PS (Equation 3.2). The HI is synonymous with PD therefore, as PD increases Heterogeneity Index (HI) increases.

Equation 3.1 $$PS = 1 - 0.5\sum_{i=1}^{S} |p_a - p_b|$$

Equation 3.2 $$PD = 1 - PS$$

The Shannon-Weiner Diversity index (H') was also calculated to evaluate the relationship between diversity and heterogeneity. The H' was computed according to Equation 3.3 with p_i representing the proportion of species cover i relative to the total cover of species in each plot. This value was expressed as the species diversity encountered along each transect.

Equation 3.3 $$H' = -\sum_{i=1}^{S} (p_i) \ln (p_i)$$

To determine whether HI and H' could be both used to described species response to disturbance, their correlation coefficient was calculated. In order to assess each disturbance hypotheses, the relationship between all environmental predictors (litter depth, canopy cover, basal area, fire occurrence) were regressed on HI or H' using linear and polynomial regression in Insightful S-Plus 7.0. The MFFH would be supported by a positive linear relationship while the FFSL would be supported by a negative relationship between HI or H’ and the environmental predictors (Figure 3.1). Finally, the IDH would be supported by a positive quadratic equation (Figure 3.1). One would assume that as HI increases; niche locations would be more available, resulting in increased species richness. The overall objective is to explore the relationship between HI and H’ and past disturbance.

3.5 Results

Although fourteen transects were considered at the onset of the research project, T8 was not completely sampled before Hurricane Ivan (9/04) made landfall. This transect had low observed rates of heterogeneity and species diversity, as a result of the late sampling period (Table 3.1). The HI, diversity, and environmental characteristics are reported in Table 3.1, however, this transect was excluded from final analysis.

Canopy cover across the thirteen transects ranged from 72% to 97% and basal area ranged from 13.3 to 25.1 m^2/ha (Table 3.1). Mean litter depth varied from a minimum of 1.8 cm to a maximum of 6.6 cm (Table 3.1). Plant taxa encountered along transects are reported in Appendix 3.1 and were identified and organized according to family and genus (Radford et al., 1968; Clewell, 1990; Miller et al., 2005). The HI was lowest along T14 with a value of 25.4% and highest along T5 at 53.4% (Table 3.1). The H’ ranged from 2.57 (T12) to a maximum of 4.19 along T14 (Table 3.1). On average, HI was 39.6% and H’ was 3.35 across the study transects. Heterogeneity and species diversity were weakly positively correlated (r = 0.46).

Prescribed fires across the EEF were consistently planned over the 55 year time frame, occurring primarily as biennial winter burns and infrequent annual spring burns. The number of fires in each compartment ranged from 14 – 18, with the compartment containing T14 having 21 prescribed fires (Table 3.1). The Fire Return Interval (FRI), or the mean number of years between subsequent fires calculated from the prescribed burns, was as low as 2.5 years and as high as 3.7 years (Table 3.1).

The HI had a non-significant but biologically significant moderate positive relationship with FRI ($r^2 = 0.20$, $p = 0.1452$) and a non-significant negative relationship with the number of fires (Figure 3.3c&d, Table 3.2). As the mean number of years between subsequent fires increased, HI increased (Figure 3.3c). The opposite is true of the relationship between HI and the occurrence of fires over the 55 year period, as an increase in the number of prescribed fire events decreased HI (Figure 3.3d). An increase in FRI increased H' ($r^2 = 0.37$, $p = 0.0362$), while an increase in number of fires reduced H' across the study site ($r^2 = 0.41$, $p = 0.0243$) (Figure 3.4a&b, Table 3.2). A quadratic relationship between number of fires and H' ($r^2 = 0.41$, $p = 0.0255$) revealed high or low fire occurrence resulted in low rates of H' while an intermediate numbers of fires maximized diversity over the 55 year period (Table 3.2). These results exclude T14, that exhibited a high value of H', and according to Cook's D test was significantly greater than ± 1.5 standard deviations and was labeled an extreme outlier (Table 3.2). Inclusion of T14 muted the occurrence of any clear trend between H' and fire frequency, but decreased any significance between HI and FRI or the number of fires.

The H' and canopy cover had a non-significant quadratic relationship, but a trend was observed indicating that moderate levels of canopy cover H' was at a maximum and at low or high canopy cover H' decreased (Figure 3.4d, Table 3.2). Basal area and canopy cover were weakly correlated (r = 0.68) indicating the environmental factors represent similar environmental characteristics in the overstory. Despite the correlation between canopy cover and BA no relationships were noted between HI or H' and BA (Table 3.2). Increasing litter depth decreased H', although the relationship was non-significant (Figure 3.4c, Table 3.2). The quadratic relationship ($r^2 = 0.28$, $p = 0.0658$) indicated that average litter depth resulted in the highest values of H' (Table 3.2). No relationship between HI and litter depth was observed (Figure 3.3b, Table 3.2).

3.6 Discussion

Heterogeneity and species diversity were correlated in this study (r = 0.46) as an increase in HI resulted in an increase in H'. This allowed consideration of some current disturbance hypotheses and their influence on HI. Species richness in this study on a second growth longleaf dominated pine forest ranged from 56 to 99 species along each transect, similar to values reported in other studies (Kirkman et al., 2001; Brockway and Lewis, 2003; Glitzenstein et al., 2003). The HI ranged from 25-53% with the lowest HI found along the transect (T14) that had been burned primarily using a combination of annual spring burns and biennial winter burns yielding a total of 21 burns (Table 3.1). The high HI was similar to observations on a study at Ichuaway, GA (Kirkman et al., 2001). High values of HI were observed along transects that were found in fire compartments that experienced cool biennial burns from 1949-2003 (Table 3.1).

The study area was impacted by disturbance in the form of hurricanes and management used to enhance longleaf pine regeneration. Between 1930 and 2004, the EEF experienced only moderate impacts by Hurricanes Opal in 1995 and Eloise in 1975, both Category 3 storms on the Saffir-Simpson scale at landfall (NOAA, 2006). Prior to 1930 other storms were recorded in 1916, 1882, 1960, and 1852, all of which may have impacted the EEF (NOAA, 2006). Other storms that could have residual effects on the landscape were Elena (Category 3, 1985) and Frederic (Category 4, 1979). After data were collected, Hurricane Ivan (2004) and Dennis (2005), both Category 3 storms, made landfall just south of Brewton, AL causing significant damage to the longleaf pine at the EEF.

The presence of canopy disturbance would have altered conditions in the understory providing variable shifts in heterogeneity and diversity. The ranges of canopy cover and basal area illustrate the variable tree cover across the plots, reflecting the different management or disturbance regimes among stands. Average canopy cover, calculated using a densitometer, was higher that visual observations in the field, especially along the transects that had an open longleaf pine canopy. High levels of canopy cover are typical in second growth longleaf as compared to virgin longleaf and is attributed to the extensive harvesting that took place in the early 1900s. Basal area and canopy cover had a fairly high correlation ($r = 0.68$), indicating that both measurements are indicative of overstory conditions. There was no significant relationship between canopy cover or basal area and heterogeneity, but overstory conditions may have some impact on understory variability. Although there was no obvious relationship between diversity and basal area, a quadratic relationship was observed between diversity and canopy cover. This may indicate that disturbance in the canopy maximizes diversity at intermediate levels following the Intermediate Disturbance Hypothesis (IDH) (Figure 3.1). Kirkman et al. (2001) were unable to document a consistent relationship between basal area and species richness and our results provide only weak evidence of the association of heterogeneity or diversity with canopy cover or basal area.

Other studies have associated variation in diversity or heterogeneity with soil characteristics (Provencher et al., 2003). Litter depth is related to overstory density, species composition, and disturbance patterns including fire regime. Litter depth can be a fairly good indicator of past fire disturbance as fire suppression leads to deep duff and litter layers that interfere with longleaf pine and herbaceous plant establishment and growth. Species diversity has shown a dramatic decrease with increasing litter layers (Brockway and Lewis, 2003). Our results didn't show a significant relationship between litter depths and H' or HI and can be attributed to the presence of fire along all transects.

Prescribed fire has been an important form of disturbance at the EEF. The number of fires at the EEF ranged from 14-21 across the plots over the 55 year time frame (Table 3.1). The fire return interval ranged from 2.5 to 3.7 and is fairly common of the natural fire regime in longleaf pine forests (Walker and Peet, 1983). A fire return interval lower than 1- 2 years could have inadequate fuel loads and a fire return interval greater than four years on this site may lead to decreased diversity due to deep litter depths and increased shading from midstory trees (Glitzenstein et al., 1995; Provencher, 2000). Fire plays a major role in shaping longleaf pine communities aiding longleaf pine regeneration and maintaining high values of species diversity (Myers, 1985; White et al., 1990).

Only a small amount of variation (r = 0.37) in H’ was explained by the number of fires and FRI. An indication of a negative relationship between number of fires and diversity did exist, but only with the exclusion of T14 (Figure 3.4b). The opposite was true of FRI and HI that showed a non-significant positive linear relationship (Figure 3.3c). The burn compartment that contained T14 had a high number of fires (21) and high values of H’ and low values of HI. This was an isolated case in the data set indicating a more robust sampling of fire regime, including numbers lower than 14 and higher than 21 could present a clearer picture of the effects of fire regime on diversity. Another study in a sandhill longleaf pine forest failed to provide evidence relating diversity and fire regime because of low statistical power (Beckage and Stout, 2000).

As FRI across the EEF study site decreased so did HI, indicating that more fires or less time between fires did not increase variability in compositional heterogeneity. Seabloom et al. (2005) observed that following a fire in grasslands the landscape was relatively homogeneous. This may be true in longleaf pine forests, making time since fire an important predictor of compositional heterogeneity. In this study, all plots had been burned either one, two, or three years prior so no clear trend between heterogeneity and time since fire was apparent. Increased values of heterogeneity as a result of a longer FRI was also seen in the fire-dominated fynbos; however diversity was increased only at high rates of FRI (Schwilk et al., 1997). In the case of diversity and the dominant fire regime, the trends were not as clear (Beckage and Stout, 2000).

The MFFH predicts a close positive relationship between species diversity and fire return interval. Similarly, fewer fires are expected to result in increased canopy cover, midstory shading and litter depth thereby decreasing species diversity

(Glitzenstein et al., 1995). This outcome supports the need for frequent fire to increase access to the mineral soil layer and reduce the litter layer (Glitzenstein et al., 2003). Our results show an increased number of fires may lead to decreased heterogeneity. Diversity also appeared to increase with FRI. There may be some evidence that the Most Frequent Fire Hypothesis may not be suitable when maintaining heterogeneity or diversity are a primary management goal (Beckage and Stout, 2000). Based on current fire data, Beckage and Stout (2000) suggest that the Saturation Hypothesis may be more appropriate when describing changes in species diversity. A threshold may be reached where less time between fires leads to decreased heterogeneity as recurrent fire creates a homogeneous forest floor (Seabloom et al., 2005).

This dichotomy between heterogeneity and diversity may also be attributed to a high spatial variability of litter depth across the environmental gradient of each study plot. This variability actually has a shadowing effect increasing the complexity of the landscape despite high average measurements. If a gradual decrease in heterogeneity was seen with increasing litter, the IDH would most accurately describe litter depth. This seems logical since research has shown that increased fire return interval or decreased number of fires results in increased canopy cover and litter as well as midstory cover thereby decreasing composition and heterogeneity across the landscape (Walker and Peet, 1983; White et al., 1990).

Areas of different historical disturbance regimes were observed to be highly variable which could be due to differences in season of fire or an underlying environmental gradient (Harcombe et al., 1993; Palik et al., 2000; Provencher et al., 2003). There were outliers in the data set that indicate some transects may be influenced by factors other than fire effects. The burn compartment that contained T14 was an outlier based on Cook's D statistical test and presents an interesting case. This compartment was regenerated utilizing a shelterwood method 7 years prior to data collection in 2003 and had been burned (FRI – 2.5) on a more regular basis when compared to the rest of the EEF. The understory composition has gradually shifted to grass cover and low to no shrub or midstory composition. The reduced competition for light availability may have benefited forb species increasing diversity. Images allow a better perspective of the obvious differences in the overstory, midstory, and understory composition across the study site (Appendix 3.8.4).

The growth forms dominant in the understory may also impact rates values of HI and H'. Kirkman et al. (2001) found that total species diversity did not decrease as dominance of grass species increased. No relationship was found to exist in this study between grass cover and species diversity although H' positively increased with forb cover (Appendix 3.8.3). This phenomenon has been observed in other longleaf pine forests as forb composition contributes heavily to species diversity (Platt, 1999). In my study, the HI also increased linearly ($r = 0.36$, $p = 0.0394$) with a forb cover, but increased grass cover reduced heterogeneity ($r = 0.23$, $p = 0.0949$) (Appendix 3.8.2b). Collins (1992) found a decrease in HI with an increase in grass cover as the landscape moved closer to homogeneity. Wiregrass-dominated longleaf pine forests appear to behave differently from bluestem-dominated systems as HI increased in a mesic longleaf pine stand as wiregrass cover increased (Kirkman et al., 2001). There is some indication that wiregrass and bluestems may impact heterogeneity differently.

It is not clear how heterogeneity and diversity fluctuate with different disturbance regimes. There is evidence that the IDH in sandhill longleaf pine forests was not appropriate in describing community structure (Schwilk et al., 1997; Beckage and Stout, 2000). The MFFH may be beneficial to some understory plant species but may be harmful to longleaf pine regeneration because short fire return intervals may not allow them to reach heights substantial enough to escape the maximum flame lengths (Glitzenstein et al., 1995). Further exploration of species composition and heterogeneity may support the Frequent Fire Species Loss Hypothesis that is often used to describe trends in grasslands (Collins, 1992). Predicting species diversity and heterogeneity is difficult as disturbance and underlying environmental characteristics are interactive and fire research is plagued by difficulty in replication and variability.

3.7 References

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Table 3.1 Heterogeneity Index (HI), H' (Shannon-Weiner Diversity Index) and environmental variables mean and standard errors calculated along sampling transects at the Escambia Experimental Forest.

Transects	**HI**	**H'**	**No. of fires (1949 – 2003)**	**FRI (year/fire)**	**Most recent burn year prior to 2005[*]**	**Mean Canopy Cover (%)**	**Mean Litter Depth (cm)**	**Estimated Basal Area (m^2/ha)**
T1	26.2	3.57	16	3.3	2001	93 ± 0.96	3.2 ± 0.12	20.4
T2	31.2	2.59	16	3.3	2001	72 ± 2.54	6.6 ± 0.23	15.8
T3	30.7	2.61	18	2.9	2001	89 ± 1.48	5.2 ± 0.15	22.9
T4	44.7	3.58	17	3.1	2001	82 ± 2.13	5.0 ± 0.17	20.4
T5	53.6	4.08	14	3.7	2001	80 ± 1.70	4.5 ± 0.13	13.3
T6	53.2	2.86	17	3.3	2001	90 ± 0.70	4.7 ± 0.12	25.1
T7	50.5	3.88	14	3.7	2001	92 ± 0.70	5.0 ± 0.14	22.4
T8	10.4	1.22	16	3.3	2002	88 ± 2.78	2.5 ± 0.14	25.1
T9	41.9	3.62	15	3.5	2002	92 ± 1.20	3.4 ± 0.15	24.0
T10	37.3	3.26	14	3.7	2002	97 ± 0.67	2.2 ± 0.11	22.2
T11	44.8	3.29	16	3.3	2002	94 ± 0.99	4.2 ± 0.13	21.4
T12	37.7	2.57	16	3.3	2002	96 ± 1.25	5.1 ± 0.15	23.7
T13	38.0	3.48	15	3.4	2002	80 ± 1.51	2.6 ± 0.13	22.7
T14	25.4	4.19	21	2.5	2002	82 ± 1.64	1.8 ± 0.08	19.2

[*] At the onset of the study prescribed fire (2003) was suspended; final burn prior to 2005 prescribed study burns.

Table 3.2 Simple and linear quadratic regression results with Heterogeneity Index (HI) and Shannon-Weiner Diversity Index (H’) as the response variables and Fire Return Interval, Number of Fires (Fire Number), Canopy Cover, Litter Depth, and Basal Area/Hectare (BA.HA) as the predictors.

Simple Linear Regression Models	**n**	**R^2**	**p-value**
H’ ~ Fire.return	12	0.37	0.0362
H’ ~ Fire.Number	12	0.41	0.0243
H’ ~ Litter	12	0.13	0.2418
H’ ~ Canopy	12	0.01	0.9278
H’ ~ BA.HA	13	0.08	0.3504
HI ~ Fire.return	12	0.20	0.1452
HI ~ Fire.Number	12	0.09	0.3212
HI ~ Litter	12	0.01	0.6616
HI ~ Canopy	12	0.01	0.9937
HI ~ BA.HA	12	0.01	0.9182
Simple Quadratic Regression Models			
H’ ~ Fire.Number	12	0.41	0.0255
H’ ~ Litter	12	0.17	0.1833
H’~ Canopy	12	0.01	0.8828
HI ~ Fire.Number	12	0.09	0.3337
HI ~ Litter	12	0.01	0.8456
HI ~ Canopy	12	0.01	0.9661

Figure 3.1 Hypotheses describing relationship between species diversity and disturbance.

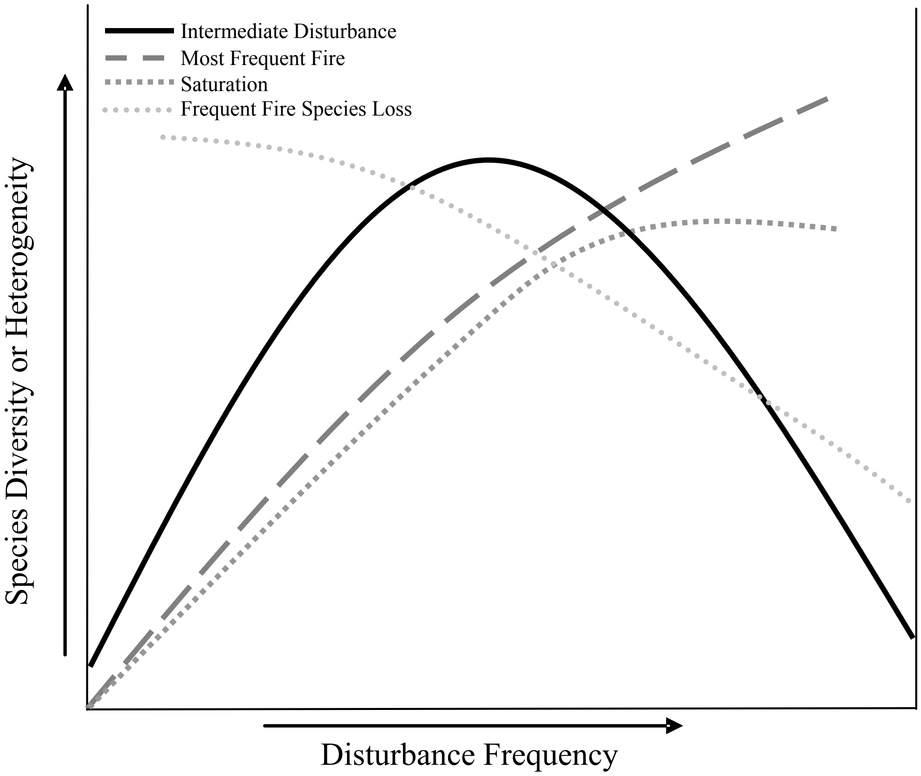
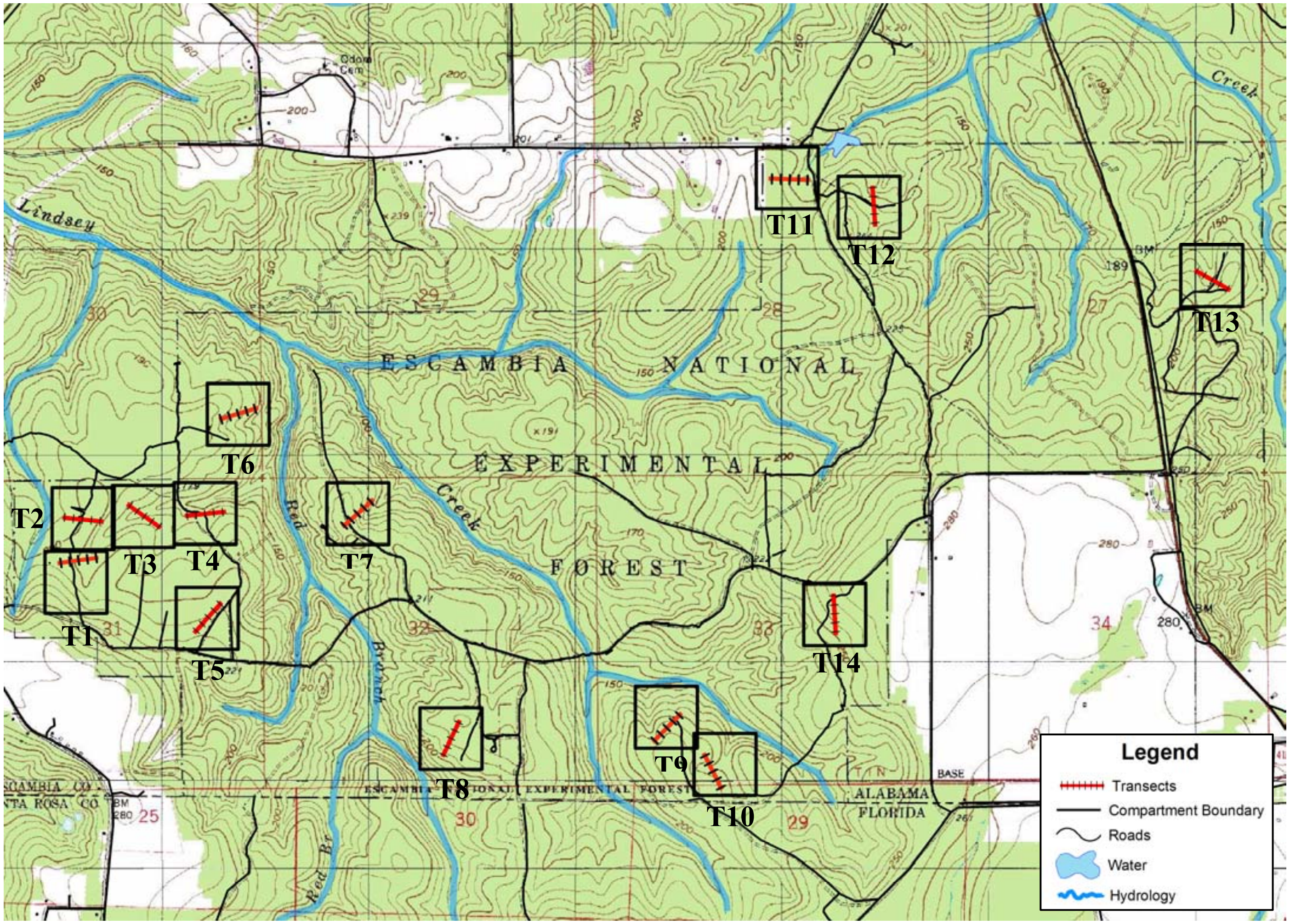


Figure 3.2 Transect locations surrounded by 9-ha CART plots at the Escambia Experimental Forest, 10 km South of Brewton, AL 31° N, 87 ° W.



Vegetation Sampling

T1 - 7/1/04
T2 - 10/15/04
T3 - 10/14/04
T4 – 6/24/04
T5 – 7/15/04
T6 – 6/16/04
T7 – 6/30/04
T8 – 1/20/04
T9 – 7/8/04
T10 – 7/21/04
T11 – 6/30/04
T12 – 6/29/04
T13 – 7/23/04
T14 – 6/24/04

Figure 3.3 Scatter plots with fitted linear regression line of Heterogeneity Index (HI) versus (a) basal area/hectare (b) litter depth (c) Fire Return Interval and (d) number of fires in a 55 year time span.

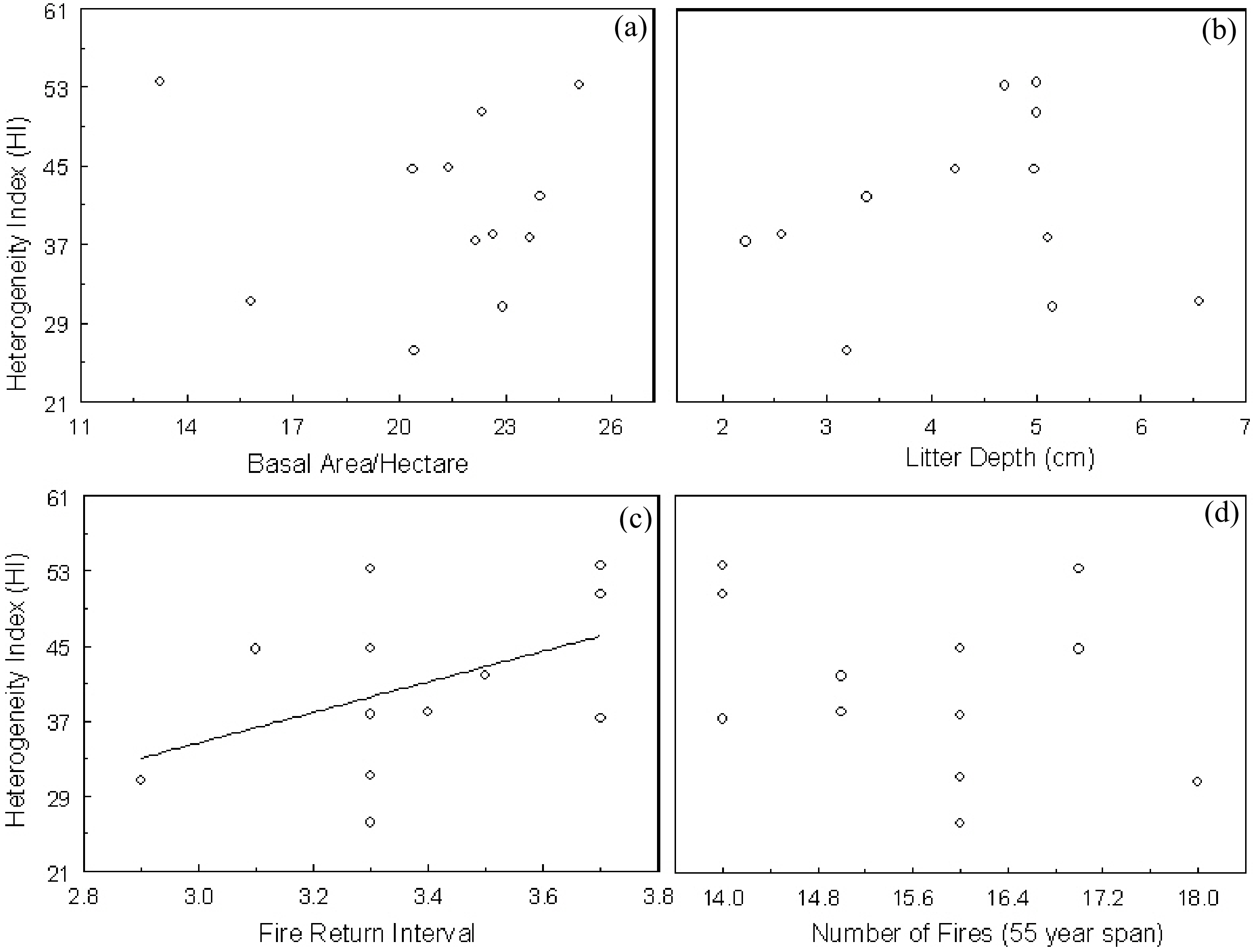
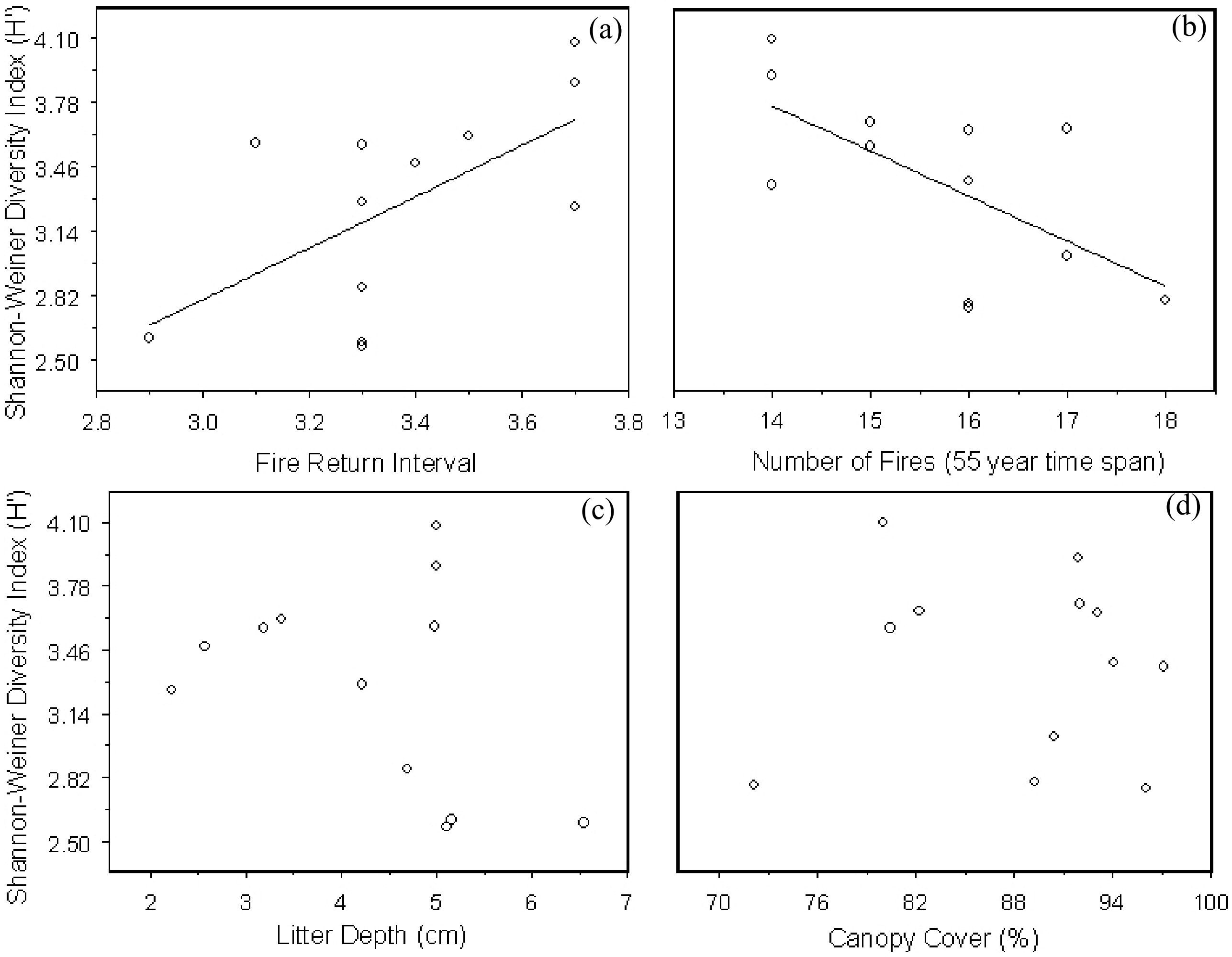


Figure 3.4 Scatter plots with fitted linear regression line of Shannon-Weiner Diversity Index (H’) versus (a) Fire Return Interval (b) number of fires in a 55 year time span (c) litter depth and (d) canopy cover



3.8 Appendices

3.8.1 List of species, genus, authority, and common name encountered on the Escambia Experimental Forest throughout sampling (Radford et al., 1968; Clewell, 1990; Miller et al., 2005; NRCS, 2006).

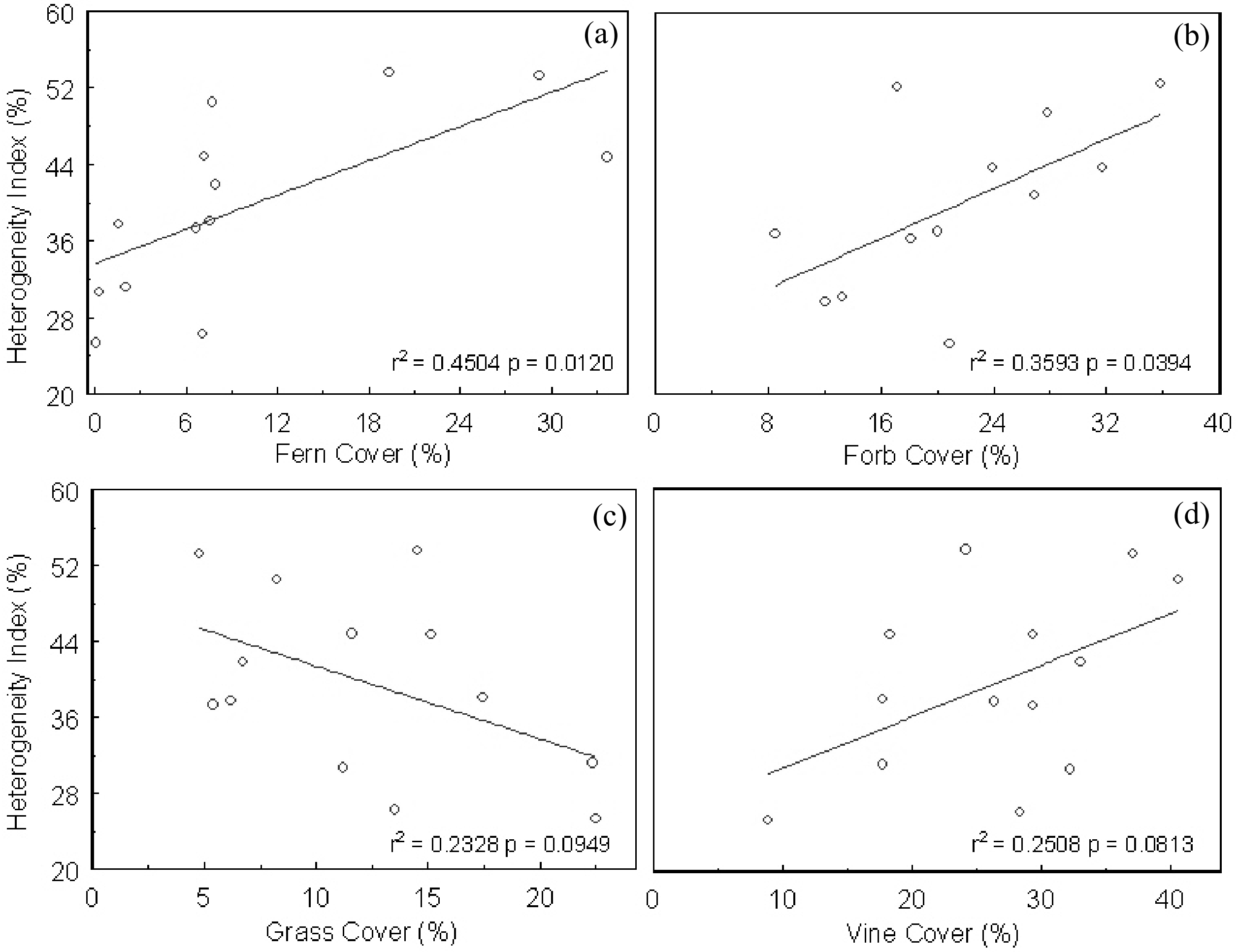
Scientific Name	Common Name	Scientific Name	Common Name
Acanthaceae			
Ruellia humilis Nutt.	wild petunia	*Elephantopus tomentosus* L.	elephant's foot
Aceraceae		*Erechtites hieracifolia* (L.) Raf. Ex DC.	Fireweed
Acer barbatum Michx.	Florida maple	*Eupatorium album* L.	white thoroughwort
Acer rubrum L.	red maple	*Eupatorium capillifolium* (Lam.) Small	dog fennell
Agavaceae		*Eupatorium compositifolium* Walter	Yankee weed
Yucca filamentosa L.	Adam's needle	*Eupatorium rotundifolium* L.	roundleaf thoroughwort
Anacardiaceae		*Euthamia tenuifolia* (Pursh) Nutt.	Slender goldentop
Toxicodendron pubescens P. Mill.	poison-oak	*Helianthus angustifolius* L.	swamp sunflower
Toxicodendron radicans (L.) Kuntze	poison-oak	*Hieracium gronovii* L.	mouseear
Rhus copallinum L.	winged sumac	*Ionactis linariifolius* (L.) Greene	whitetop aster
Annonaceae		*Liatris elegans* (Walt.) Michx.	Pinkscale blazing star
Asimina triloba (L.) Dunal	pawpaw	*Liatris pilosa* (Ait.) Willd. Var. pilosa	blazing star
Apiaceae		*Pityopsis graminifolia* (Michx.) Nutt.	Narrowleaf silkgrass
Eryngium yuccifolium Michx.	button eryngo	*Pseudognaphalium obtusifolium* Hilliard & Burtt (L.)	rabbittobacco
Aquafoliaceae		*Rudbeckia hirta* L.	blackeyed Susan
Ilex coriacea (Pursh) Chapman	large gallberry	*Sericocarpus asteroides* (L.) B.S.P.	toothed whitetop aster
Ilex glabra (L.) Gray	gallberry	*Sericocarpus tortifolius* (Michx.) Nees	Dixie whitetop aster
Ilex opaca Ait.	American holly	*Silphium compositum* Michx.	Kidneyleaf rosinweed
Ilex vomitoria Ait.	yaupon	*Solidago odora* Ait.	Anisescented goldenrod
Asclepidaceae		*Symphyotrichum depauperatum* (Fern.) Nesom	serpentine aster
Asclepias spp. L.	milkweek	*Symphyotrichum dumosum* (L.) Nesom var. dumosum	rice button aster
Asteraceae		*Symphyotrichum patens* (Ait.) Nesom var. *patens*	late purple aster
Ageratina aromatica (L.) Spach var. *aromatica*	lesser snakeroot	*Vernonia angustifolia* Michx.	ironweed
Ambrosia artemisiifolia L.	ragweed	**Betulaceae**	
Aster spp. L.	aster	*Ostrya virginiana* (P. Mill.) K. Koch	hophornbeam
Baccharis halimifolia L.	eastern baccharis	**Buddlejaceae**	
Berlandiera pumila (Michx.) Nutt.	soft greeneyes	*Polypremum procumbens* L.	rustweed
Carphephorus odoratissimus (J.F. Gmel.) Herbert	vanillaleaf		

Campanulaceae		**Euphorbiaceae**	
Lobelia brevifolia Nutt. Ex A.DC.	shortleaf lobelia	*Acalypha gracilens* L.	slender threeseed mercury
Chrysobalanaceae		*Cnidoscolus stimulosus* (Michx.) Engelm. & Gray	stinging nettle
Licania michauxii Prance	gopher apple	*Croton argyranthemus* Michx.	silver croton
Clethraceae		*Croton capitatus* Michx.	woolly croton
Clethra alnifolia L.	pepperbush	*Croton michauxii* G.L. Webster	rushfoil
Clusiaceae		*Euphorbia pubentissima* Michx.	false flowering spurge
Hypericum gentianoides (L.) B.S.P.	pineweed	*Tragia smallii* Shinners	smalls' noseburn
Hypericum hypericoides (L.) Crantz	St. John's Wart	*Tragia urticifolia* Michx.	nettleleaf noseburn
Hypericum sphaerocarpum Michx.	roundseed St. Johnswort	**Fabaceae**	
Convolvulaceae		*Baptisia lanceolata* (Walter) Ell.	gopherweed
Bonamia spp. Thouars	lady's nightcap	*Centrosema virginianum* (L.) Benth.	spurred butterfly pea
Ipomoea spp. L.	morning-glory	*Chamaecrista fasciculata* (Michx.) Greene	sleepingplant
Jacquemontia tamnifolia (L.) Griseb.	hairy clustervine	*Chamaecrista nictitans* (L.) Moench	partridge pea
Stylisma patens (Desr.) Myint subsp. *patens*	coastalplain dawnflower	*Clitoria mariana* L.	Atlantic pigeonwings
Cornaceae		*Crotalaria rotundifolia* Walt. Ex J.F. Gmel	rabbitbells
Cornus florida L.	flowering dogwood	*Desmodium laevigatum* (Nutt.) DC.	smooth ticktrefoil
Nyssa sylvatica Marsh.	blackgum	*Desmodium obtusum* (Muhl. Ex Willd.) DC.	stiff ticktrefoil
Cyperaceae		*Desmodium ciliare* (Muhl. Ex Willd.) DC.	hairy small-leaf ticktrefoil
Carex spp. L.	sedge	*Desmodium strictum* (Pursh) DC.	pinebarren ticktrefoil
Cyperus echinatus (L.) Wood	roundhead sedge	*Galactia volubilis* (L.) Britt.	milkpea
Rhynchospora cephalantha Gray	bunched beaksedge	*Galium hispidulum* Michx.	B\bedstraw
Dennstaedtiaceae		*Kummerowia striata* (Thunb.) Schindl.	Japanese clover
Pteridium caudatum (L.) Maxon	southern brackenfern	*Lespedeza hirta* (L.) Hornem.	hairy lespedeza
Ebenaceae		*Lespedeza procumbens* Michx.	trailing lespedeza
Diospyros virginiana L.	common persimmon	*Lespedeza repens* (L.) W. Bart.	creeping lespedeza
Ericaceae		*Mimosa microphylla* Dry.	littleleaf sensitive-briar
Gaylussacia dumosa (Andr.) Torr. & Gray	dwarf huckleberry	*Mimosa quadrivalvis* L.	sensitive briar
Gaylussacia frondosa (L.) Torr. & Gray ex Torr.	blue huckleberry	*Rhynchosia reniformis* DC.	kidney leaf
Oxydendrum arboreum (L.) DC.	sourwood	*Stillingia sylvactica* Garden ex L.	toothleaf
Rhododendron spp. L.	rhododendron	*Strophostyles umbellata* (Muhl. Ex Willd.) Britt.	pink fuzzybean
Vaccinium arboreum Marsh.	sparkleberry	*Stylosanthes biflora* (L.) B.S.P.	pencil flower
Vaccinium elliottii Chapman	Elliott's blueberry	*Tephrosia hispidula* (Michx.) Pers.	sprawling hoarypea
Vaccinium myrsinites Lam.	shiny blueberry	*Tephrosia spicata* (Walt.) Torr. & Gray	spiked hoarypea
Vaccinium stamineum L.	deerberry		

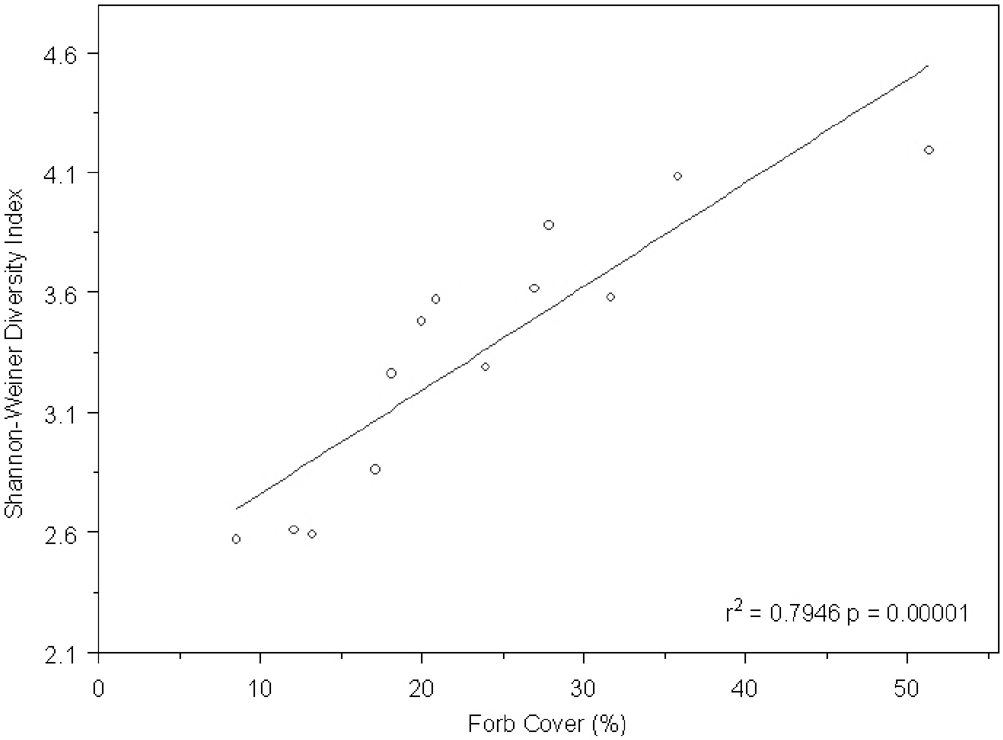
Fagaceae		**Myricaceae**	
Castanea pumila (L.) P. Mill.	chinkapin	*Morella cerifera* (L.) Small	wax myrtle
Fagus grandifolia Ehrh.	American beech	**Onagraceae**	
Quercus falcata Michx.	Southern red oak	*Oenothera* spp. L.	evening primrose
Quercus incana Bartr.	bluejack oak	**Orchidaceae**	
Quercus laevis Walt.	turkey oak	*Spiranthes* spp. L.C. Rich.	ladies'-tresses
Quercus laurifolia Michx.	laurel oak	**Oxalidaceae**	
Quercus marilandica Muenchh.	bluejack oak	*Oxalis* spp. L.	woodsorrel
Quercus nigra L.	water oak	**Phytolaccaceae**	
Quercus stellata Wangenh.	post oak	*Phytolacca americana* L.	common pokeweed
Geraniaceae		**Pinaceae**	
Geranium carolinianum L.	Carolina geranium	*Pinus palustris* P. Mill.	longleaf pine
Hamamelidaceae		*Pinus taeda* L.	loblolly pine
Liquidambar styraciflua L.	sweetgum	**Plantaginaceae**	
Iridaceae		*Plantago virginica* L.	Virginia plantain
Iris spp. L.	iris	**Poaceae**	
Juglandaceae		*Andropogon* spp. L.	bluestem grass
Carya spp. Nutt.	hickory	*Aristida stricta* Michx.	pineland threeawn
Lamiaceae		*Centium aromaticum* (Walt.) Wood	toothache grass
Collinsonia serotina Walt.	horsebalm	*Chasmanthium laxum* (L.) Yates	Indian woodoats
Hyptis alata (Raf.) Shinners	clustered bushmint	*Danthonia sericea* Nutt.	downy danthonia
Monarda punctata L.	spotted beebalm	*Dichanthelium* spp. (A.S. Hitchc. & Chase) Gould	low panicgrass
Pycnanthemum incanum (L.) Michx.	mountain mint	*Eragrostis spectabilis* (Persh.) Steud	purple lovegrass
Scutellaria integrifolia L.	larger skullcap	*Gymnopogon ambiguus* (Michx.) B.S.P.	skeleton grass
Lauraceae		*Lolium arundinaceum* (Schreb.) S.J. Darbyshire	tall fescue
Sassafras albidum (Nutt.) Nees	sassafrass	*Muhlenbergia* spp. Schreb.	muhly grass
Loganiaceae		*Panicum* spp. L.	panicgrass
Gelsemium sempervirens (L.) St. Hil.	yellow jessamine	*Paspalum spp.* L.	crowngrass
Magnoliaceae		*Saccharum giganteum* (Walt.) Pers.	sugarcane plumegrass
Liridodendron tulipifera L.	tulip tree	*Schizachyrium scoparium* (Michx.) Nash	little bluestem
Magnolia virginiana L.	sweetbay	*Sorghastrum secundum* (Ell.) Nash	lopsided Indiangrass
Malvaceae		*Sorghum halepense* (L.) Pers.	Johnson grass
Hibiscus aculeatus Walt.	comfortroot	*Sporobolus junceus* (Beauv.) Kunth	pineywoods dropseed
Melastomataceae		*Tridens flavus* (L.) A.S. Hitchc.	Purpletop tridens
Rhexia mariana L.	Maryland meadowbeauty		

Polygonaceae		**Vitaceae**	
Eriogonum tomentosum Michx.	dogtongue buckwheat	*Parthenocissus quinquefolia* (L.) Planch.	Virginia creeper
Rhamnaceae		*Vitis* spp. L.	grape
Ceanothus americanus L.	New Jersey tea		
Rosaceae			
Crataegus spp. L.	hawthorne		
Prunus serotina Ehrh.	black cherry		
Rubus spp. L.	blackberry		
Rubus spectabilis Pursh.	salmonberry		
Rubiaceae			
Diodia teres Walt.	poor joe		
Houstonia procumbens (Walt. Ex J.F. Gmel.) Standl.	roundleaf bluet		
Mitchella repens L.	partridgeberry		
Richardia scabra L.	Florida pusley		
Salicaceae			
Populus deltoides Bartr. Ex Marsh.	cottonwood		
Scrophulariaceae			
Agalinis purpurea (L.) Pennell	purple gerardia		
Smilcaceae			
Smilax spp. L.	greenbrier		
Solanaceae			
Solanum americanum P. Mill.	American nightshade		
Symplocaceae			
Symplocos tinctoria (L.) L'Hér.	common sweetleaf		
Verbeanaceae			
Callicarpa americana L.	American beautyberry		

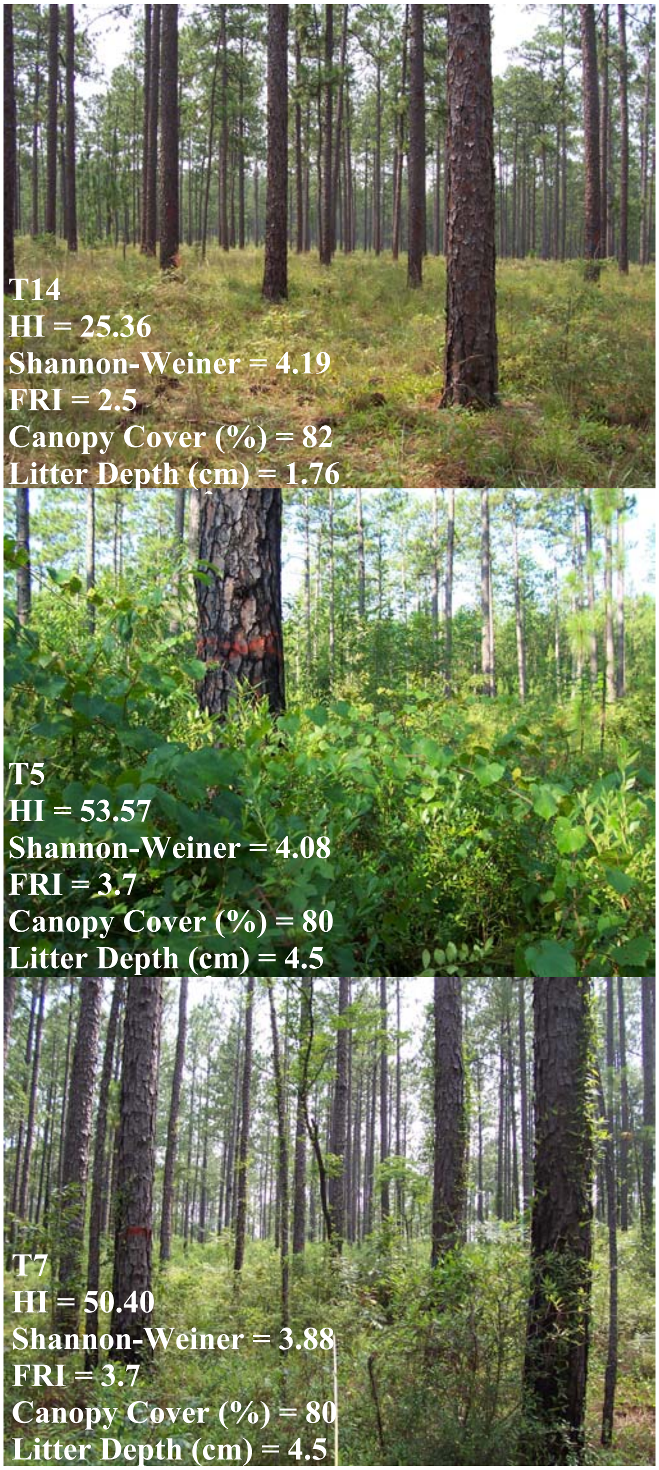
3.8.2 Scatter plots with fitted linear regression line of Heterogeneity Index and a) fern percent cover b) forb percent cover c) grass percent cover and d) vine percent cover.



3.8.3 Scatter plot with fitted linear regression line of Shannon-Weiner Diversity Index and forb percent cover.



3.8.4 Photographs highlighting diversity indices, basal area/hectare, canopy cover, and Fire Return Interval on three transects at the Escambia Experimental Forest (Photos taken by Becky Estes – July/August 2004).



4 SPATIAL PATTERNS OF FIRE INTENSITY OF FUELS IN A LONGLEAF PINE FOREST

4.1 Abstract

Predicting fire impacts on the environment is limited by the variable nature of fire in space and time. Frequent low-intensity burns are important in maintaining variable structure in longleaf pine forests. Fire intensity is a major determinant of post-fire effects and is influenced by fuel load, type, arrangement and moisture as well as climate and topography. Five forest management treatments: irregular and uniform shelterwood, single and group selection, and a no harvest treatments were conducted on the Escambia Experimental Forest creating a variable fuel complex prior to prescribe burning. In order to determine the spatial scale of fire intensity, maximum temperature was assessed using pyrometers located at 1-m intervals along a 200-m transect centered in the middle of the 9 ha forest management compartments. Fuel characteristics were assessed to explain the variation in fire behavior. The prescribed burns had a maximum fire temperature range greater than 232-259°C in more than 50% of the pyrometers. Peak variance according to Three Term Local Quadrat Variance occurred at block size 33-34 along the transects located in the no harvest forest management compartments with several peaks indicating variable spatial influence. Peak variance along the transects located in the compartments that utilized some type of active management ranged from a block size of 34 to 55, indicating that fire intensity varied at a moderate yet variable scale. Litter depth explained 20% of the variability in fire temperature along transects in no harvest compartments while those transects in the harvested compartments had larger mean patch and gap sizes for maximum temperature that was primarily explained by variation in 10 and 100-hr fuels (30%). The fuel complex was modified by harvesting and wind disturbance caused by Hurricane Ivan and subsequent salvaging operations. The ability to predict fire intensity is important when prescribing fires following overstory and ground disturbance.

Key Words: fire intensity, fuel loads, fire temperature, fuel consumption, disturbance, *Pinus palustris* P. Mill.

4.2 Introduction

Fires and hurricanes are two of the natural disturbances that create variation at different temporal and spatial scales in longleaf pine forests (Whelan, 1995; Turner and Dale, 1998). Frequent low intensity burns, occurring every 1-3 years, are important in maintaining variable horizontal structure in fire dependent communities such as longleaf pine ecosystems (Landers et al., 1995; Palik and Pederson, 1996; Carter and Foster, 2004). Disturbance regimes play an important role in determining ecological patterns due to differential survival of plant species (Platt and Connell, 2003). Fire and hurricane intensity can influence post-burn plant species patterns independently, but these disturbances can also have a distinct interactive effect (Passmore, 2005). Characterizing the spatial patterns of fire intensity has only been partially explored but could be a useful tool in understanding patterns of post-burn recovery.

Variation in fire effects is a function of fire intensity and rate of spread and occurs in both wildland and prescribed fires, creating post-burn heterogeneity characterized as a mix of unburned, moderately burned and severely burned patches (Platt and Connell, 2003; Rocca, 2004). Fire intensity is a measure of the heat that is released during a fire, expressed as the amount of fuel, the specific fuel's heat of combustion, and the rate of spread (Whelan, 1995). Rate of spread is critical because it identifies the residence time of the flaming front and indicates lethal fire temperatures (Whelan, 1995). Fire intensity is influenced by characteristics such as fuel load, arrangement, type and moisture, as well as climate and topography (Hobbs and Atkins, 1988; Whelan, 1995; Archibold et al., 1998). Measurement of the spatial structure of fuel components is important in assessing fire intensity as the energy stored in the fuel is a primary driver of fire spread (Whelan, 1995).

Fuel loading (dry weight/surface area) is the amount of energy stored in the fuel and is important in determining fire intensity (Whelan, 1995). This amount is usually expressed as potential fuel as fuel arrangement, type, and moisture limit what fuel is available for flame consumption. There is direct evidence that high fine fuel loads increase fire intensity (Stinson and Wright, 1969; Thaxton and Platt, 2006). Natural and anthropogenic disturbance regimes impact the accumulation and arrangement of fuel across landscapes. Hurricanes cause both immediate and delayed mortality in the overstory that contribute to heavy fuel loads, affecting fire intensity and residence time

(Myers and van Lear, 1998; Platt et al., 2002). Land management objectives that promote tree regeneration can involve overstory tree removal that also increases fuel loads. Fire intensity becomes more homogeneous as fuel loads increase, creating a more severe and complete fire and possibly reducing spatial variation (Hobbs and Atkins, 1988; Franklin et al., 1997; Slocum et al., 2003). This decrease in patchiness may result in a less variable landscape making it unsuitable for a wide range of species.

Fuel arrangement is an important variable in determining the packing ratio and fuel continuity (Whelan, 1995). Packing ratio provides a measure of compactness: tightly packed fuel allows less available oxygen to the flaming front (Whelan, 1995). This becomes important in overstory thinning where piles of logging debris occur alter fire continuity and intensity. Fuel continuity contributes to the vertical and horizontal movement of a fire. It can affect evenness of a burn by creating heterogeneous effects (Franklin et al., 1997). This variation in continuity is the result of differential rates of disturbance. Hurricane disturbance can decrease continuity of fuels by creating natural fire breaks in the form of coarse woody debris and tip-up mounds (Myers and van Lear, 1998). Heavy machinery used in harvesting also impacts fuel continuity, resulting in skid trails and logging decks that typically have reduced or no fuel. A discontinuous burn results in lower fire intensity and reduced patchiness.

Live plant composition is as important in determining fire intensity as downed woody debris (Breininger et al., 2002). Plant growth type can have a substantial effect on both fire intensity and rate of spread. Fuel chemistry varies by plant species and has a considerable impact on flammability (Kalabokidis and Omi, 1992). Flammability then plays a role in determining the spread of fire (Williams et al., 1994). Less flammable plants can serve as fire breaks and create variable microsite patches (Whelan, 1995). Past natural and anthropogenic disturbance can impact vegetation patterns and alter fire intensity (Franklin et al., 1997). This patchiness is often a goal of managers and spatial analysis provides a method whereby spatial variability can be determined based on the community type (Williams et al., 1994; Kennard and Outcalt, 2006). Fuel moisture and prevailing climatic conditions are very important determinants of fire intensity and exhibit variability due to spatial and temporal differences that occur before and during a burn (Ferguson et al., 2002). All of these variables have a profound effect on how fuels react in the flame front, impacting fire intensity and therefore vegetation recovery.

Fire does not burn continuously across the landscape; rather, it creates patches caused by variation in fuel loadings, moisture, weather conditions, slope, and residence time (Williams et al., 1994). These patches are characterized by differences in ash depth, remaining soil nutrition, variable soil heating and changed populations of microflora. Fire intensity alters the response of vegetation, creating structural variability and influencing succession patterns, competition, and species stability (Williams et al., 1994; Whelan, 1995). This patchiness allows for colonization by a number of species that are able to capitalize on the resources following the burn. For instance, in longleaf pine communities, hot spots create critical openings in continuous wiregrass cover that can be occupied by other less tolerant species such as *Pityopsis graminifolia* (Brewer et al., 1996). Knowledge of spatial patterning of fuel components could provide useful information to managers, helping them to understand the impacts on fire variability and subsequent recovery.

Exploring spatial patterns that are created by varying disturbance intensity may provide an invaluable method of evaluating recovery in longleaf pine communities. This research represents both exploratory analyses to detect and characterize patterns and to identify fuel predictors driving fire intensity. The objectives are to: 1) identify the presence of spatial patterns in fire temperature 2) identify the spatial pattern of fuel components located in compartments with different rates of overstory disturbance and 3) describe the functional relationship between pre-fire fuels and fire intensity.

4.3 Study Area

The Escambia Experimental Forest (EEF) (31° 01’ N, 87° 04’ W) is located ten kilometers south of Brewton, Alabama and consists of 1,214 hectares of second-growth longleaf pine (Figure 4.1). The EEF is managed by the USDA Forest Service Southern Research Station through a lease with the T.R. Miller Company of Brewton, AL. The EEF is located within the upper coastal plain. The climate is subtropical with abundant annual precipitation arriving primarily during the long growing season, occurring from April to October. Mean average temperatures range from 16 to 33°C in spring and summer with the warmest months in July and August and the coldest ranging from 5 to 20° C (Alabama Cooperative Extension Agency, 2006). Predominant soils are in the Troup series which are typically coarse sands, silts and clays that are low in organic matter and nutrients and have average water holding capacity. Surface slopes range from 5-15% with numerous drainages across the landscape (Mattox, 1975).

The dominant tree species at the EEF is second-growth longleaf pine (80%) that was naturally established from the 1958 seed crop (Boyer and Miller, 1994). The remaining 20% of the site is in pine-hardwood bottoms. In the longleaf pine stands all stages of growth are represented from seedlings to saplings to mature trees ranging from 9 to 88 years of age. The midstory is occupied by a variety of scrub oaks and the understory consists of grasses, forbs, shrubs, and vines.

4.4 Methods

This research is a part of a larger study conducted by the USDA Forest Service, Southern Research Station. The Comparative Analysis of Forest Reproduction Treatments (CART) study's primary objective is to evaluate the short- and long-term management and ecological consequences of forest regeneration methods on the overstory, midstory, and understory across three longleaf pine sites in the Southeast (Brockway and Outcalt, 2004).

Eight 200-m Transects (T), each surrounded by 9-ha compartments of high quality longleaf pine forest, were considered in the fire intensity analysis (Figure 4.1). The area surrounding each transect consisted of compartments utilized by the CART study and represented five forest management treatments. Each transect was located in the center of the eight compartments and was laid out at a random azimuth. Metal stakes were located at the center and the ends of each transect and each location was mapped with a Global Positioning System (GPS) for ease of relocation. Only eight transects were considered due to logistical constraints following Hurricane Ivan and subsequent salvage operations that left compartments with high amounts of coarse woody debris and bare soil, along with low residual basal area. The compartment that contained T1 was dropped from the analysis because a logging deck that was placed in the center of the plot resulted in a discontinuous prescribed fire that passed along only 50 m of the transect. Transects where fire intensity was observed remained relatively intact and were representative of the original forest management goals.

4.4.1 Overstory Removal

Five forest management treatments were conducted on the EEF involving various types of overstory removal to promote regeneration in late summer and early fall of 2004 (Table 4.1). Transects 7 and 4 were located in the shelterwood management compartments and were reduced to 7 m^2/ha BA with the major difference between the uniform (T7) and irregular shelterwood (T4) being the retention of all or part of the overwood in the latter (Table 4.1). The group (T3 and T6) and single tree (T8) selection treatments were reduced to 9-14 m^2/ha (Table 4.1). The group selection created large gaps by removing trees in groups and single tree removed individual trees uniformly to form canopy openings (Table 4.1). The “no harvest” compartment (T2 and T5) had no regeneration method planned and therefore retained overstory cover from 16-23 m^2/ha (Table 4.1).

One month following the completion of logging, Hurricane Ivan (Category 3) struck the Gulf Coast on September 16, 2004. Hurricane Ivan was the fourth most costly Atlantic hurricane to strike the United States throughout recorded history (NOAA, 2006).

Damage to the EEF was due in part to high winds (speeds up to 150 kph) and possible tornado touchdowns. The EEF suffered substantial overstory mortality that occurred in patches across the landscape. Forest management compartments harvested to a shelterwood were highly vulnerable to windthrow and breakage, while the selection-treated compartments sustained minor damage. Hurricane impact resulted in reduced basal area across the forest management compartments compared to the projected treatment residual BA including the "no harvest" plots (Table 4.1, 4.3).

The remaining trees that were damaged during the storm were salvaged. The order of events (harvest, hurricane, and salvage) substantially increased fuel loads and created a more discontinuous forest floor as a result of ground disturbance caused by heavy logging machinery.

4.4.2 Fuel Sampling

All fuel woody debris (FWD) lag classes (1, 10, and 100 hr) were recorded using the line-intercept method along each 200-m transect recording the number encountered at every 1m increment. The resulting numbers were transformed into biomass based on samples that were taken every 25 m at a distance of 10 m from each transect to avoid destructive harvesting along the sampling plane. Each sample was separated into 1, 10, and 100-h fuels and a mean dry biomass was calculated. The number of each type of FWD along each transect was then converted into biomass using these calculations. Coarse woody debris (CWD) (> 100 hr) was also recorded along each transect noting location along transect, species, diameter, and length. Each piece of CWD was then converted into a volume using the measurements collected. Litter, fuel, and humus depths were measured every 1m along each of the seven 200m transects. Fuelbed depth or the height of the tallest shrub, tree, grass, or piece of woody debris was recorded also at every meter to denote the influence of the standing fuel component. Shrub cover was recorded along the 200 meters of each transect recording a percent cover at every 1-m increment. Every time a shrub crossed the sampling plane in each 10 cm section a hit was recorded for a total of 10 hits per 1 meter segment. Shrub cover was recorded as a visual projection up to a maximum of 100%. Finally, bare soil was recorded along the transect as a percent at each 1-m segment as a measure of fuel continuity.

4.4.3 Fire Intensity

All of the forest management compartments were burned in either Winter (February) or Spring (April) fires in 2005. Originally, all of the compartments were to be burned on a spring fire regime but Hurricane Ivan created high fuel loads and a dangerous situation for residual longleaf pine trees, so the prescribed fire plan was changed to low intensity winter burns. The compartment containing T6 was an exception due to the late completion of salvage operations and was burned in the spring.

Fire intensity was estimated by measuring the maximum temperature that occurred during the prescribed fires. Fire temperature (°C) was estimated using pyrometers. These use industrial heat-sensitive paints manufactured to melt at a specific minimum temperature (Wally et al., 2006). The pyrometers measure only the maximum fire temperature incurred and not the residence time of the flame front. Pyrometers have been used to predict temperature and provide information on spatial variability and post-fire effects (Hobbs et al., 1984; Perez and Moreno, 1998). The pyrometers were two copper plates sandwiched together and painted on the inside with 15 dots of Omegalaq® heat sensitive paints that made up 14 categories: 1 – ≤78°C (no heat sensitive paints melted), 2 - 79 to 92°C, 3 – 93 to 120°C, 4 – 121 to 148°C, 5 – 149 to 176°C, 6 – 177 to 203°C, 7 – 204 to 231°C, 8 – 232 to 259°C, 9 – 260 to 287°C, 10 – 288 to 315°C, 11 – 316 to 342°C, 12 – 343 to 370°C, 13 – 371 to 426°C, 14 – 427 to 481°C, 15 – 482 to 537°C, and 16 – 538 to 592°C and 17 - ≥593°C above (Figure 4.2a). The lower temperature in each range represents the melting point of each paint while the upper temperature range represents the highest melting point before reaching the lower range of the next paint. Copper pyrometers have proven to be successful at predicting the 1-minute mean temperatures found using thermocouples and are, therefore, an inexpensive accurate way of estimating fire temperature (Wally et al., 2006) The pyrometers were placed at 2 heights to document fire intensity at the forest floor (0 cm) and at average shrub height (30 cm) which is often the height of the highest flame length in longleaf pine understory burning (Figure 4.2b) (Perez and Moreno, 1998; Kennard et al., 2005). Both of the pyrometers were placed at every 1m along the seven 200 meter transects. The pyrometer data were collected along the same points as fuel data collection. To standardize the recording procedure of the maximum temperatures, all temperature ranges on the pyrometers were subjected to known temperatures in a muffle oven. So that each pyrometer used in the field would be given the same rating, each paint was assessed for its melting characteristic.

Fuel moisture was determined before each burn at samples taken at every 25 meters along each transect at a distance of 10 meters from the center line for a total of 8 samples along each transect. All types of fuels were collected (soil, duff, litter, live fuel, and all hour class fuels). The green weights were recorded using a balance located at the field office and the samples were then placed in a drying oven for 48 hours at 70°C. Following the drying time, samples were reweighed and fuel moisture was calculated. Flame height and rate of spread were also estimated from observations by the prescribed fire crew on the day of each burn.

4.4.4 Data Analysis

To visualize the spatial patterns in each plot all of the factors were plotted against location and are presented in Appendices 4.7.1-4.7.7. These figures revealed the presence of patches and gaps along the transects and minimum, maximum, and mean patch and gap length. To assess spatial patterns in the data sets, a blocked quadrat variance method was utilized. These methods allow for the observer to identify pattern scale and intensity or the average length of the gaps and patches (Dale and MacIssac, 1989).

All of the blocked variance analyses were performed using PASSAGE: Pattern Analysis, Spatial Statistics And Geographic Exegesis (Rosenberg, 2001). In order to identify the mean size of the patches and gaps, Three-Term Local Quadrat Variance (3TTLQV) (Equation 4.1) was employed (Hill, 1973; Dale, 1999). The 3TTLQV analyzes the difference between overlapping blocks and identifies the pattern, avoiding the peak shift often seen in Two-Term Local Quadrat Variance (TTLQV) (Guo and Kelly, 2004). The terms in the equation x_j represent density of the jth quadrat, *n* is number of samples, and *b* is block size, (Dale, 1999).

Equation 4.1 $$V_3(b) = \sum_{i=1}^{n+1-3b} \left(\sum_{j=1}^{i+b-1} x_j - 2\sum_{j=i+b}^{i+2b-1} x_j + \sum_{j=i+2b}^{i+3b-1} x_j\right)^2 / 8b(n+1-3b)$$

The 3TTLQV analysis yields a distinct variance peak that estimates the mean patch/gap size exhibited in the data or the mean distance between the center of a patch and gap (Guo and Kelly, 2004). A Monte Carlo randomization test was performed at every scale using 1,000 permutations (Galiano et al., 1987). While this is not a formal statistical test, it does provide a means to determine whether the observed pattern is naturally occurring or is a result of a stochastic occurrence (Rosenberg, 2001). The order of the samples is randomized and the statistic is recalculated for each selected scale. The mean and the 95% confidence intervals are plotted alongside the observed variance patterns. This was accomplished using PASSAGE 1.0 (Rosenberg, 2001). Peaks occurring above the upper confidence interval are interpreted as a naturally occurring scale at an alpha level of 0.15 based on the number of randomizations. The analyses were presented in graphical form to determine similarities in patterns amongst the fuel biomass and fire temperature data.

Finally, in order to determine the relationship between the fuel component predictors and the fire temperature, linear stepwise regressions were performed for all seven transects and forest management treatments using SAS 9.1. All models were selected based on an entry and exit alpha levels of 0.05.

4.5 Results

All of the management compartments were burned in the Winter of 2005 with the exception of the compartment with T6 that was burned in the Spring after completion of salvage operations following Hurricane Ivan. The Winter burns had a mean air temperature range from 2 – 12°C while the Spring burn (T6) was 15°C and mean relative humidity ranged from 63 – 82% during both the Winter and Spring burns (Table 4.2). Similar ignition patterns were used on the burns including backfiring along roads and natural fire breaks and strip headfires within the plots. Each burn compartment had rainfall in excess of 0.7 cm 1-2 days prior to prescribed burns allowing for moderate fuel moisture (Table 4.2). Flame height and rate of spread ranged from 0.5 – 1.0m and 0.5 – 1.3 m/min, respectively in burn compartments with T5 and T4, while burn compartments with T6 and T3 had moderate intensity with flame heights of 0.5 – 2 m and flame spread of 1 -2 m/min (Table 4.2). Compartments surrounding T7 and T8 had maximum flame heights of 2 m and a rate of spread of up to 4 m/min (Table 4.2).

Maximum fire temperatures varied along the 200-m transects resulting in gaps of low temperatures and patches of high temperatures. The highest fire temperature range occurred in T2 (288-315°C) while the lowest fire temperature range occurred in T5 (121-148°C) (Figure 4.3, Table 4.3). Burn compartments that were harvested to a shelterwood had two varying ranges of maximum temperatures with T4 showing a range of 149-176°C and T7 having a high temperature range of 232-259°C (Figure 4.3, Table 4.3). Burn and selection harvest compartments had similar ranges of maximum temperatures with T3 and T6 both harvested in groups of trees having ranges of 204-231°C and 232-

259°C and T8, in a single tree harvest compartment, had a temperature range of 232-259°C (Figure 4.3, Table 4.3).

Some of the pyrometers had no melted paints and, therefore, either did not burn or burned at a temperature lower than 78°C. These particular pyrometers occurred at a 19% frequency, mostly along T4 and T5, indicating the low intensity of those burns (Figure 4.3). Other pyrometers could not be rated because of charring on the copper tag although it appeared they did not reach the melting point of copper (971°C). These pyrometers were recorded at a range above 593°C and occurred more frequently along T2, T8, and T6, however the frequency across the EEF was under 1% (Figure 4.3). Overall, 63% of the pyrometers along T2 ranged from 260-593°C and only 18% ranged from 78-260°C, while pyrometers along T3, T6, T7, and T8 had approximately equal frequencies occurring above and below the 260-287°C range (Figure 4.3). Finally, pyrometers observed along T5 and T4 had a 70% frequency of temperatures ranging from 78-260°C (Figure 4.3).

The fuel components sampled along the transects varied along a disturbance gradient with low disturbance in the no harvest compartments and high disturbance in the compartments where forest management objectives required overstory removal. The disturbance gradient was reflected in the residual basal area left within each compartment following the multiple disturbances with T2 and T5 having 19-20 m^2/ha, the selection compartments (T3, T6, and T8) retained 7-14 m^2/ha, and the shelterwood plots had a low residual basal area ranging from 1.4-2.4 m^2/ha (Table 4.3). The 1-hr fuels were high along T5 (8.1 g) and T2 (12.8 g) when compared to harvested plots (T4, T7, T3, T6, and T8) (Table 4.3). The opposite was true of 100-hr fuels as increased biomass was noted in the plots that had some form of overstory removal (Table 4.3). Litter depth was fairly consistent along all of the transects and ranged from 2.1-3.7 cm (Table 4.3).

The maximum temperatures recorded by the pyrometers varied along the transects resulting in heterogeneity (Figures 4.4-4.6). In the "no harvest" compartments, pyrometers were rated as below 78°C and were a consequence of extreme fire patchiness, resulting in unburned areas (Figure 4.4). This was reflected in the variance measures as T5 had several peak variances (6, 17 and 34) indicating varying mean patch and gap size (Figure 4.7a). Only the largest scale at 34 coincides is similar to a scale in T2 that was observed at a block size of 33 (Figure 4.7a). Mean patch and gap size along T5 and T2 in the no harvest compartments is 34, although considerable variability can be seen due to the changes in fuel and fire characteristics along the transect. The two group selection compartments (T3 and T6), although burned in different seasons, appear to show similar patch and gap sizes occurring at a large block size (44-49) with smaller scale patterns occurring at 14 and 30, indicating the same variability in spatial pattern as seen along T2 and T5 (Figure 4.5, Figure 4.8a,g). The only transect sampled in the single tree selection (T8) compartment had different scales, with mean patch and gap size occurring at block size 12 with a variable scale at 26 (Figure 4.5 and Figure 4.9a). Along T4 and T7 in the shelterwood compartments a similar mean patch and gap sizes as the "no harvest" transects occurred with a peak variance at a block size of 34 and a secondary variance peak of 18 along T4 and a smaller and larger peak at 11 and 55 along T7 (Figure 4.6 and Figure 4.10a,g).

Fuels sampled along the transects yielded distinct spatial patterns. The transects within the "no harvest" compartments (T2 and T5) had similar variance peaks observed in the 1-hr fuel biomass at a scale of 45, although T5 had peaks evident at smaller scales (Figure 4.7b,h). Similar scale was observed for litter depth that had a small variance peak at block 31 along T5 and a maximum of 64 along T2 (Figure 4.7d,j). Shrub density occurred at two patterns of scale along T5 with peak variance at 17 while T2 had a similar pattern to 1-hr fuel biomass at block size 49 (Figure 4.7f,l).

The mean gap and patch size associated with 1-hr fuel biomass along T3 in the selection plots was only significant at a peak variance of 25 (Figure 4.8b). Spatial patterns occurred in the 10-hr fuel biomass at a block size of 37 in both T6 and T8 (Figure 4.8h and Figure 4.9c). Both of these plots had a similar mean 10-hr fuel biomass around 60 g and could have contributed to the similarity in scale (Table 4.3). There was not a clear trend of pattern size in the 100-hr biomass as T3 had a small and large mean patch and gap size (14, 62) and T6 and T8 hovered around a more intermediate scale of 23-38 (Figure 4.8c,i and Figure 4.9d). Litter depth had a maximum variance around block size 36 in T8, while T3 and T6 had a small peak variance occurring at 14 with a second peak at 46 in T3 (Figure 4.8d,j and Figure 4.9e). The observed peak variance in fuel bed depth occurred in both T6 and T8 from 44-57 (Figure 4.8 k and Figure 4.9f). The maximum variance that occurred in shrub density occurred at a small scale in T8 at 28 and a larger block size (45) in T3 and T6 (Figure 4.8f,l and Figure 4.9g).

The mean patch and gap size along the transects (T4 and T7) sampled in the shelterwood compartments were variable for all fuel sizes. The 1-hr biomass occurred at two scales in T7, both having similar variance (19,49) while T4 had one variance peak occurring at a scale of 22 (Figure 4.10b,h). The 10-hr biomass had a mean patch and gap size of 12 in T4 while three peaks were identified in T7 with a maximum variance of 62

(Figure 4.10c,i). The patch and gap size that was identified in the 100-hr fuel biomass was similar occurring at a block size of 25 (Figure 4.10d,j). Litter depth had a scale that ranged from 29-35 (Figure 4.10e,k). Shrub density was different along the two transects with a large scale of pattern occurring along T4 at 39 and a small scale occurring in T7 (17) that may be attributed to high shrub cover creating more frequent patch and gaps along the transect (Figure 4.10f,l, Table 4.3).

The results of stepwise regression indicate different fuel predictors explain the variability in fire intensity pattern that was observed along the transects in the 3TTLQV analysis. The model explaining fire intensity variability along the transects sampled in the "no harvest" plots explained only a small amount of variability (20%), with litter depth, bare soil and shrub cover entering the model (Table 4.4). When considering T5 and T2 individually, neither model explained a substantial amount of variability, but litter depth and 1-hr fuel biomass were consistently important predictors (Table 4.4). The models explaining fire intensity along the transects in the selection and shelterwood treatments explained 28-33% of the variation (Table 4.4). The important factors in these models were 10-hr fuel biomass, litter and fuelbed depth, as well as shrub cover while the model explaining the variability in the fire temperature in the shelterwood treatment added 100-hr fuel biomass (Table 4.4). Bare soil (%) was a significant predictor in all models, but explained more variability in the shelterwood and selection plots (Table 4.4).

4.6 Discussion

Fire intensity along the transects in the prescribed fire compartments had variable prevailing weather conditions, but were fairly characteristic of prescribed fires conducted as low intensity surface fires. Higher wind speeds, lower relative humidity, and high mean temperatures may have influenced the fire intensity along T2, T3 and T4 that were burned on the same day in a large acreage prescribed fire. In addition to the predominant climate, small changes in wind speed and direction may have created microhabitat variability altering fire intensity. Temperature and humidity during the remaining prescribed fires ranged from 6.1-15°C and 72-82%, respectively (Table 4.2). The prevailing winds also impacted the relative humidity as it was marginally reduced on the 2/16/05 burn day (Table 4.2). There were two seasons of burning applied in this study due to constraints incurred by the salvage operations post-hurricane. Distinct differences in fire intensity between winter and spring burns were not observed despite a higher mean air temperature (23.9°C) in the April burn (T6). Gliztenstein et al. (1995) determined that fire season may be of less consequence to fire intensity than to vegetation and this appears to be the case in this study .

Prescribed fires are a common form of management on the EEF used to accomplish longleaf pine restoration objectives. A control or area that was treated as unburned was not a treatment in this study as the negative effects of fire suppression in longleaf pine forests are widely acknowledged in the literature (Heyward, 1939; Myers, 1985; Gilliam and Platt, 1999). The maximum fire temperatures that were observed across the EEF (121 - 315°C) are fairly typical of other reported values occurring in similar longleaf pine communities where temperatures ranged from 52 – 335°C (Gibson et al., 1990; Glitzenstein et al., 1995; Grace and Platt, 1995). Kennard and Outcalt (2006) reported mean temperatures of 154-236°C in longleaf pine in spring burns at the Solon Dixon Forestry Center in Andalusia, AL that were slightly lower than the observed temperatures in this study. The method of ignition patterns (i.e., backing – Dixon versus heading fire - EEF) could have affected maximum temperatures (Kennard and Outcalt, 2006). Fire temperatures have been documented in other forested and grassland communities using pyrometers: Northern mixed prairie mean temperature of 432°C, aspen mean temperature of 710°C, Eucalypt forest mean temperature of 600°C, palmetto shrub 135°C at 5 cm in the soil, tallgrass prairie mean of 230°C, upland pine savanna 400°C, and mixed white pine-hardwood 200°C (Raison et al., 1986; Hobbs and Atkins, 1988; Olson and Platt, 1995; Archibold et al., 1998; Clinton et al., 1998; Hierro and Menges, 2002).

A major unplanned component in this research was the wind damage from Hurricane Ivan in 2004. Hurricanes have two major impacts on forested ecosystems: reduction of overstory canopy cover and addition of substantial fuel loads in the form of pine straw and hardwood litter, downed woody fuel, and coarse woody debris (Passmore, 2005). Both of these impacts occurred in the EEF, as well as ground disturbance from multiple salvage operations. Increased fuel loads could have contributed to increased fire intensity. The transects sampled in the shelterwood compartments (T4 and T7) had a residual basal area of 1.42 m^2/ha and substantial bare soil (13%) creating a discontinuous fuel layer and reducing fire intensity across the transect (149 - 176°C in T4 and 232 - 259°C in T7). The occurrence of natural disturbance, such as hurricanes and salvage operations, can alter fuel loads and continuity creating areas of variable fire intensity that recover with different types of vegetation (Platt et al., 1988; Provencher et al., 2003).

Prescribed fires in longleaf pine forests are fueled by fine woody debris that is primarily composed of needle litter. Any addition of fuel increased fire temperature along the transects. High biomass of fine fuel can often increase temperature more than the addition of coarse woody debris (Table 4.3). This in turn influences heterogeneity and alters patterns of plant mortality (Archibold et al., 1998; Passmore, 2005; Thaxton and Platt, 2006). Properties of fuel biomass affect fire intensity as increased density of coarse woody debris decreases ignition and thus reduced fire spread and intensity (Archibold et al., 1998). In contrast, some studies have observed an increase in fireline intensity following salvage or harvesting operations due in part to the extensive layer of slash and the removal of overstory canopy (Stephens, 1998; Passmore, 2005). In the context of the EEF, results were variable as T4 (sampled in the shelterwood compartment) was characterized by a discontinuous fuel layer, but had a low observed fire temperature range, while T7 (2.4 m^2/ha) had high biomass of all down woody material and a high maximum temperature range (Table 4.3, Figure 4.3). The same variability was seen along the transects (T2 and T5) in the "no harvest" compartments that had minimal damage from Hurricane Ivan and subsequent salvage operations. T2 had a high mean maximum temperature range of (288-315°C) while the lowest fire temperature range occurred in T5 (121-148°C) (Figure 4.3, Table 4.3).

There was considerable variation in temperatures recorded by the pyrometers at adjacent locations. Variation in temperature could be attributed to changes in the fuel complex or moisture content of the vegetation (Hobbs et al., 1984; Hobbs and

Gimingham, 1984; Raison et al., 1986). Results from the 3TTLQV analysis indicated variable mean patch and gap size with peak variance occurring at both small and larger patterns of scale. Additionally, the pattern analysis relates the average length of gaps to areas of low fire temperature and average length of patches to areas of high fire temperature (Franklin et al., 1997). Although 3TTLQV does not directly determine the contribution of patches and gaps to the overall mean, inspection of the location data along each transect can help to distinguish this pattern. It appears that the smaller scale of pattern observed along T5 in the "no harvest" compartment was similar to variance peaks observed in 1- and 10-hr fuel biomass and litter depth (Figure 4.7b,c,d). This is in contrast to T2, which had moderate to high block sizes in fire temperature, 1- and 10-hr fuel biomass, litter depth, fuelbed depth, and shrub cover (Figure 4.7g-l). The maximum temperature ranges along these transects indicated T5 to be a cooler more heterogeneous burn while T2 burned hotter and more homogeneously. Other research has reported that surface fires with higher maximum temperatures burn more continuously or homogenously across the landscape (Franklin et al., 1997). The transects in the group selection and shelterwood burn compartments had a larger scale of pattern and more closely resembled the scale of pattern in the 10- and 100-hr fuel biomass. In conclusion, the prescribed fires at the EEF were had extremely variable maximum temperature ranges and produced fires with heterogeneous and homogeneous patterns with each fire and between fires.

Variance peaks in the 3TTLQV analysis not only provide the mean patch and gap size of the maximum fire temperature, but also indicated peak variance along the fire intensity transects. Litter fires exhibit low variability as they typically burn fuel completely and are of low intensity. As fuel loads increase and variability across the stand increases, fire intensity variance increases and then levels off. Wildfires or slash fires also exhibit high variance, but as fuel biomass is maximized the burns become hotter and more homogeneous (Williams et al., 1994). Only severe fires with extreme fuel loads and weather conditions would result in a uniform fire treatment and low fire intensity variability (Hobbs and Atkins, 1988). The variance observed in the analysis of the EEF data showed similar trends with transects in the "no harvest" compartments having a relatively low peak variance while the transects in the selection and shelterwood compartments had substantially increased variance. This may indicate, that as the fuel complex became more variable, so did fire intensity, although none of the burns appeared to plateau and decrease in variance as was expected in slash fires.

Many techniques have been used to extrapolate patterns of scale from ecological data. The use of both local quadrat block variance methods and semivariance analysis may be a useful combination for determining the variation relative to the pattern in area or in distance, respectively (Franklin et al., 1997). Kennard and Outcalt (2006) examined the spatial patterns of a longleaf pine forest in an upland site and found that fire temperature varied over moderate scales. Although the technique used in our study related pattern to area (3TTLQV), similar moderate scales of maximum fire temperature, ranging from 12-55 m, were observed. These patterns of scale were not isolated within plot heterogeneity, as small and large patterns were also observed, indicating the considerable variability that occurred during each burn.

Other studies have implied similar variability associated with maximum fire temperatures (Franklin et al., 1997; Rocca, 2004). In this study, at 1-m scales the mean difference in maximum fire temperature ranged from 112 -142°C which resembles the difference found in Florida scrub (mean difference of 150°C) rather than upland longleaf pine, where the mean difference was 50°C (Wally et al., 2006). Transects sampled across the EEF had the high degree of heterogeneity that is common in forests with frequent fires. Landscapes that have a longer time interval between burns have a high fire intensity as fuel loads build up, increasing the homogeneity of the burn (Gibson et al., 1990).

Shrub cover did not have a significant role in determining maximum fire temperatures. In most cases, shrub cover entered the regression model with a negative coefficient which was unexpected. This may indicate that factors important in explaining the variability in maximum fire temperature may not have been sampled. Along T2, slope may account for the remaining unexplained variability in fire temperature as the transect crossed a small stream bottom and then returned to upland longleaf pines. If the strip head was ignited downslope, the fire traveling north along the transect could have increased rate of spread due to a predominant northwest wind. This observation may explain the high maximum temperature shown along T2.

Bare soil was an important predictor in all regression models and was mainly caused by skid trails and logging decks as well as small disturbance from tip up mounds that occurred during Hurricane Ivan (Robichaud and Miller, 1999; Iverson et al., 2004). These locations interrupted fuel continuity and the spread of the flame front. Fuel characteristics that explained fire temperature varied across the management compartments and were a consequence of residual basal area left on the sites. Transects (T2 and T5) that occurred in compartments with minimal disturbance (high BA) had fire temperature variability explained by litter depth. The transects in the selection plots (T3, T6, and T8) or those with moderate residual BA had fire temperature variability explained by 1 and 10-hr fuel biomass as well as litter and shrub cover. Transects that were sampled in compartments with less than 5 m^2/ha residual basal area (T4 and T7) had variability explained by the full model that included all variables. These observations indicate that, as disturbance increases so does the heterogeneity of the fuel complex and the variability of fire intensity.

Litter depth contributed to fire temperature variability in all of the forest management treatments (Table 4.4). The amount of continuous litter biomass was clearly related to the density of trees on the sites as a higher longleaf pine density produced a greater amount of continuous litter biomass (Grace and Platt, 1995). Litter depths were greater along T2 and T6, consequently both had a high mean maximum fire temperatures range (Table 4.3). Other studies have shown higher maximum fire temperature occurring directly underneath longleaf pine crowns (Grace and Platt, 1995). The proximity of pyrometers to longleaf pine crowns along the transects was reduced in the shelterwood compartments, while the majority of pyrometers in the selection and “no harvest” compartments occurred close to or directly under a crown. This may help to better explain the high fire temperature along these transects (personal observation).

It was not apparent on the EEF that fuel buildup and/or ground disturbance altered the maximum temperature along transects in the shelterwood (T4 and T7) or the selection (T3, T4, and T15) forest management compartments. The highest maximum temperature range was recorded along T2 (“no harvest”) indicating that a continuous litter layer may have contributed to overall fire intensity. The disruption of the litter layer due to increased harvesting traffic on the removal transects increased litter heterogeneity, although most of these transects had high maximum temperature ranges due to increases in 10- and 100-hr fuel biomass. Although fire intensity increased due to addition of fuel biomass, negative consequences on vegetation may not be observed on a landscape level, but rather may occur on a small scale with plant survival varying from quadrat to quadrat (Hierro and Menges, 2002). Determining the spatial pattern and the predictors of fire intensity may be important in evaluating the impacts of overstory removal, wind damage from hurricanes, and salvage operations on planning prescribed burns and predicting post-fire effects.

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Table 4.1 Experimental regeneration treatments applied to forest management plots in the Escambia Experimental Forest.

Harvest	200-m Sampling Transect	Regeneration Method	Projected Residual BA	Description	Projected Canopy Openings (ha)	Prescribed Fire
Irregular Shelterwood (SH)	T4	Two-aged	6-7 m^2/ha	Canopy openings progressively expanded and some mature trees are retained	<0.01 to 0.1 at onset with larger openings over time	Winter
Uniform Shelterwood (SH)	T7	Even	6-7 m^2/ha	Initial cut leaves overstory trees as protective cover then overwood is harvested	<0.01 to 0.1 ending in open conditions	Winter
Group Selection (GS)	T3,T6	Uneven	9-14 m^2/ha	Small groups of trees harvested	0.1 to 0.8	Winter/Spring
Single Tree Selection (SS)	T8	Uneven	9-14 m^2/ha	Individual trees removed maintaining continuous cover	0.01 to 0.1	Winter
No Harvesting (NH)	T1,T2,T5	None	N/A	N/A	N/A	Winter

Table 4.2 Conditions occurring during the Escambia Experimental Forest prescribed fires. All values in ( ) indicate the range of the variable.

Date	**Transect**	**Mean Air Temp (°C)**	**Mean RH (%)**	**Mean Wind Speed (km/hr)**	**Wind Dir.**	**Precip (mm)**	**Date of Precip**	**Flame Height (m)**	**Rate of Spread (m/min)**	**Fuel moisture (%)**			
										Live	**Dead**	**Litter**	**Soil**
2/16/05	T4	12 (11-13)	63 (35-77)	11 (10-11)	NW	1.5	2/14/05	0.5-1	0.3-1	81	26	23	18
2/11/05	T7	2 (-2-11)	78 (41-100)	4 (0-13)	NW	1.3	2/9/05	0.5–2	2-4	39	30	17	23
2/16/05	T3	11.6 (11-13)	62.5 (35-77)	11 (10-11)	NW	1.5	2/14/05	0.5-2	1-2	44	40	20	15
4/28/05	T6	15 (8-24)	74 (43-100)	3 (0-6)	SE	1.3	4/26/05	0.5-2	1-2	73	*	25	2
2/6/05	T8	8.9 (4-17)	72 (51-92)	2.75 (2-10)	NE	0.7	2/3/05	0.5 -2	2-4	75	35	18	14
2/5/05	T5	6 (1-15)	82 (44-100)	2.4 (0-10)	N	0.7	2/3/05	0.3-1	0.5-1	63	36	25	19
2/16/05	T2	11.6 (11-13)	62.5 (35-77)	11.3 (10-11)	NW	1.5	2/14/05	*	*	78	33	21	10

* Values for these characteristics were unavailable the day of the burn due to inaccessibility to the plot.

Table 4.3 Mean and standard error of maximum temperature and fuel variables in plots at the Escambia Experimental Forest.

Transect	Median and Range of Maximum Temperature (°C)	Fine Woody Biomass (g)			Coarse Woody Debris (cm^3)	Bare Soil (%)	Litter (cm)	Fuelbed Depth (cm)	Shrub Cover (%)	Residual Basal Area (m^2/ha)
		1-hr	*10-hr*	*100-hr*						
T4	121 (121-148)	9.3 ± 1.3	90.1 ± 6.6	64.0 ± 9.3	2340 ± 1050	14 ± 2	2.9 ± 0.3	22.7 ± 2.6	14 ± 1	1.4
T7	204 (204-231)	7.1 ± 1.0	120.7 ± 8.1	124.2 ± 12.6	4453 ± 979	7 ± 1	3.0 ± 0.1	26.0 ± 2.1	25 ± 2	2.4
T3	232 (232-259)	9.7 ± 1.0	46.8 ± 4.1	23.4 ± 4.8	247 ± 138	11 ± 2	2.1 ± 0.1	14.8 ± 1.8	6 ± 1	7.2
T6	260 (260-287)	7.7 ± 1.0	67.3 ± 5.5	40.8 ± 7.0	3291 ± 1600	10 ± 2	3.2 ± 0.2	28.9 ± 2.4	23 ± 2	11.5
T8	232 (232-259)	5.5 ± 1.1	53.9 ± 4.7	25.5 ± 5.6	1558 ± 1078	16 ± 3	2.4 ± 0.5	17.1 ± 1.6	11 ± 2	14.3
T5	121 (121-148)	8.1 ± 1.0	66.5 ± 3.9	27.6 ± 4.6	2049 ± 1445	9 ± 1	2.5 ± 0.1	11.7 ± 1.4	16 ± 2	19.3
T2	288 (288-315)	12.8 ± 1.2	70.6 ± 4.5	16.8 ± 3.9	254 ± 170	1 ± 1	3.7 ± 0.1	19.6 ± 2.4	6 ± 1	20.9

Table 4.4 Results from stepwise regression of fuel predictors on fire temperature. Results include coefficient values, significance level for each variable F-test and the percent of fire temperature variation explained by each model.

Transect/ Forest Management	***n***	**Fine Woody Biomass (g)**			**Bare Soil (%)**	**Litter (cm)**	**Fuelbed Depth (cm)**	**Shrub Cover (%)**	**% Temp variance explained**
		1-hr	*10-hr*	*100-hr*					
T4	169				-1.4261 (0.0006)	15.3357 (0.0208)			17%
T7	180		0.4027 (0.0001)	0.1772 (0.0083)		14.0434 (0.0318)	1.7163 (0.0001)		35%
T3	197	1.8855 (0.0014)			-1.8813 (0.0001)	16.3904 (0.0068)			30%
T6	185		0.3297 (0.0068)		-1.5760 (0.0001)	6.9712 (0.0269)	0.8690 (0.0043)	1.5831 (0.0008)	39%
T8	171	1.5162 (0.0352)			-1.9697 (0.0001)		1.8112 (0.0017)	1.0650 (0.0666)	33%
T5	197				-0.8795 (0.0200)	9.7452 (0.0383)	1.0568 (0.0035)		12%
T2	194					18.5177 (00023)		-2.0066 (0.0005)	11%
No Harvest (T2,T5)	391				-1.6591 (0.0001)	25.9149 (0.0001)		-1.1011 (0.0011)	20%
Selection (T3,T6,T8)	553	1.4565 (0.0003)	0.1963 (0.0215)		-1.8082 (0.0001)	7.0615 (0.0078)	0.8244 (0.0002)	0.7638 (0.0085)	33%
Shelterwood (T4,T7)	349		0.3474 (0.0001)	0.1595 (0.0021)	-0.9220 (0.0082)	13.7200 (0.0057)	0.6892 (0.0054)	1.1308 (0.0015)	28%

Figure 4.1 Plot layout and regeneration methods at the Escambia Experimental Forest, 10 km south of Brewton, AL.

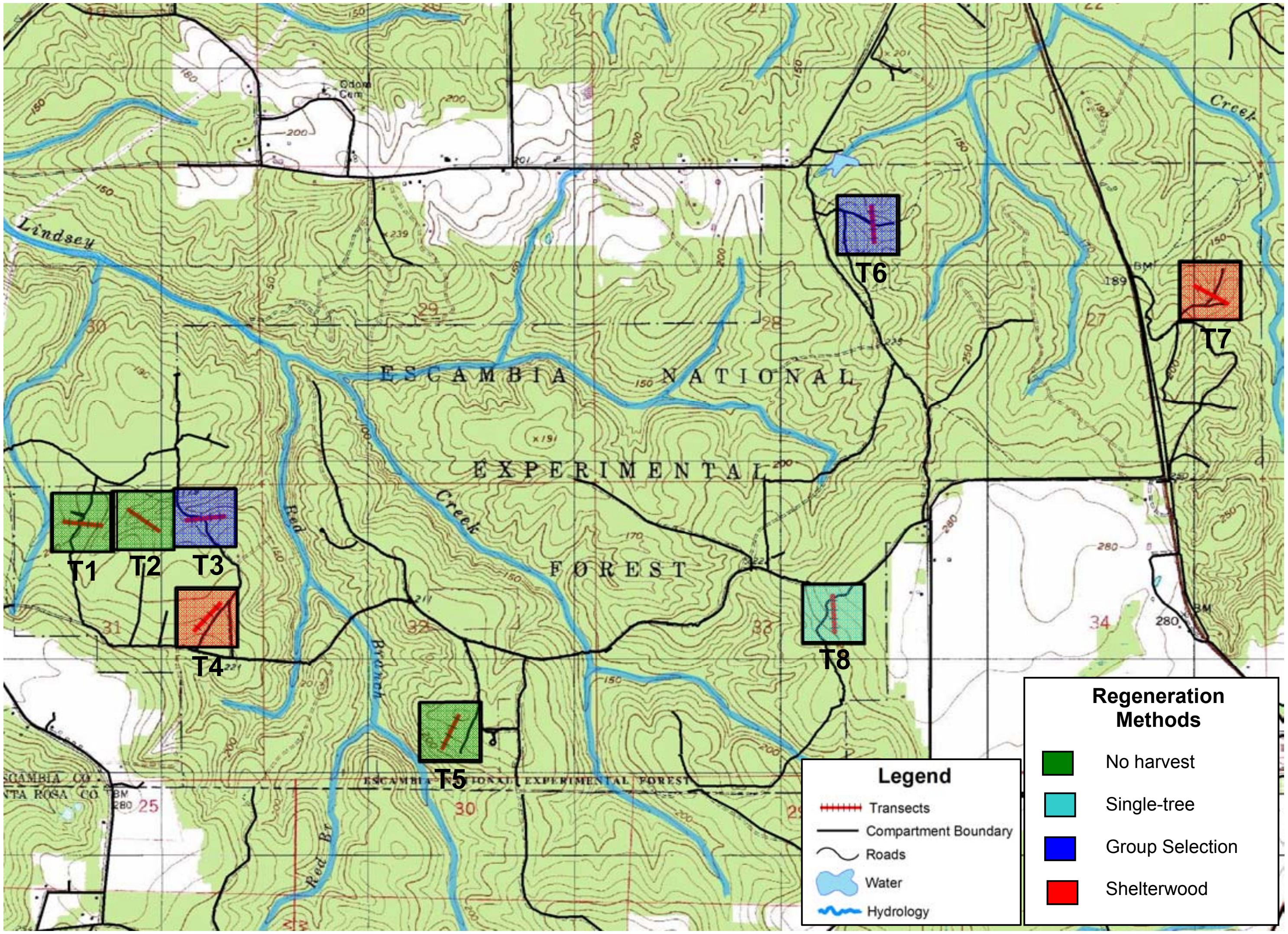


Figure 4.2 Design of the pyrometers(a) and placement (b) during the prescribed fires at the Escambia Experimental Forest.

Figure 4.3 Histogram of the Maximum Fire Temperatures (°C) of pyrometers placed at 30-cm height (shrub height).

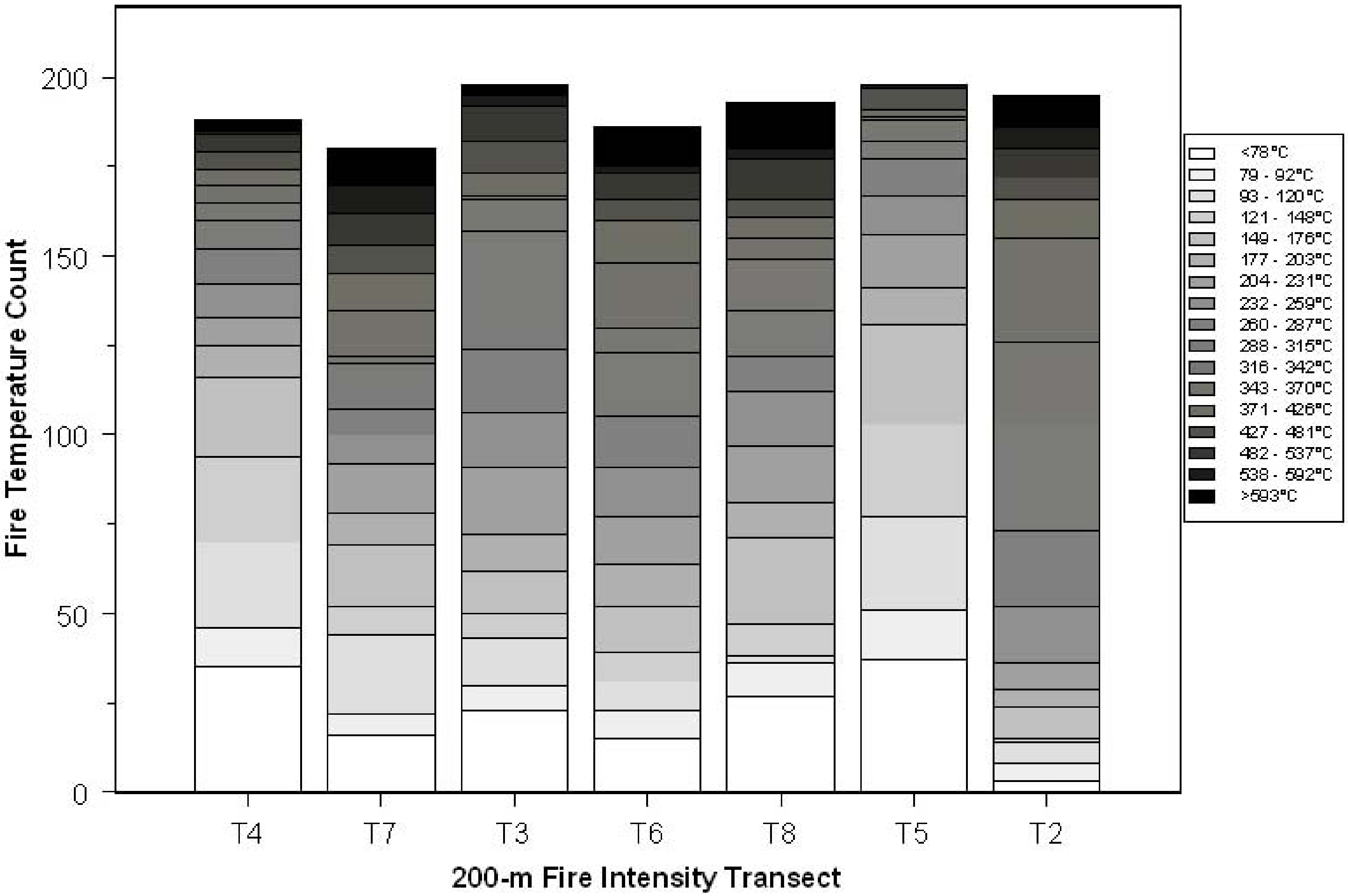


Figure 4.4 Maximum temperatures of pyrometers at 30-cm height along 200-m transects in no harvest management compartments along (a) T2 and (b) T5.

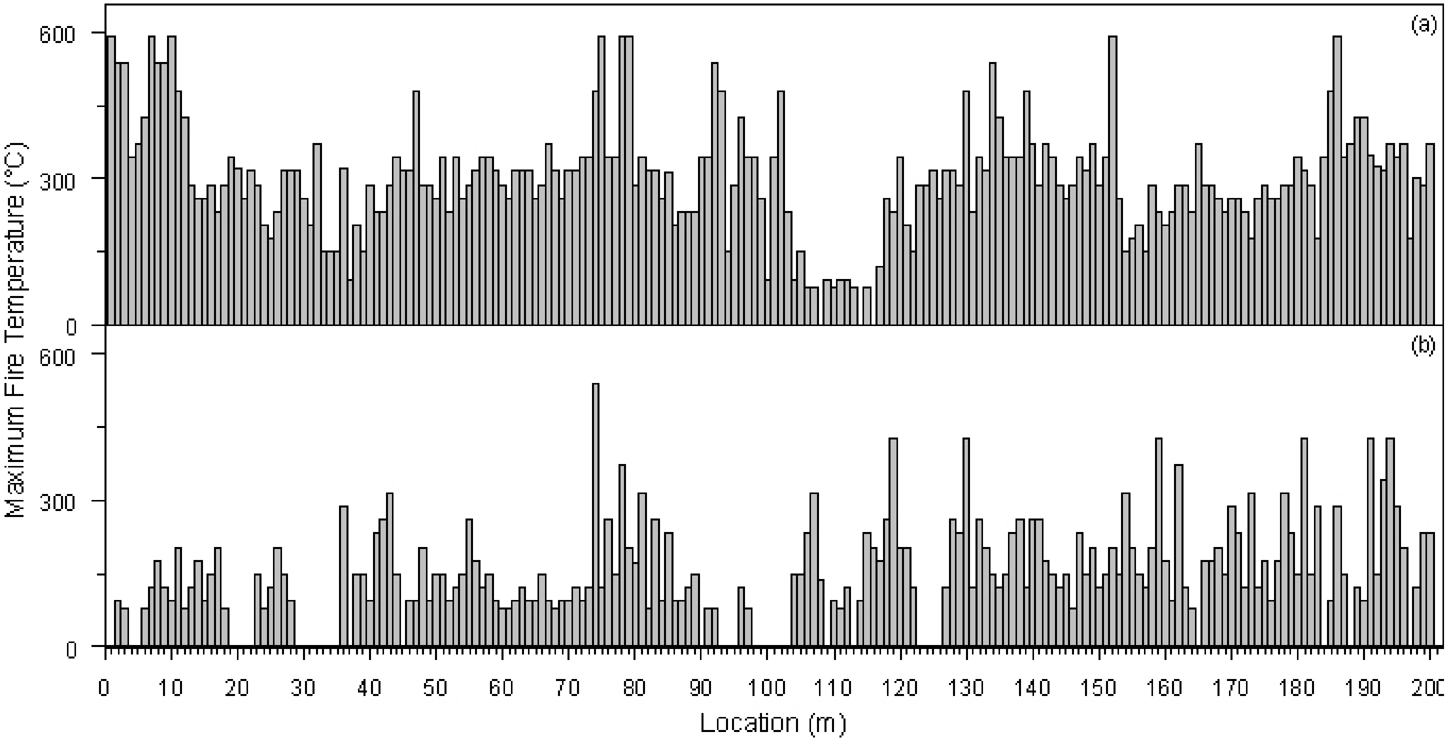


Figure 4.5 Maximum temperatures of pyrometers at 30-cm height along 200-m transects in group selection (a) T3 and (b) T6 and single-tree (c) (T8) forest management compartments.

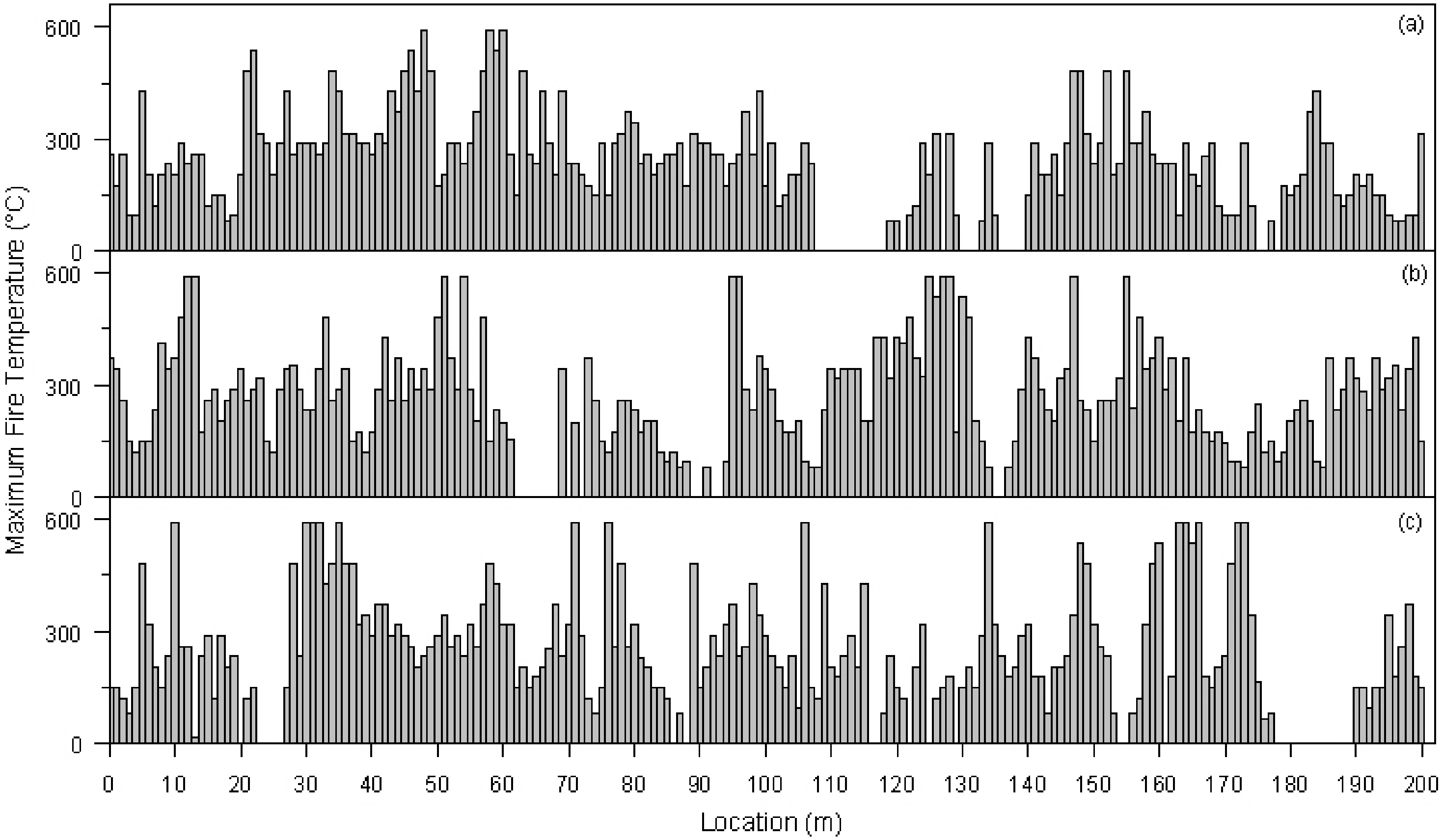


Figure 4.6 Maximum temperatures of pyrometers at 30-cm height along 200-m transects in irregular shelterwood (a) T4 and uniform shelterwood (b) T7 forest management compartments.

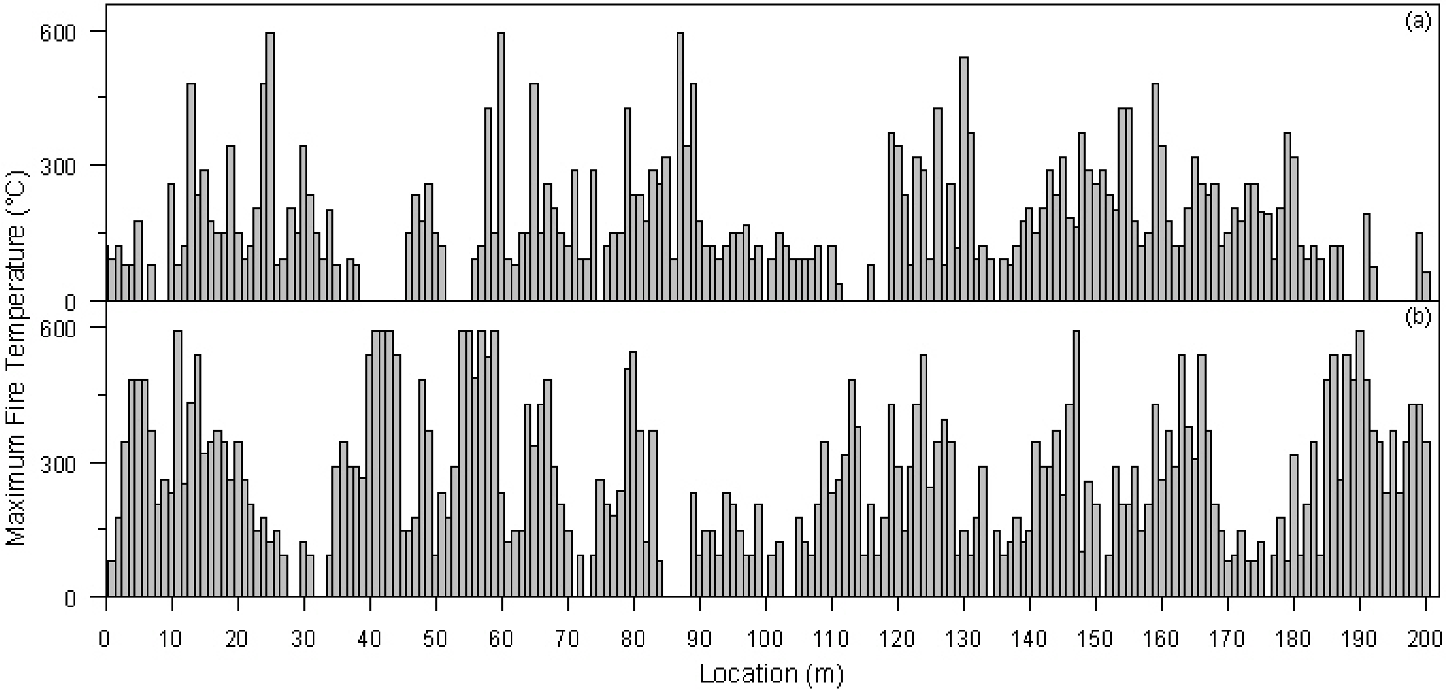


Figure 4.7 Pattern intensity determined by Three-Term Local Quadrat Variance (3TTLQV) for variables from the no harvest fire compartments (a-f collected from T5 and g-l from T2) at the Escambia Experimental Forest. Large dotted line indicates the mean of 1,000 randomization tests performed on the variance results and small dotted lines indicate the confidence intervals for each randomization test; (a) & (g) maximum temperature (°C), (b) & (h) 1-hr fuel biomass (g), (c) & (i) 10-hr fuel biomass (g), (d) & (j) litter depth (cm), (e) & (k) fuelbed depth (cm), and (f) & (l) shrub cover (%).

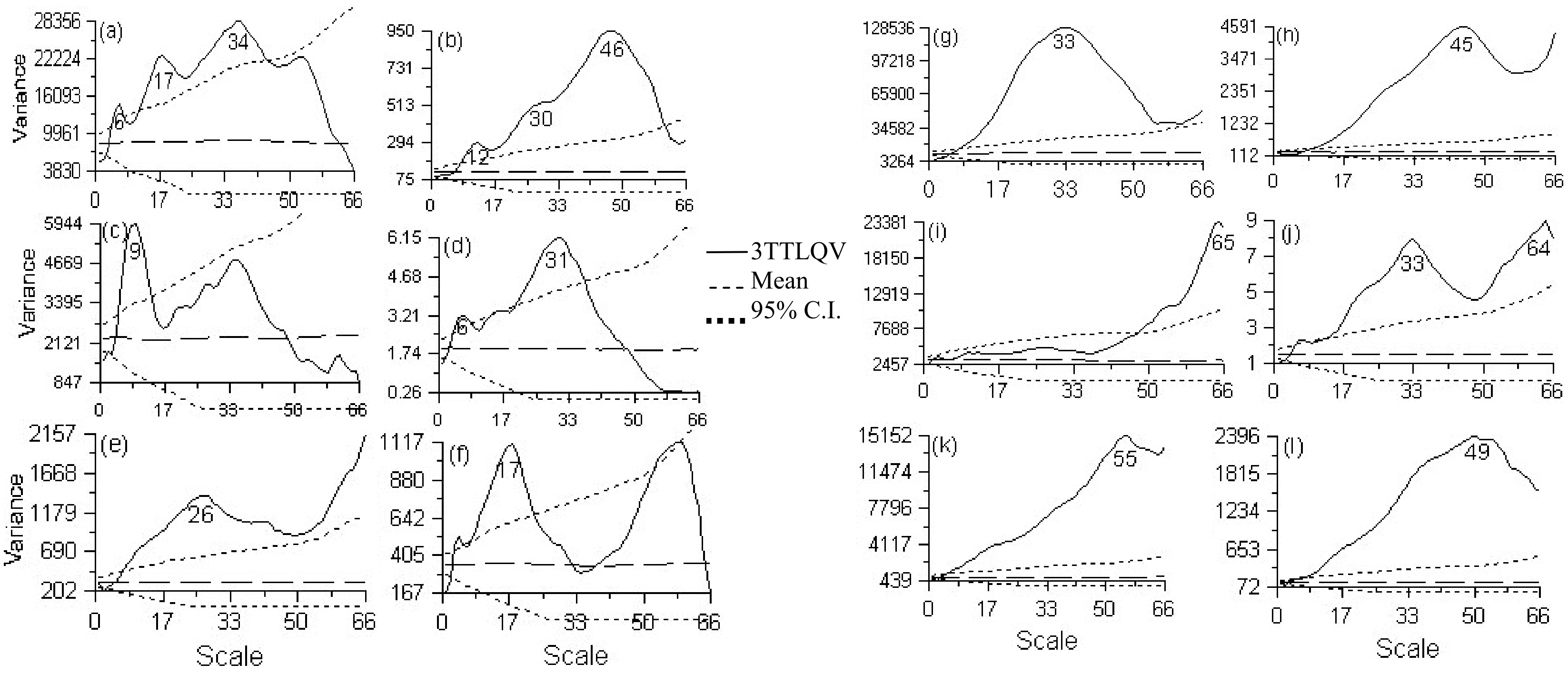


Figure 4.8 Pattern intensity determined by Three-Term Local Quadrat Variance (3TTLQV) for variables from the group selection fire compartments (a-f collected from T3 and g-l from T6) at the Escambia Experimental Forest. Large dotted line indicates the mean of 1,000 randomization tests performed on the variance results and small dotted lines indicate the confidence intervals for each randomization test; (a) & (g) maximum temperature (°C), (b) 1-hr fuel biomass (g), (h) 10-hr fuel biomass (g), (c) & (i) 100-hr fuel biomass, (d) & (j) litter depth (cm), (e) & (k) fuelbed depth (cm), and (f) & (l) shrub cover (%).

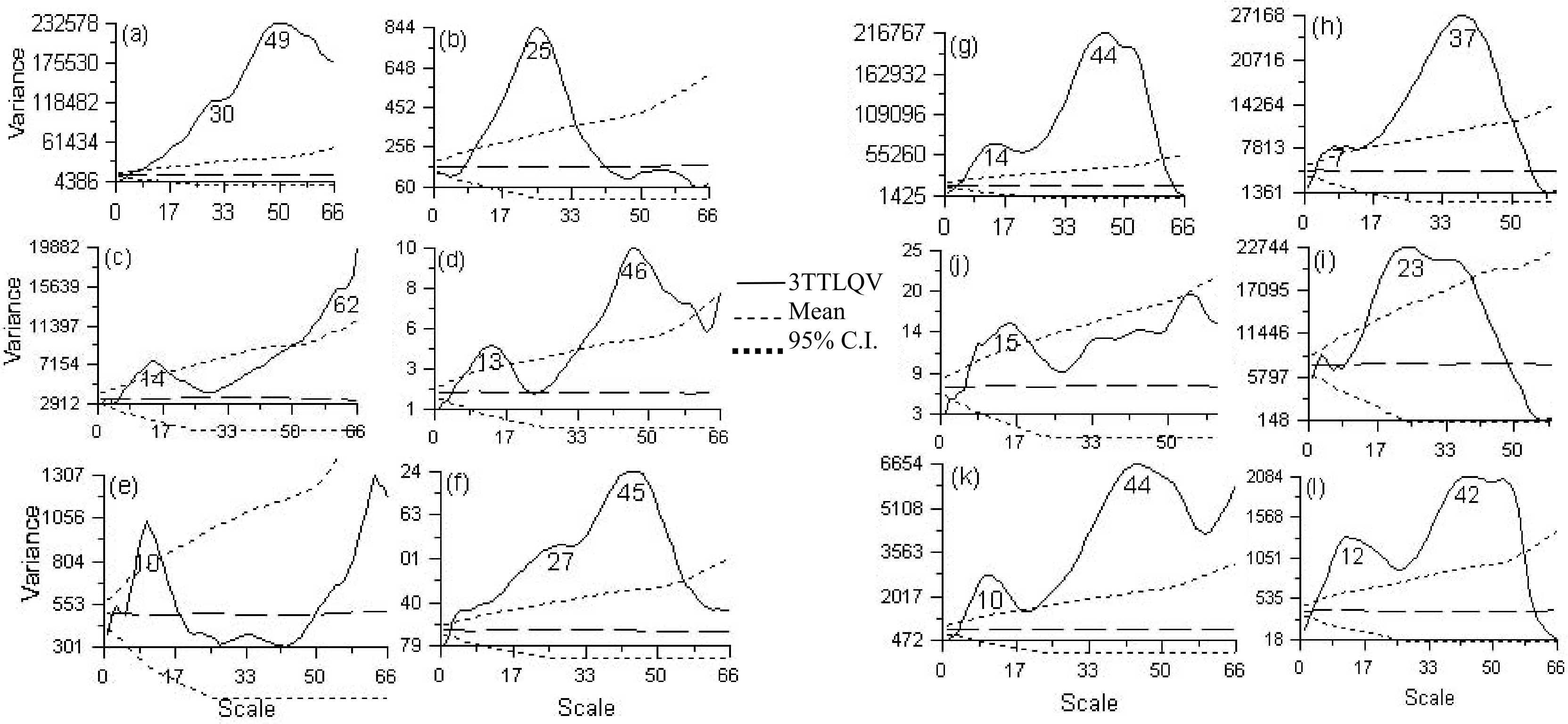


Figure 4.9 Pattern intensity determined by Three-Term Local Quadrat Variance (3TTLQV) for variables from the single tree selection fire compartments (a-g collected from T8) at the Escambia Experimental Forest. Large dotted line indicates the mean of 1,000 randomization tests performed on the variance results and small dotted lines indicate the confidence intervals for each randomization test; (a) maximum temperature (°C), (b) 1-hr fuel biomass (g), (c) 10-hr fuel biomass (g), (d) 100-hr fuel biomass (g), (e) litter depth (cm), (f) fuelbed depth (cm), and (g) shrub cover (%).

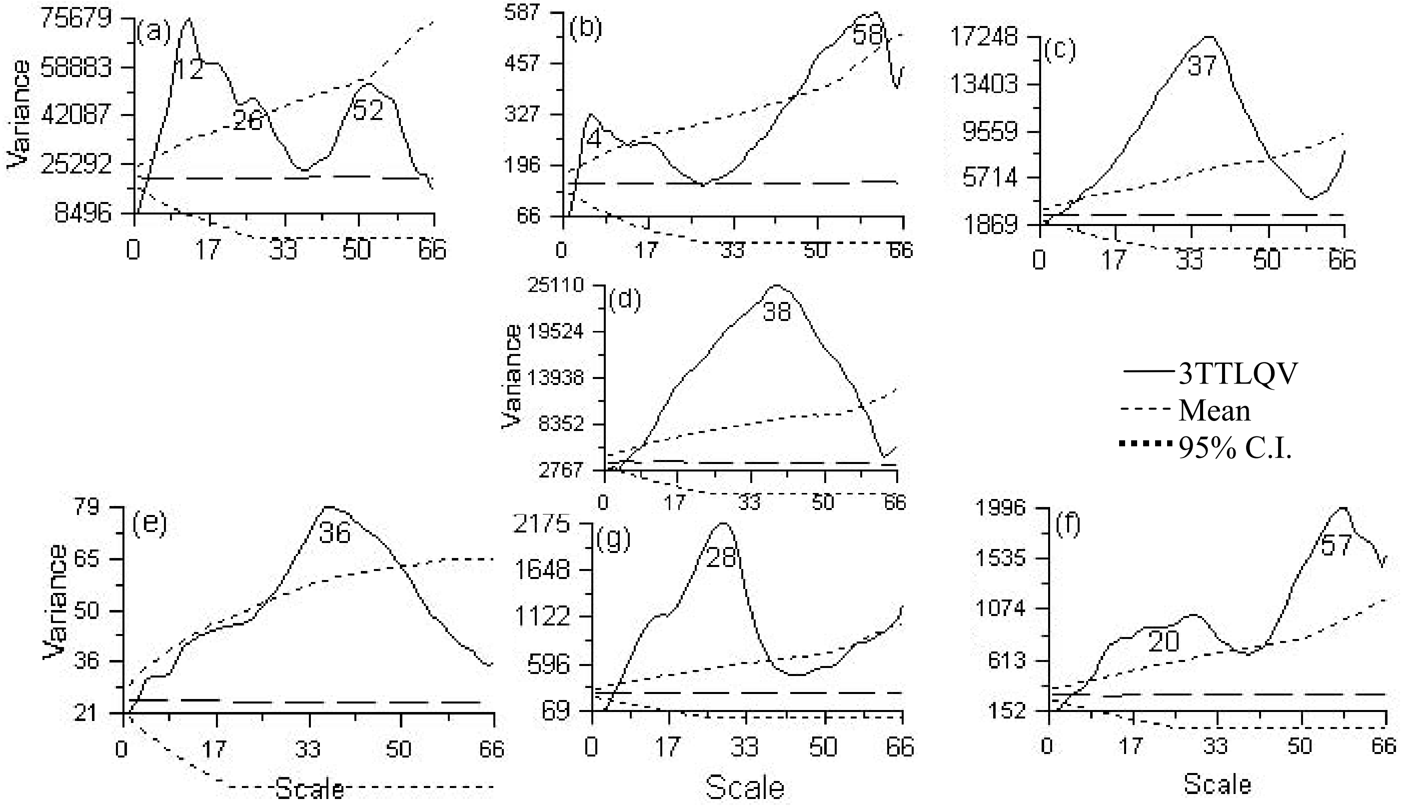
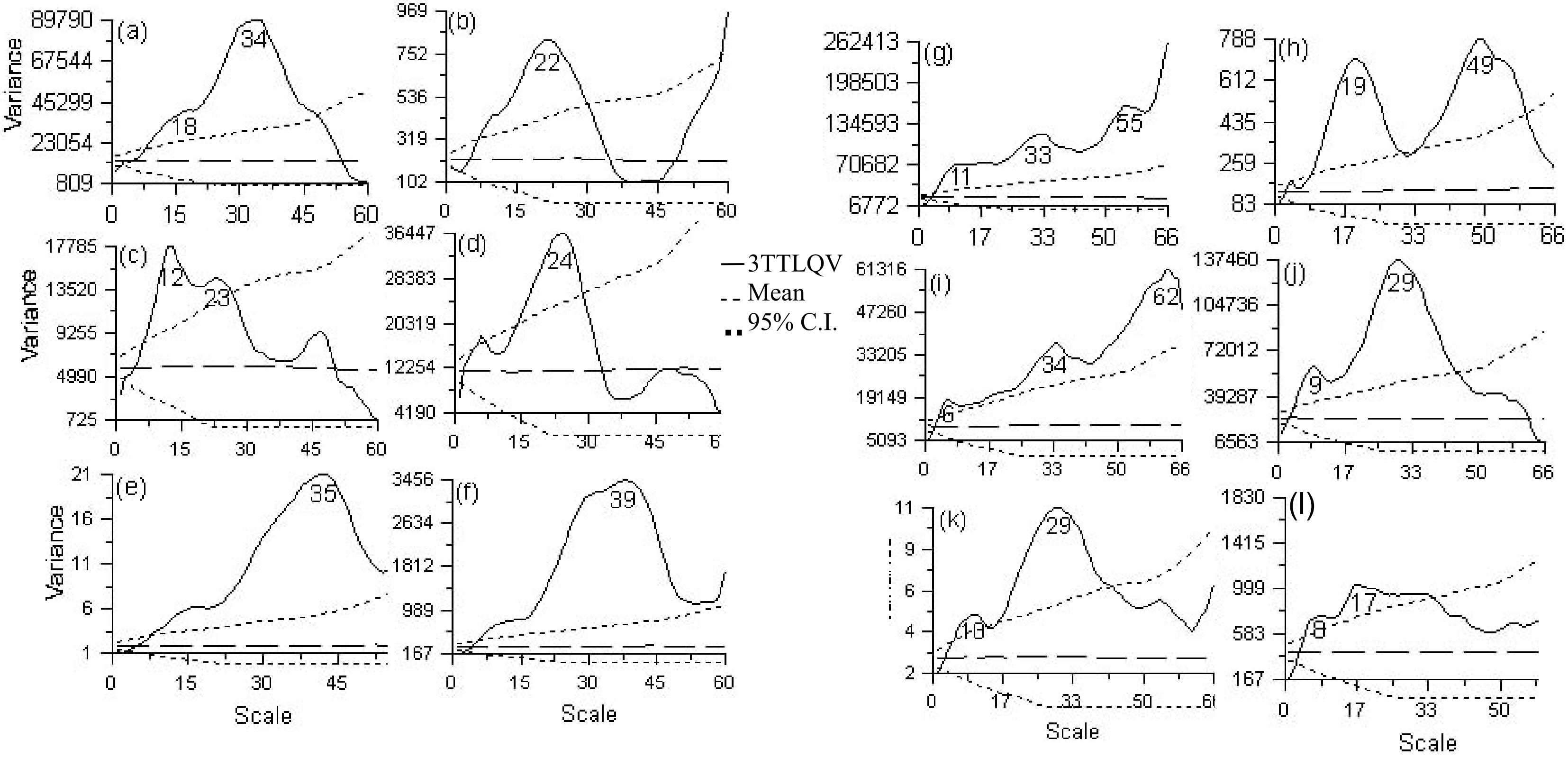
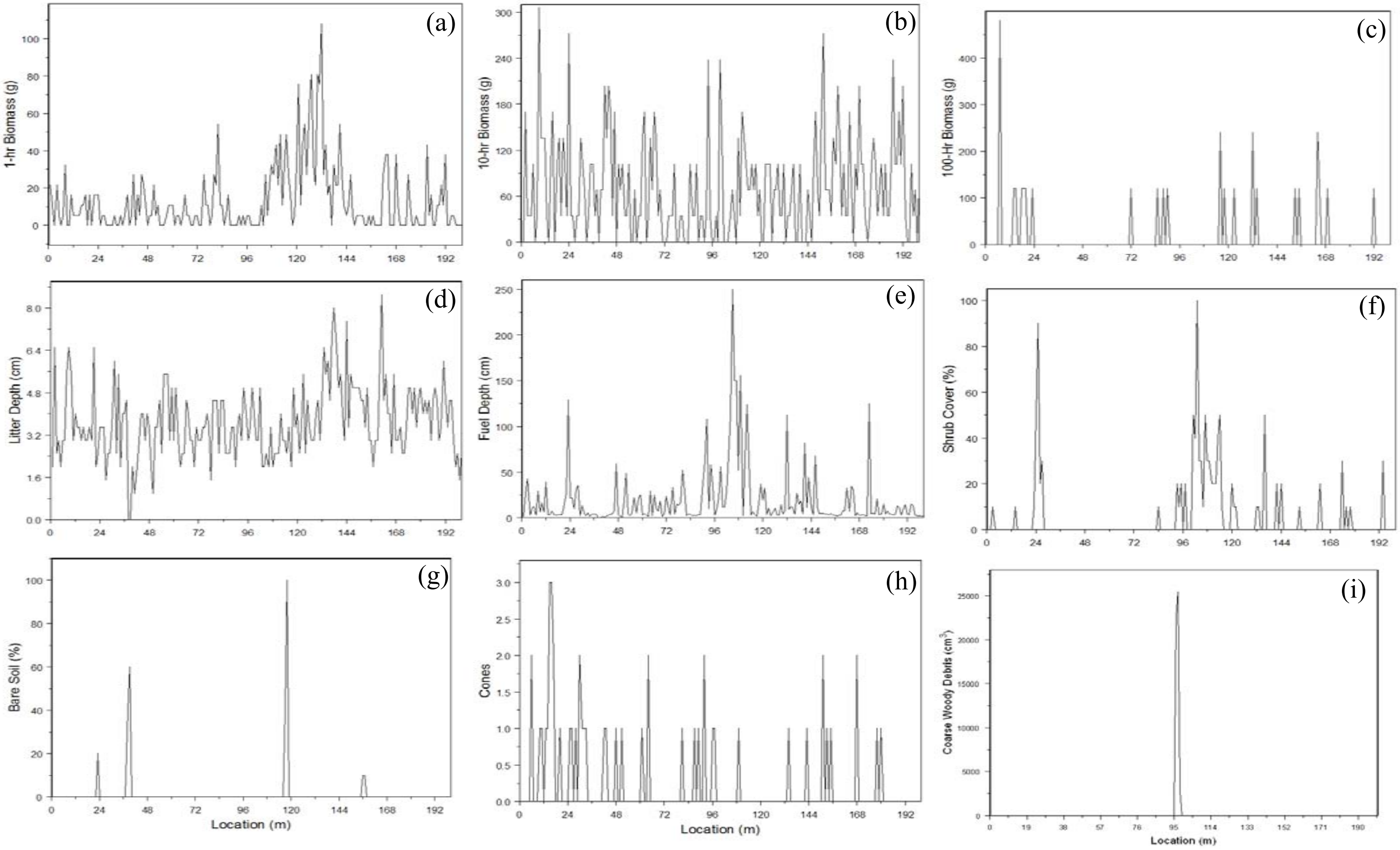


Figure 4.10 Pattern intensity determined by Three-Term Local Quadrat Variance (3TTLQV) for variables from the shelterwood fire plots (a-f collected from T4 and g-l from T7) at the Escambia Experimental Forest. Large dotted line indicates the mean of 1,000 randomization tests performed on the variance results and small dotted lines indicate the confidence intervals for each randomization test; (a) & (g) maximum temperature (°C), (b) & (h) 1-hr fuel biomass (g), (c) & (i) 10-hr fuel biomass (g), (d) & (j) 100-hr fuel biomass (g), (e) & (k) litter depth (cm), and (f) & (l) shrub cover (%).

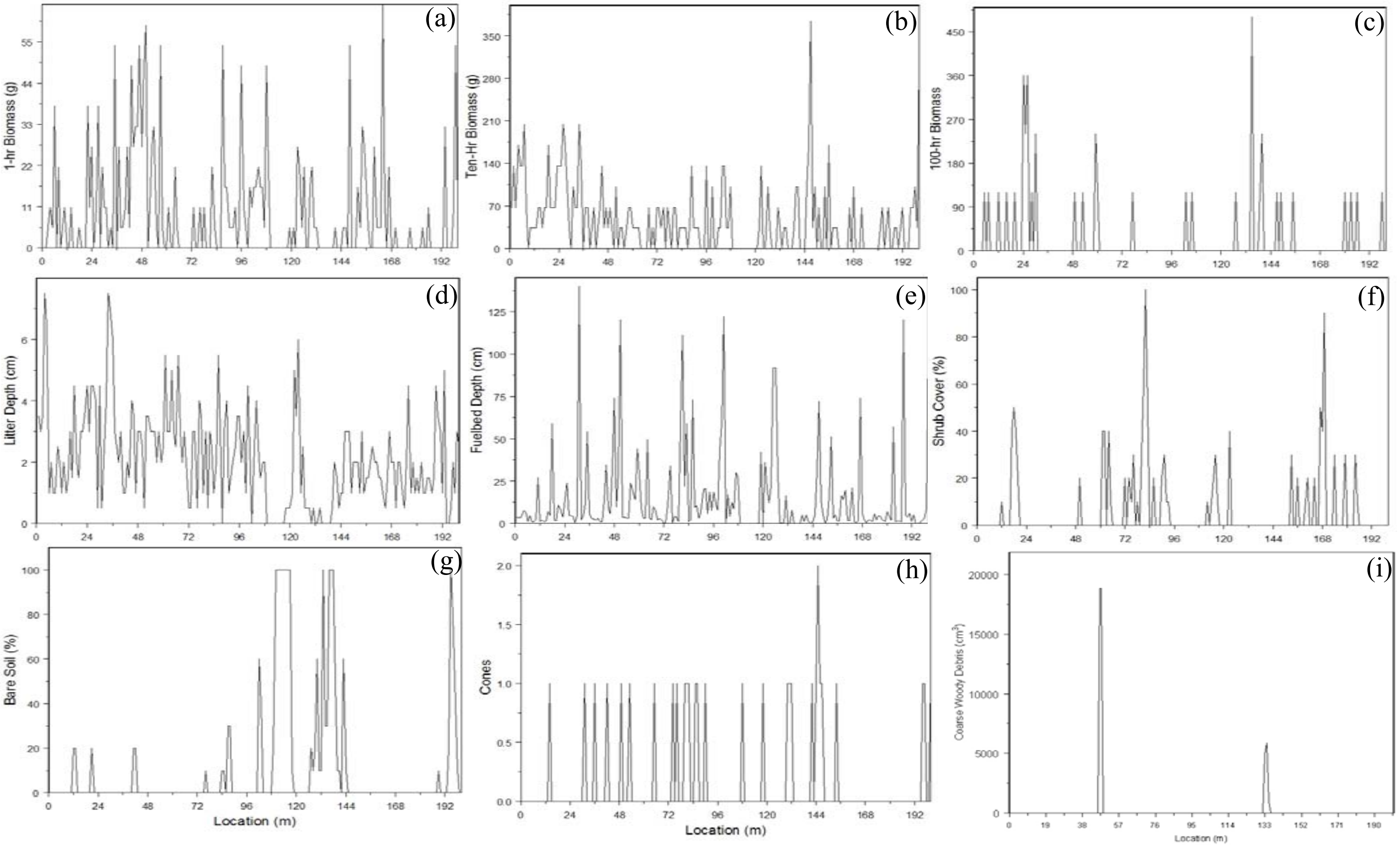


4.7 Appendices

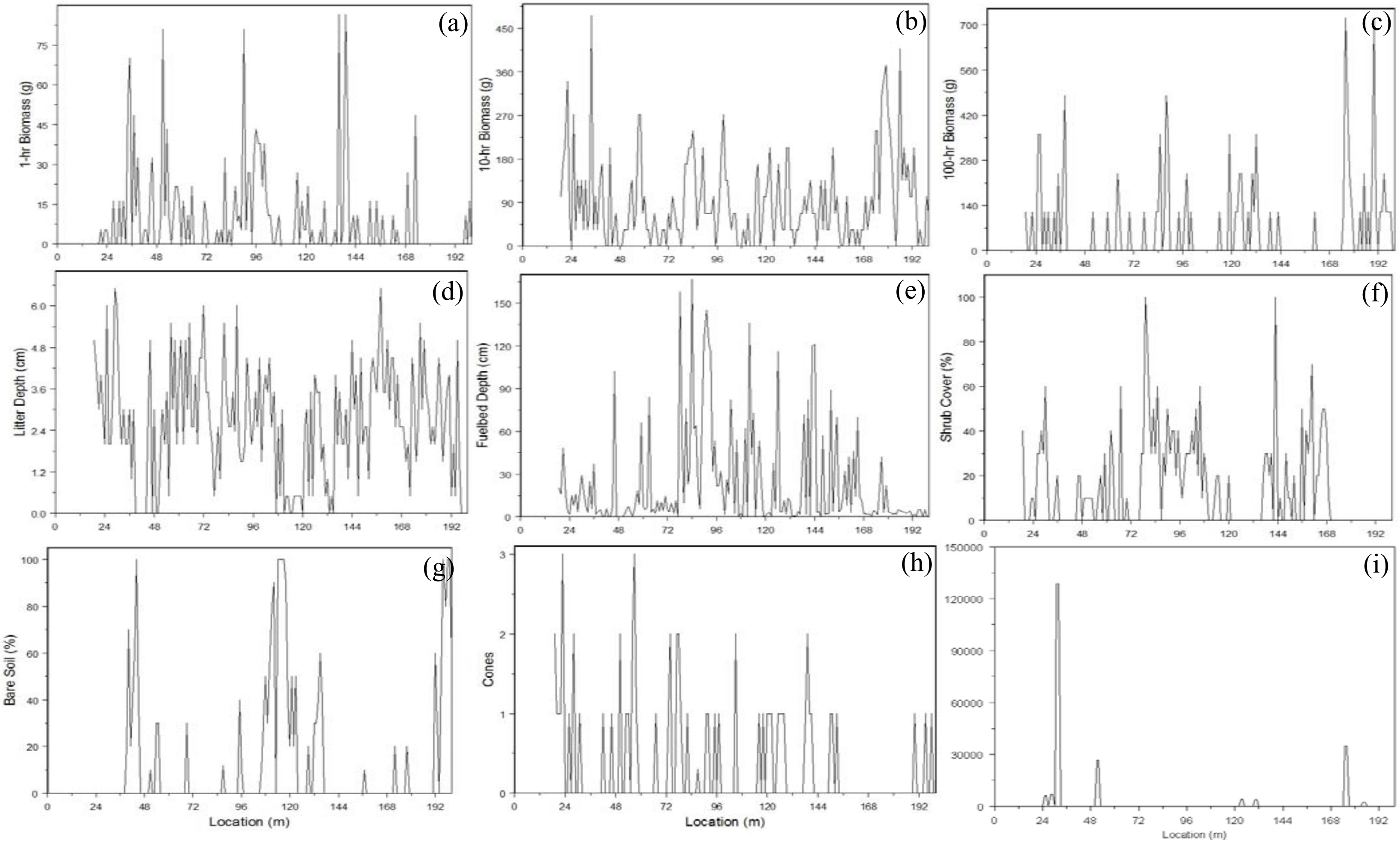
4.7.1 Patterns along T2: a) 1-hr, b) 10-hr, c) 100-hr fuels, d) litter, e) fuelbed depth, f) shrub cover, g) bare ground, h) cones, and i) coarse woody debris.



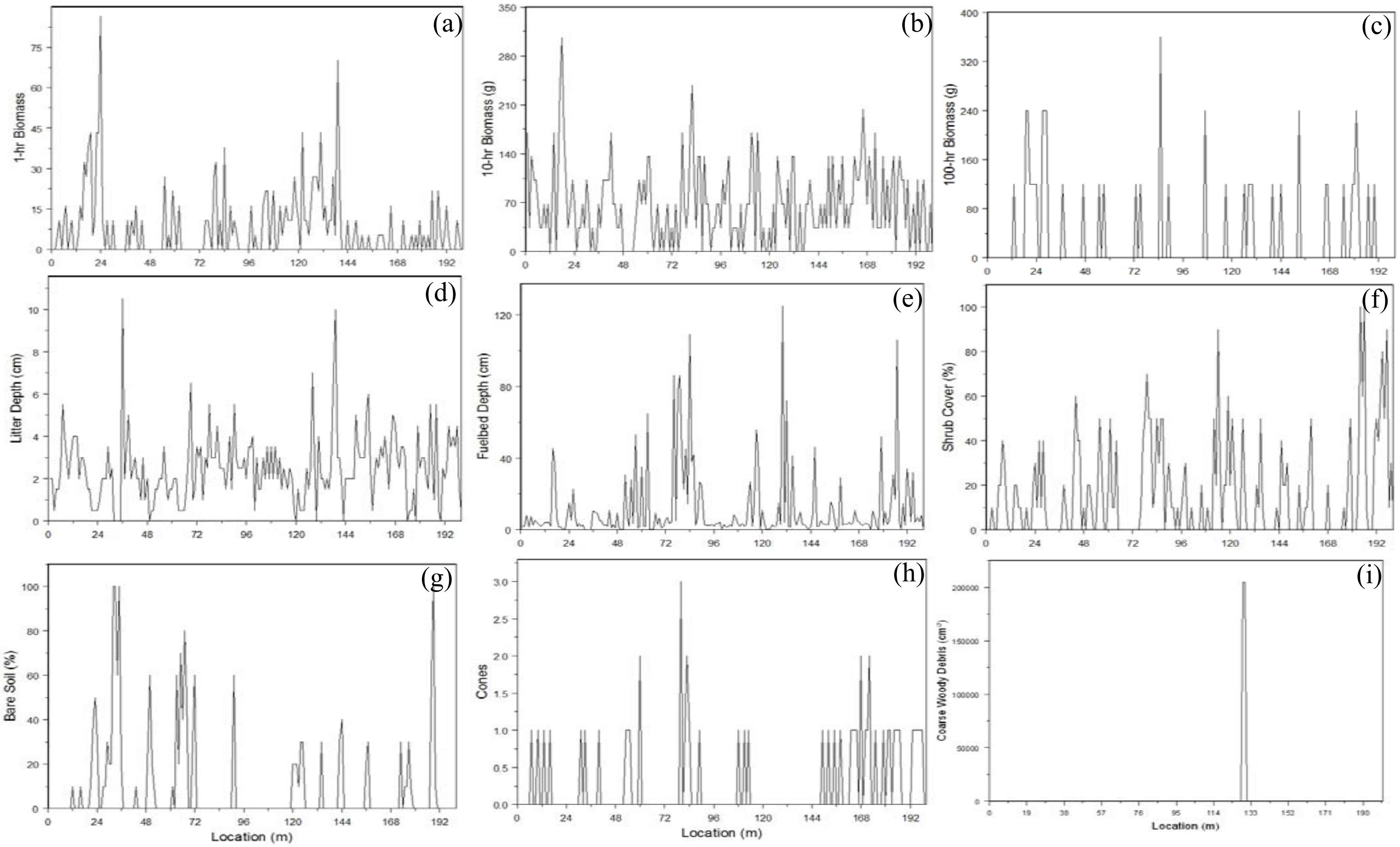
4.7.2 Patterns along T3: a) 1-hr, b) 10-hr, c) 100-hr fuels, d) litter, e) fuelbed depth, f) shrub cover, g) bare ground, h) cones, and i) coarse woody debris.



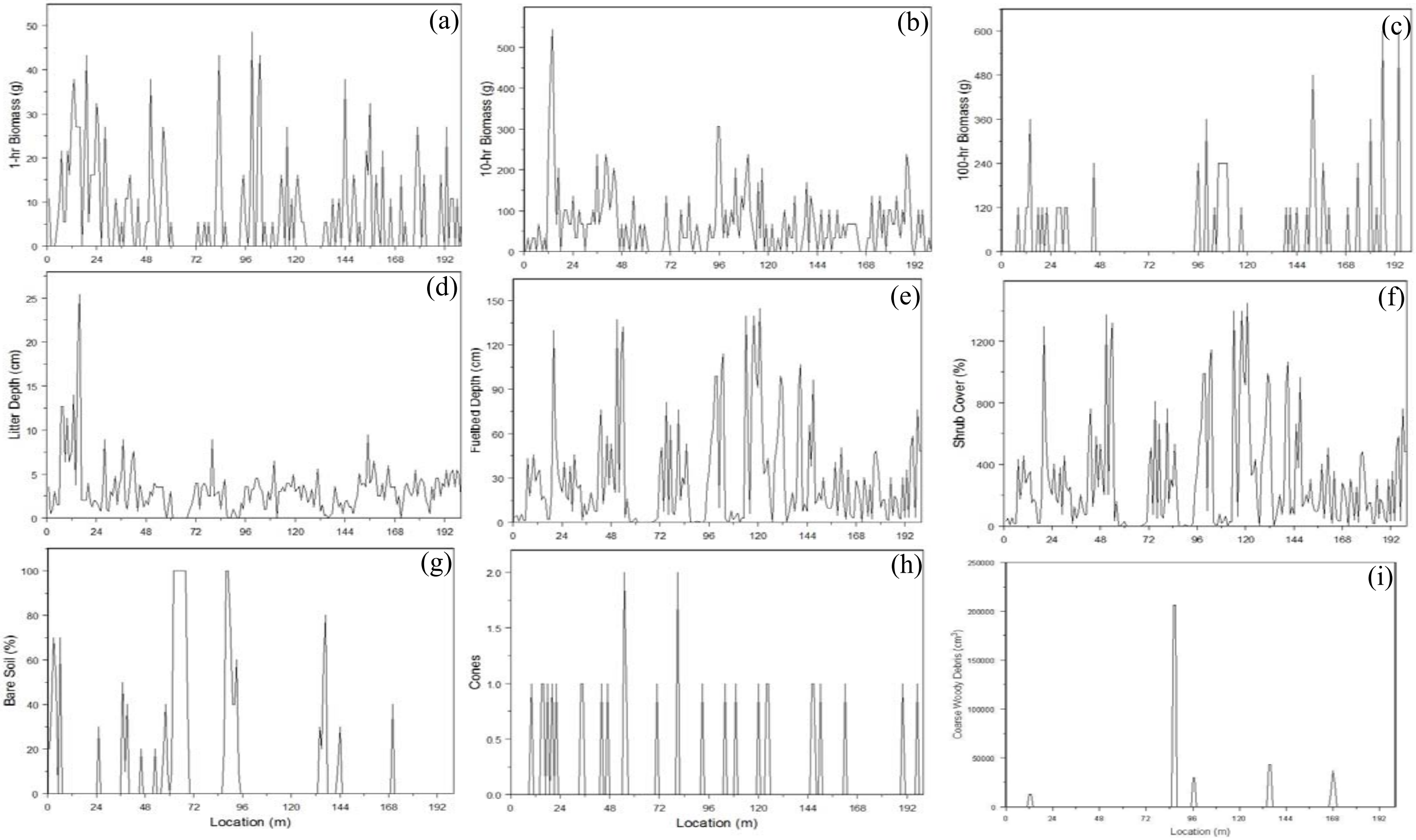
4.7.3 Patterns along T4: a) 1-hr, b) 10-hr, c) 100-hr fuels, d) litter, e) fuelbed depth, f) shrub cover, g) bare ground, h) cones, and i) coarse woody debris.



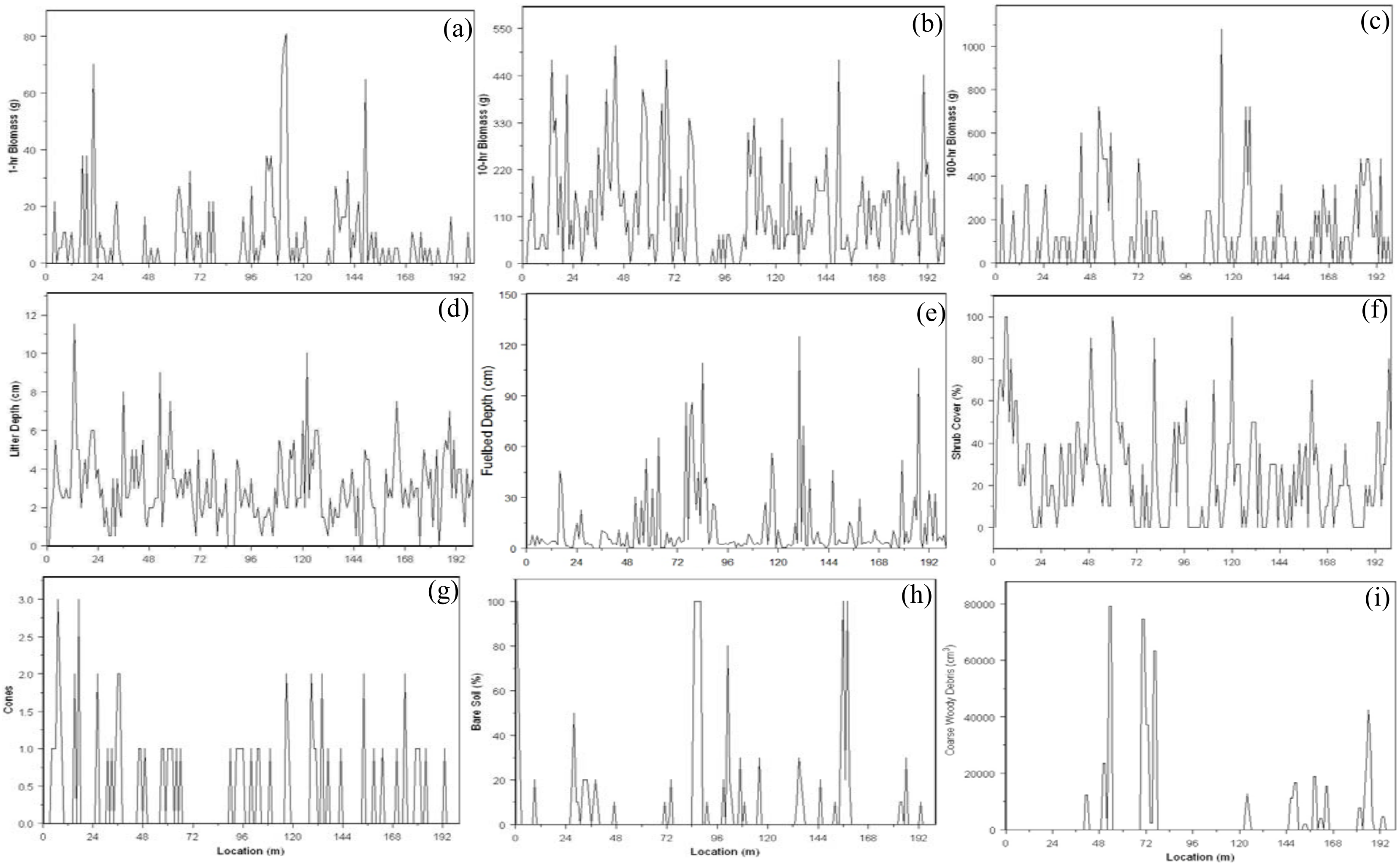
4.7.4 Patterns along T5: a) 1-hr, b) 10-hr, c) 100-hr fuels, d) litter, e) fuelbed depth, f) shrub cover, g) bare ground, h) cones, and i) coarse woody debris.



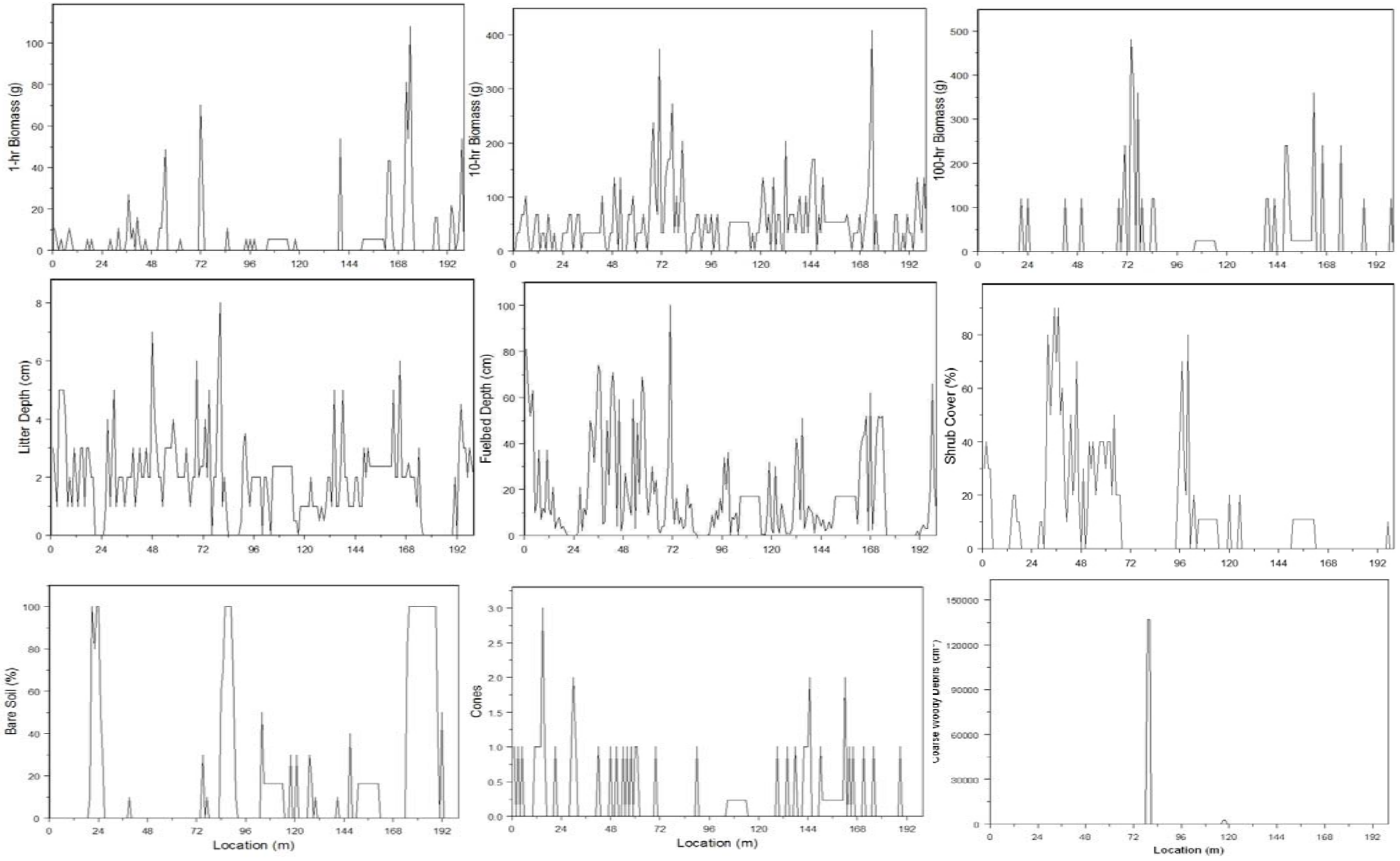
4.7.5 Patterns along T6: a) 1-hr, b) 10-hr, c) 100-hr fuels, d) litter, e) fuelbed depth, f) shrub cover, g) bare ground, h) cones, and i) coarse woody debris.



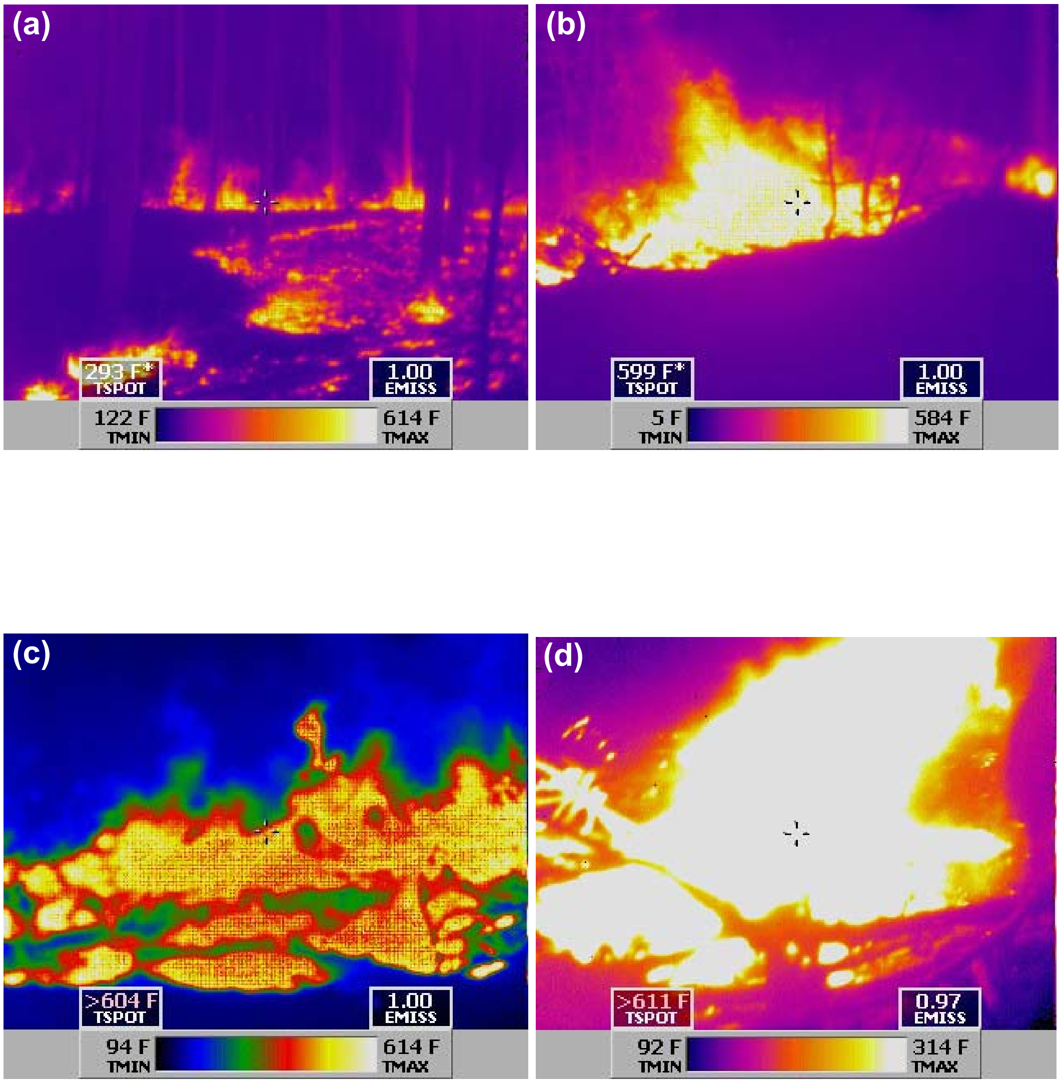
4.7.6 Patterns along T7: a) 1-hr, b) 10-hr, c) 100-hr fuels, d) litter, e) fuelbed depth, f) shrub cover, g) bare ground, h) cones, and i) coarse woody debris.



4.7.7 Patterns along T8: a) 1-hr, b) 10-hr, c) 100-hr fuels, d) litter, e) fuelbed depth, f) shrub cover, g) bare ground, h) cones, and i) coarse woody debris.



4.7.8 Captures from infrared camera: along (a) & (b) T4 (group selection), (c) & (d) T7 (shelterwood plot). The temperature in the left corner indicates approximate scale and mean where point was taken.



5 PATTERNS OF VEGETATION RECOVERY IN RESPONSE TO FIRE INTENSITY

5.1 Abstract

Disturbance, especially fire, influences vegetation recovery in longleaf pine forests. Fire intensity and post-disturbance characteristics were assessed at the Escambia Experimental Forest to determine impacts on the composition of the understory community in longleaf pine forests. Data were collected along seven 200 meter transects that had differential regeneration methods applied in the summer of 2004: no harvest, selection and shelterwood harvest. Community species composition in each plot was further altered by Hurricane Ivan (September 2004). Maximum temperature was determined at 1-meter intervals during prescribed fires (Winter 2005) utilizing pyrometers. Forest floor consumption (percent of litter burned) and bare soil cover were determined post-burn at each pyrometer station. Percent cover was recorded by plant species along the transects in each plot one growing season post-burn. Ordination techniques indicated that *Pityopsis graminifolia*, *Lespedeza procumbens*, *Solidago odora, Sassafras albidum*, *Cornus florida, Andropogon* spp., *Aristida* spp., *Ilex glabra*, *Gaylussacia dumosa*, *Prunus serotina*, *Nyssa sylvatica*, and *Quercus falcata* recovery may have been increased by the prescribed fires. These species colonize with various

methods of recovery often found in fire-dependent communities: re-sprouters from rhizomes and dormant buds, clonal growth, and seed germination. Other species such as *Dichanthelium* spp., *Smilax* spp., *Ceanothus americanus, Carphephorus odoratissimus, Rubus* spp., and *Panicum* spp. appeared to require bare soil to re-colonize areas in the longleaf pine understory. Small-scale fire intensity variation is a common denominator in recovery following fire disturbance and has a variable impact on species composition in the community.

5.2 Introduction

Landscape and small scale disturbances affect both structure and composition of ecological communities. Response of vegetation to disturbance depends on three factors associated with the disturbance regime: frequency, intensity, and severity (Sousa, 1984; White and Pickett, 1985; Chaneton and Facelli, 1991; Williams et al., 1994). Community structure and species characteristics are also important in determining post-disturbance plant response (Whelan, 1995). Longleaf pine communities are disturbance-mediated by frequent low intensity surface fires and infrequent wind disturbance in the form of hurricanes (Wahlenberg, 1946). These dominant disturbances have different impacts on stand physiognomy and understory composition (Gilliam et al., 2006).

Fire is an important factor in the persistence of longleaf pine communities. Frequent low intensity fires, occurring every 1-3 years, are important in maintaining vertical and horizontal structure in fire-dependent communities (Heyward, 1939; Landers et al., 1995; Palik and Pederson, 1996; Carter and Foster, 2004). These fires were historically ignited naturally by sporadic lightning strikes and the process has been maintained with prescribed fires (Wahlenberg, 1946; Campbell, 1955; Komarek, 1977). The shift from naturally occurring wildfire to prescribed fire could alter fire-dependent communities. This is especially true of prescribed fires that are conducted in cooler seasons that may lack the spatial variability of naturally occurring growing season fires (Franklin et al., 1997; Slocum et al., 2003; Rocca, 2004).

Fire exclusion has more obvious effects in longleaf pine forests altering structural heterogeneity, increasing litter depth and changing species composition. These changes eventually lead to crown closure and succession to shade tolerant overstory species that reduce understory species richness (Frost et al., 1986; Bridges and Orzell, 1989; Kush and Meldahl, 2000). Longleaf pines also decrease in importance as their seedlings cannot adequately establish without access to mineral soil and reduced competition from shrubs (Kush and Meldahl, 2000).

Some have hypothesized that longleaf pines are self-perpetuating by producing large pyrogenic needles that facilitate fire (Grace and Platt, 1995). Longleaf pines and associated forb and grass species (i.e., *Aristida* spp., wiregrass, and *Andropogon* spp., bunchgrasses) are extremely resilient to the historically occurring surface fires (Abrahamson and Hartnett, 1990). Fires allow these species to persist and flourish in this disturbance prone environment (Landers et al., 1995). Longleaf pines have adapted to frequent fire in a number of ways: 1) regenerating in relatively open patches characteristically low in adult tree density, 2) remaining in the grass stage to protect the terminal bud, 3) bolting several feet to escape the flame lengths common in surface fires, 4) natural pruning of bottom limbs to reduce ladder fuels and 4) thick bark to protect vascular cambium from lethal heat (Chapman, 1932; Grace and Platt, 1995; Abrahamson and Abrahamson, 1996).

Patterns of fire spread and intensity are very important in determining vegetation composition and structure (Rebertus et al., 1989). Fire intensity is a measure of the heat that is released during a fire expressed as the amount of fuel, the specific fuel's heat of combustion and the rate of spread (Whelan, 1995). Rate of spread is critical because it determines the residence time of the flaming front and lethal fire temperature (Whelan, 1995). Fire intensity is influenced by characteristics such as fuel load, type, arrangement, and moisture, as well as climate and topography (Hobbs and Atkins, 1988; Whelan, 1995; Franklin et al., 1997; Archibold et al., 1998). Maximum fire temperature is often used as an indicator of fire intensity can have dramatic impacts on vegetation, influencing growth and survival of rhizomes as well as seed germination (Glitzenstien et al., 1995; Iverson et al., 2004; Thaxton and Platt, 2006).

Fire intensity, spread, and residence time vary among fires, but more importantly can vary within a single fire across a landscape thereby increasing fire patchiness and resource heterogeneity (Franklin et al., 1997). The post-fire environment is a function of fuel consumption, subsurface heating, and fire behavior. Following a fire, physical and biological changes occur in soil microbe populations, plant root survival, soil moisture, available organic matter and nutrient availability (Whelan, 1995). These changes influence the response of individual plants to the post-burn environment.

Fire affects plant communities directly through mortality but also indirectly through changes in the post-burn environment. Post-fire survival of an organism depends on the morphological and structural traits of the specific species, resulting in variable spatial patterns (Thaxton and Platt, 2006). Species respond to the resource changes by seed release, re-sprouting, clonal growth and seedling establishment (Hobbs and Atkins, 1988; Franklin et al., 1997; Menges and Hawkes, 1998). Some species rely on fire to scarify seeds, while others sprout prolifically in the post-burn environment (Olson and Platt, 1995; Menges and Hawkes, 1998; Drewa et al., 2002a). Fire also stimulates flowering of a variety of native plants, thus increasing recruitment but often having little effect on population structure (Brewer and Platt, 1994; Brewer et al., 1996; Kirkman et al., 1998).

Effects of disturbance on the landscape are patchy, creating gaps characterized by increased light and nutrients and decreased litter depth (Robichaud and Miller, 1999; McConnell and Menges, 2002). Various plant species react differently to these changes in the microenvironment. In this study, species composition was sampled along 7 transects in the Escambia Experimental Forest where fire behavior was observed during winter and spring prescribed burns. Composition was assessed one growing season following the prescribed fires. Species composition was subjected to ordination do determine whether plant population patterns were influenced by the disturbance environment.

5.3 Study Area

The Escambia Experimental Forest (EEF) (31° 01’ N, 87° 04’ W) is located ten kilometers south of Brewton, Alabama and consists of 1,214 hectares of second-growth longleaf pine (Figure 5.1). The EEF is managed by the USDA Forest Service Southern Research Station through a lease with the T.R. Miller Company of Brewton, AL. The

EEF is located within the upper coastal plain. The climate is subtropical with abundant annual precipitation arriving primarily during the long growing season occurring from April to October. Mean average temperatures range from 16 to 33°C in spring and summer with the warmest months in July and August and the coldest ranging from 5 to 20° C (Alabama Cooperative Extension Agency, 2006). Predominant soils are in the Troup series which are typically coarse sands, silts and clays that are low in organic matter and nutrients and have average water holding capacity. Surface slopes range from 5-15% with numerous drainages across the landscape (Mattox, 1975).

The dominant tree species at the EEF is second-growth longleaf pine (80%) that was naturally established from the 1958 seed crop (Boyer and Miller, 1994). The remaining 20% of the site is in pine-hardwood bottoms. In the longleaf pine stands, all stages of growth are represented from seedlings to saplings to mature trees ranging from 9 to 88 years of age (Boyer et al., 1997). The midstory is occupied by a variety of scrub oaks and the understory consists of grasses, forbs, shrubs, and vines.

5.4 Methods

This research is a part of a larger study conducted by the USDA Forest Service, Southern Research Station. The Comparative Analysis of Forest Reproduction Treatments (CART) study's primary objective is to evaluate the short- and long-term management and ecological consequences of forest regeneration methods on the overstory, midstory, and understory across three longleaf pine sites in the Southeast (Brockway and Outcalt, 2004).

Eight 200-m Transects (T), each surrounded by 9-ha compartments of high quality longleaf pine forest, were considered in the post-fire vegetation analysis (Figure 5.1). The area surrounding each transect consisted of compartments utilized by the CART study and represented five forest management treatments. Each transect was located in the center of the eight compartments and was laid out at a random azimuth. Metal stakes were located at the center and the ends of each transect and each location was mapped with a Global Positioning System (GPS) for ease of relocation. Only seven transects were analyzed due to logistical constraints following Hurricane Ivan and subsequent salvage operations that left the compartments with high amounts of coarse woody debris and bare soil, along with low residual basal area (Estes, Ch. 4). The compartment that contained T1 was dropped from the analysis because a logging deck that was placed in the center of the plot resulted in a discontinuous prescribed fire that passed along only 50 m of the transect. Transects where fire intensity was observed remained relatively intact and were representative of the original forest management goals.

5.4.1 Overstory Removal

Five forest management treatments were conducted on the EEF involving various types of overstory removal to promote regeneration in late summer and early fall of 2004 (Table 5.1). Transects 7 and 4 were located in the shelterwood management compartments and were reduced to 7 m^2/ha BA with the major difference between the uniform (T7) and irregular shelterwood (T4) being the retention of all or part of the overwood in the latter (Table 5.1). The group (T3 and T6) and single tree (T8) management treatments were reduced to 9-14 m^2/ha (Table 5.1). The group selection created large gaps by removing trees in groups and single tree removed individual trees uniformly to form canopy openings (Table 5.1). The “no harvest” compartment (T2 and T5) had no regeneration method planned and therefore retained overstory cover from 16-23 m^2/ha (Table 5.1).

One month following the completion of logging, Hurricane Ivan (Category 3) struck the Gulf Coast on September 16, 2004. Hurricane Ivan was the fourth most costly Atlantic hurricane to strike the United States throughout recorded history (NOAA, 2006). Damage to the EEF was due in part to high winds (speeds up to 150 kph) and possible tornado touchdowns. The EEF suffered substantial overstory mortality that occurred in patches across the landscape. Forest management compartments harvested to a shelterwood were highly vulnerable to windthrow and breakage, while the selection-treated compartments sustained minor damage. Hurricane impact resulted in reduced basal area across the forest management compartments compared to the projected treatment residual BA including the “no harvest” plots (Estes, in Chapter 4).

The remaining trees that were damaged during the storm were salvaged. The order of events (harvest, hurricane, and salvage) substantially increased fuel loads and created a more discontinuous forest floor as a result of ground disturbance caused by heavy logging machinery.

5.4.2 Vegetation Sampling

Vegetation data were collected along 7 transects at every meter so that each had a set of point referenced data. Vegetation was sampled in the same time frame as earlier data collection and can be found in Figure 5.1. This resulted in a data set documenting vegetation patterns along all seven transects. Trees, shrubs, vines, grasses, and forbs were recorded using a line-transect method along the 200 meters recording a total at every 1-m increment. Every time a species crossed the tape in each 10 cm section a hit was recorded for a total of 10 hits per 1 meter segment. Species and genus were recorded for all vegetation encountered following the specific taxonomic authorities (Radford et al., 1968; Clewell, 1990; Miller et al., 2005; NRCS, 2006).

5.4.3 Fire Intensity

All of the forest management compartments were burned in either Winter (February) or Spring (April) fires in 2005. Originally, all of the compartments were to be burned on a spring fire regime but Hurricane Ivan created high fuel loads and a dangerous situation for residual longleaf trees so the prescribed fire plan was changed to low intensity winter burns. The compartment containing T6 was an exception due to the late completion of salvage operations and had to be burned in the spring.

Fire intensity was estimated by measuring the maximum temperature that occurred during the prescribed fires. Fire temperature (°C) was estimated using pyrometers. These use industrial heat sensitive paints that are manufactured to melt at a specific minimum temperature (Wally et al., 2006). The pyrometers measure only the maximum fire temperature incurred and not the residence time of the flame front. Pyrometers have been used to predict temperature and provide information on spatial variability and post-fire effects (Hobbs et al., 1984; Perez and Moreno, 1998). The pyrometers were two copper plates sandwiched together and painted on the inside with 15 dots of Omegalaq® heat sensitive paints that made up 14 categories: 1 – ≤78°C (no heat sensitive paints melted), 2 - 79 to 92°C, 3 – 93 to 120°C, 4 – 121 to 148°C, 5 – 149 to 176°C, 6 – 177 to 203°C, 7 – 204 to 231°C, 8 – 232 to 259°C, 9 – 260 to 287°C, 10 – 288 to 315°C, 11 – 316 to 342°C, 12 – 343 to 370°C, 13 – 371 to 426°C, 14 – 427 to 481°C, 15 – 482 to 537°C, and 16 – 538 to 592°C and 17 - ≥593°C above. The lower temperature in each range represents the melting point of each paint while the upper temperature range represents the highest melting point before reaching the lower range of the next paint. To find out detailed information of the results of the fire intensity study refer to Estes, Ch. 4 in this publication.

Copper pyrometers have proven to be successful at predicting the 1-minute mean temperatures found using thermocouples and are, therefore, an inexpensive accurate way of estimating fire temperature (Wally et al., 2006) The pyrometers were placed at average shrub height (30 cm) which is often the height of the highest flame length in longleaf pine understory burning (Perez and Moreno, 1998; Kennard et al., 2005). Pyrometers were placed at every 1m along the seven 200 meter transects. To standardize the recording procedure of the maximum temperatures, all temperature ranges on the pyrometers were subjected to known temperatures in a muffle oven. So that each pyrometer used in the field would be given the same rating, each paint was assessed for its melting characteristics.

5.4.4 Forest Floor Consumption and Bare Soil Percent

Immediately following cessation of smoldering, post-burn characteristics were assessed. Prior to each prescribed burn, duff pins (long metal nails) were placed at every meter next to pyrometers with the nail head flush with the top of the litter layer. As the flame front passed over the duff pins, litter was reduced partially or totally and this was recorded as the difference between pre-burn forest floor depth and post-burn forest floor depth. Bare soil percent was also recorded at every meter along the transect to indicate the degree of disturbance caused by harvesting and salvage operations.

5.4.5 Data Analysis

Species composition was generated as a 200 x n matrix with all n species names abbreviated using USDA codes (NRCS, 2006). The codes along with the genus and species name are found in Appendices 5.8.1-5.8.7. Descriptive statistics were calculated with PC-ORD 4.0 and included species frequency, average cover, and species counts or the number of non-zero species occurrences in each sampling unit (Appendices 5.8.1 – 5.8.7). Following the analysis that included all species, rare species (< 5% presence in each 1 meter section) were excluded from the data which left data sets consisting of 25 - 35 species sampled along the transects at the EEF. Environmental variables (maximum fire temperature, forest floor consumption, and bare soil) were also presented in a 200 x 3 matrix and all values were relativized by the maximum.

The hypothesis that was tested in this study was the H_o: There is no linear relationship between the species matrix and the environmental matrix. To assess this hypothesis, a Canonical Correspondence Analysis (CCA) ordination was chosen. Ordination is an important technique that attempts to take multivariate ecological data and to represent it in n-dimensional space so that the distance similarities provide insight into complex community relationships that can be related to environmental pattern (McCune and Grace, 2002). All CCA models were performed using PC-ORD 4.0 (McCune and Meddord, 1999). In this direct ordination technique, species scores are optimized as weighted mean site scores and standardized to the column totals (McCune and Grace, 2002). After standardization, the distances are averaged and a regression is performed. The distance was approximated using chi-square techniques and this yielded the Weighted Averaging (WA) scores (Palmer, 1993; McCune and Grace, 2002). A multiple linear regression least squares analysis was performed using site scores and the environmental matrix produced the Linear Combination (LC) scores (Palmer, 1993). The site scores were then rescaled so the mean is equal to 0 and the variance is 1. Monte Carlo tests were then conducted with 999 randomizations to test if the eigenvalues differed from what would occur at random and whether a linear relationship between the species and environmental matrices existed.

For each CCA, the first axis was interpreted. Biplot figures were created using the scaled LC plot scores derived from species scores and environmental variables were represented as arrows on the figures (McCune and Grace, 2002). These arrows indicate the correlation of the variable with species composition with varying length indicating strength and angle indicating correlation (Palmer, 1993). The location of the species scores with respect to the environmental arrows may indicate environmental requirements for each species (Palmer, 1993). Biplot figures were also presented where each species score was represented as plant growth habit.

5.5 Results

All of the study plots were burned in the Winter of 2005 with the exception of T6 that was burned in the Spring after completion of salvage operations following Hurricane Ivan. The compartment containing T1 was not included in the analysis as the prescribed burn was incomplete due to increased litter disturbance from subsequent salvage operations. Observation of fire weather and fire intensity are presented and discussed in Chapter 4 of the dissertation.

Species frequency, average cover, and counts of all plants along the transects can be found in Appendices 5.8.1 – 5.8.7. A summary of all axis data and the results from the multiple regression analysis are presented in Appendix 5.8.8 and 5.8.9, respectively. The weighted correlation matrix showed fire intensity variables had weak to moderate correlations with one another indicating they were independent predictors of species distribution (Table 5.2).

The eigenvalues associated with Axis 1 in T2 was below 0.100 although Monte Carlo randomization tests indicated the value was significant ($p = 0.046$) (Table 5.3). The species-environment correlation was not significant despite high intraset correlations between the environmental variables and Axis 1 (Table 5.3 and 5.4). Similar results were seen along T5 as the eigenvalue was significant according to the Monte Carlo tests (p = 0.0170), but the plant species-environmental correlation was only moderately significant (p = 0.0711) despite high intraset correlations (Table 5.5 and 5.6). The biplots although not interpreted are presented in Appendix 5.8.10 for T2 and 5.8.11 for T5.

The transect in the SS treatment (T8) had a moderately high eigenvalue and was significant (p = 0.0010) according to the Monte Carlo tests (Table 5.7). The plant species composition was weakly associated with all three environmental characteristics (p = 0.0801) (Table 5.7 and 5.8). The biplot showed species such as *Dichanthelium* spp., *Smilax* spp., as well as *Rubus* spp. and *Eupatorium album* were influenced by bare soil (Figure 5.2a). Maximum fire temperature and duff consumption both determined species composition as indicated by their shallow angle (Figure 5.2a). Other species appear to be influenced by maximum fire temperature, namely *Pityopsis graminifolia*, *Lespedeza procumbens*, and *Solidago odora* (Figure 5.2a). Some hardwood species also occurred along a fire temperature gradient: *Sassafrass albidum* and *Cornus florida* (Figure 5.2a). Species composition was represented by growth form in the biplot and revealed a trend (Figure 5.2b). Axis 1 can be interpreted as a disturbance gradient with higher intensity disturbance occurring in the higher range. A cluster of forb/herb occurs on the lower end of the disturbance gradient while growth forms associated with ruderal species becomes more prevalent to the high end of Axis 1 (Figure 5.2b).

Along T6 in the GS treatment, the eigenvalue was significant (p = 0.0010) when compared to those expected by chance and the null hypothesis of no relationship between the species data and the environmental data were rejected (p = 0.0070) (Table 5.9). The intraset correlation also indicate that along T6, Axis 1 is correlated with all three environmental variables (>50%) (Table 5.10). Similar results were seen along T3, as the eigenvalue was significant (p = 0.0010) and the species-environmental correlation was also significant (p = 0.0010) (Table 5.11). The intraset correlations were similar to that observed along T6 (Table 5.12). On inspection of the biplots, the relationship between the environmental variables and the species data appear to quite complex (Figure 5.3, 5.4).

The biplots yielded similar results to T8 sampled in the SS treatment (Figure 5.2). Species composition along T6 was influenced by the post-disturbance variables. Certain species such as *Dichanthelium* spp., *Smilax* spp., *Ceanothus amerciana,* and *Carphephorus odoratissimus* were positively associated with increasing bare ground (Figure 5.3a). It is more difficult to determine the contribution of maximum fire temperature and duff consumption, as it appears the two may be acting in conjunction (Figure 5.3a). Certain species such as *Ilex glabra*, *Aristida* spp., *Gaylussacia dumosa*, *Prunus serotina* and *Nyssa sylvatica* were positively associated with fire temperature (Figure 5.3a). In the biplot organized by growth habit, forb/herb and grasses appear to occur in groups along Axis 1 (Figure 5.3b). Along T3, species composition was not influenced by any single measured environmental characteristics rather all three seem to influence species composition (Figure 5.4a,b).

The eigenvalue representing Axis 1 along T7 was significant and intraset correlations were high although it was low in comparison to the other transects (Table 5.13, 5.14). The biplot representing T7 was not interpreted but can be found in Appendix 5.8.12. The transect in the SH (T4) treatment had a substantially high eigenvalue (0.15) and Monte Carlo tests indicated both axes had a higher probability (p = 0.0010) of occurring than by chance alone (Table 5.15). Only the first axis along T4 was interpreted and the randomization tests indicated a species-environment interaction that was associated with all 3 factors (p = 0.0010) (Table 5.15). The intraset correlations also indicated a strong negative relationship between Axis 1 and fire temperature and bare soil and a positive relationship between Axis 1 and duff consumption (Table 5.16). The biplot overlay indicates a number of species may require fire: *Andropogon* spp., *Pinus palustris*, *Quercus falcata* and *Ilex glabra* (Figure 5.5a). *Panicum* spp., another species of similar habit to *Dicanthelium* spp., showed a positive relationship with bare soil (Figure 5.5a). A number of species in the Asteraceae family were also observed to require both adequate duff consumption and/or maximum fire temperature (Figure 5.5a). Lumping the species according to growth habit also showed forb/herb habit occurring in groups as well as the forbs from the Asteraceae family (Figure 5.5b).

5.6 Discussion

Fire intensity, estimated by maximum fire temperature, exhibited high rates of variability across the EEF prescribed fires (in Chapter 4, dissertation). Dominant fire-adapted species capitalized on the newly formed microsites as colonization niches. Variability in fire intensity may be attributed to post-burn resource availability and is a complex function in fire-dominant systems.

It was unusual not to see a more pronounced correlation between fire temperature and post-burn fire variables. Typically, forest floor consumption is closely related to the intensity of the flaming front (Clinton et al., 1998; Stanturf et al., 2002; Thaxton and Platt, 2006). In this study, the pyrometers were located 30 cm above the ground and mean litter depth was 2-4 cm coupled with some isolated cases where mounding occurred during harvest and litter depth exceeded 15 cm. As a result, the pyrometer temperature recorded at the shrub height may not have correlated with forest floor consumption. A sub-sample of pyrometer data from the soil surface resulted in 90% of the pyrometers exceeding the maximum measured temperature range of 593°C (unpublished). The complete consumption of the forest floor across the transects may have a greater correlation with the surface maximum temperature ranges. There was also observed smoldering that may have had a greater effect on consumption than the initial flaming front. While fire temperature was spatially variable, forest floor consumption had low spatial variability, as more than 50% of sampling points had complete consumption. Consumption of all available pine litter is common in prescribed fires in longleaf pine forests (Chapman, 1932; Wahlenberg, 1946).

The reduced percent of variance explained by CCA models indicates that unmeasured variables (soil characteristics, slope, light availability) may be equally important in determining vegetation composition (Appendix 5.8.8) (Rome, 1988; Gilliam et al., 1993; Kirkman et al., 1996; Drew et al., 1998; Carter et al., 1999; Rodgers and Provencher, 1999; Smith et al., 1999; Drewa et al., 2002b). In all cases, Axis 1 had high intraset correlations with the measured environmental variables. This shows the complex nature of the interaction between ground and fire disturbance and its effect on species composition.

The majority of species sampled post-disturbance are commonly found in the longleaf pine understory. A number of species observed at the EEF have documented interaction with the fire and/or surface disturbance. *Pityopsis graminifolia* was associated with fire along T8 in the single tree selection compartment and was abundant where it occurred. Brewer (1996; 2006) in two studies noted populations of this particular species was positively influenced by growing season fires. This rhizomatous forb often occupies areas that are devoid of vegetation or patches created by high fire intensity (Brewer et al., 1996). In this study, the creation of patches located in areas of high fire temperature may have increased ramet production by this plant.

Dominant grass species in this area are *Andropogon* spp. (bluestem grass) along with small pockets of *Aristida* spp. (wiregrass). Both perpetuate through clonal growth (Chapman, 1932). Both wiregrass and bluestem species were positively associated with fire temperature in the CCA ordinations (Figure 5.2-5.5). This response to fire intensity allowed species such as wiregrass to take advantage of patches associated with high fire intensity to aggressively re-colonize (Menges and Hawkes, 1998). The influence of fire on bluestem grass has not been sufficiently documented, but there is some evidence that high fire intensity can create patches where re-colonization would be successful (Brockway and Lewis, 1997). Wiregrass occurred at a low frequency across the sampling area in the EEF, so no conclusive statements can be made on the influence of fire intensity. The majority of research links *Aristida* spp. populations to spring fires where fire-induced flowering increases their population (Abrahamson, 1984; Mulligan et al., 2002).

Spatial patterns of vegetation recovery in response to variable fire intensity and ground disturbance differed by species and growth habit (Menges et al., 1993). Shrub species had variable response to fire intensity. This response could have determined rates of re-sprouting that is directly related to canopy cover and shrub density (Abrahamson, 1984; Hierro and Menges, 2002). Although some shrubs appeared to be positively influenced by fire temperature, the overall impact on shrub species was negligible following one dormant season fire, as significant re-growth was apparent along all transects (Figure 5.4, 5.5 and 5.8). Similar rates of shrub canopy cover following fire disturbance have been documented by Hierro and Menges (2002).

Following the fires, shrubs varied in density, but spatial patterns were similar to pre-burn due to clonal growth from dormant buds and re-sprouting. High fire frequency and season of burn may play a larger part in determining shrub composition as shrub re-sprouting is more susceptible to high intensity growing season burns that occur during active growth. Vegetative regeneration is a function of fire patchiness caused by variable fuel cover, fuel moisture, season of burn, and microclimate variability (Matlack and Good, 1989; Matlack et al., 1993).

Other species occurred along the bare soil gradient: *Dichanthelium* spp. and *Panicum* spp. and a number of vine species (*Rubus* spp., *Vitis* spp. and *Gelsemium sempervirens*) are all associated with various degree of disturbance (Swindel et al., 1987; Brockway and Lewis, 1997). Ruderal species respond to fire by capitalizing on the disturbed area and increasing cover dramatically. This is followed by a slow decline as competition increases.

Considerable evidence links increased fuel accumulation to increased fire intensity and, therefore, differential vegetation recovery (Hierro and Menges, 2002; Kennard et al., 2002; Thaxton and Platt, 2006). In this study, an increase in fuel load occurred as a result of harvest, hurricane and salvage disturbance varying in scale and altering litter continuity and fine and coarse woody debris . The majority of studies in longleaf pine communities have focused on the presence or absence of fire and its impacts on vegetation composition and little on vegetation recovery following multiple disturbances (Menges et al., 1993; Brockway and Lewis, 1997).

A number of species capitalized on ground disturbance and the presence of bare soil while other species utilized patches created in response to the variable prescribed fire. Further research could attempt to further partition species into groups reflecting low, moderate, or high levels of fire and surface disturbance.

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Table 5.1 Experimental regeneration treatments applied to forest management plots in the Escambia Experimental Forest.

Harvest	200-m Sampling Transect	Regeneration Method	Projected Residual BA	Description	Projected Canopy Openings (ha)	Prescribed Fire
Irregular Shelterwood (SH)	T4	Two-aged	6-7 m^2/ha	Canopy openings progressively expanded and some mature trees are retained	<0.01 to 0.1 at onset with larger openings over time	Winter
Uniform Shelterwood (SH)	T7	Even	6-7 m^2/ha	Initial cut leaves overstory trees as protective cover then overwood is harvested	<0.01 to 0.1 ending in open conditions	Winter
Group Selection (GS)	T3,T6	Uneven	9-14 m^2/ha	Small groups of trees harvested	0.1 to 0.8	Winter/Spring
Single Tree Selection (SS)	T8	Uneven	9-14 m^2/ha	Individual trees removed maintaining continuous cover	0.01 to 0.1	Winter
No Harvesting (NH)	T1,T2,T5	None	N/A	N/A	N/A	Winter

Table 5.2 Weighted correlations among fire intensity variables.

Transect		Fire Temperature	Duff Consumption	Bare Soil
	Temperature	1	0.28	-0.114
T2	Duff Consumption	0.28	1	-0.034
	Bare Soil	-0.114	-0.034	1
	Temperature	1	-0.175	0.101
T5	Duff Consumption	-0.175	1	-0.256
	Bare Soil	0.101	-0.256	1
	Temperature	1	-0.378	0.188
T8	Duff Consumption	-0.378	1	-0.393
	Bare Soil	0.188	-0.393	1
	Temperature	1	-0.4	0.105
T6	Duff Consumption	-0.4	1	-0.012
	Bare Soil	0.105	-0.012	1
	Temperature	1	-0.334	0.262
T3	Duff Consumption	-0.334	1	-0.29
	Bare Soil	0.262	-0.29	1
	Temperature	1	-0.161	0.325
T7	Duff Consumption	-0.161	1	-0.303
	Bare Soil	0.325	-0.303	1
	Temperature	1	-0.317	0.301
T4	Duff Consumption	-0.317	1	-0.462
	Bare Soil	0.301	-0.462	1

Table 5.3 Monte Carlo test results for eigenvalues and species-environment correlations based on 999 runs with randomized data along T2.

		Randomized data			
Axis		Mean	Minimum	Maximum	*p*
	Eigenvalue				
1	0.091	0.058	0.023	0.241	0.0460
2	0.038	0.036	0.016	0.078	0.3604
3	0.029	0.023	0.007	0.046	0.1522
	Spp-Env Corr.				
1	0.486	0.414	0.261	0.792	0.0801
2	0.339	0.343	0.233	0.491	0.5285
3	0.352	0.281	0.162	0.431	0.0410

Table 5.4 Intraset correlations indicating influential variables in ordination along T2.

Variable	Axis 1	Axis 2	Axis 3
Fire Temperature	-0.85	-0.47	0.23
Duff Consumption	-0.68	0.32	-0.66
Bare Soil	-0.15	0.79	0.59

Table 5.5 Monte Carlo test results for eigenvalues and species-environment correlations based on 999 randomizations along T5.

		Randomized data			
Axis		Mean	Minimum	Maximum	*p*
	Eigenvalue				
1	0.09	0.054	0.025	0.121	0.0170
2	0.065	0.035	0.018	0.066	0.0020
3	0.033	0.021	0.005	0.048	0.0290
	Spp-Env. Corr.				
1	0.445	0.385	0.271	0.532	0.0711
2	0.444	0.327	0.228	0.457	0.0040
3	0.295	0.269	0.135	0.396	0.2402

Table 5.6 Intraset correlations indicating influential variables in ordination along T5.

Variable	Axis 1	Axis 2	Axis 3
Fire Temperature	-0.79	0.37	0.49
Duff Consumption	0.72	0.57	0.39
Bare Soil	-0.09	-0.76	0.63

Table 5.7 Monte Carlo test results for eigenvalues and species-environment correlations based on 999 randomizations along T8.

		Randomized data			
Axis		Mean	Minimum	Maximum	*p*
	Eigenvalue				
1	0.147	0.055	0.026	0.123	0.0010
2	0.047	0.037	0.020	0.073	0.1031
3	0.044	0.025	0.009	0.046	0.0030
	Spp-Env. Corr.				
1	0.486	0.414	0.261	0.792	0.0801
2	0.339	0.343	0.233	0.491	0.5285
3	0.352	0.281	0.162	0.431	0.0410

Table 5.8 Intraset correlations indicating influential variables in ordination along T8.

Variable	Axis 1	Axis 2	Axis 3
Fire Temperature	-0.61	0.33	-0.73
Duff Consumption	0.96	0.25	-0.16
Bare Soil	-0.51	0.71	0.49

Table 5.9 Monte Carlo test results for eigenvalues and species-environment correlations based on 999 randomizations along T6.

		Randomized data			
Axis		Mean	Minimum	Maximum	*p*
	Eigenvalue				
1	0.161	0.064	0.033	0.146	0.0010
2	0.077	0.041	0.022	0.082	0.0020
3	0.042	0.027	0.011	0.054	0.0200
	Spp-Env. Corr.				
1	0.610	0.441	0.299	0.632	0.0070
2	0.508	0.380	0.258	0.559	0.0030
3	0.379	0.322	0.191	0.452	0.0810

Table 5.10 Intraset correlations indicating influential variables in ordination along T6.

Variable	Axis 1	Axis 2	Axis 3
Fire Temperature	-0.80	-0.58	-0.18
Duff Consumption	0.87	-0.50	0.02
Bare Soil	-0.17	-0.24	0.96

Table 5.11 Monte Carlo test results for eigenvalues and species-environment correlations based on 999 randomizations along T3.

Axis		Randomized data			
		Mean	Minimum	Maximum	*p*
	Eigenvalue				
1	0.106	0.041	0.019	0.085	0.0010
2	0.036	0.026	0.010	0.049	0.0591
3	0.032	0.016	0.005	0.031	0.0010
	Spp-Env. Corr.				
1	0.566	0.377	0.263	0.528	0.0010
2	0.334	0.315	0.217	0.429	0.2873
3	0.343	0.254	0.147	0.371	0.0060

Table 5.12 Intraset correlations indicating influential variables in ordination along T3.

Variable	Axis 1	Axis 2	Axis 3
Fire Temperature	-0.64	-0.36	-0.69
Duff Consumption	0.92	-0.36	-0.18
Bare Soil	-0.51	-0.72	0.47

Table 5.13 Monte Carlo test results for eigenvalues and species-environment correlations based on 999 randomizations along T7.

		Randomized data			
Axis		Mean	Minimum	Maximum	*p*
	Eigenvalue				
1	0.077	0.040	0.021	0.107	0.0100
2	0.035	0.026	0.012	0.05	0.0791
3	0.017	0.017	0.006	0.032	0.4384
	Spp-Env. Corr.				
1	0.497	0.407	0.283	0.591	0.0220
2	0.430	0.353	0.254	0.473	0.0190
3	0.293	0.295	0.184	0.418	0.5185

Table 5.14 Intraset correlations indicating influential variables in ordination along T7.

Variable	Axis 1	Axis 2	Axis 3
Fire Temperature	-0.94	-0.34	-0.07
Duff Consumption	0.38	-0.69	0.61
Bare Soil	-0.60	0.59	0.54

Table 5.15 Monte Carlo test results for eigenvalues and species-environment correlations based on 999 randomizations along T4.

		Randomized data			
Axis		Mean	Minimum	Maximum	*p*
	Eigenvalue				
1	0.150	0.054	0.028	0.103	0.0010
2	0.070	0.036	0.018	0.072	0.0020
3	0.039	0.023	0.009	0.040	0.0030
	Spp-Env. Corr.				
1	0.593	0.427	0.321	0.576	0.0010
2	0.499	0.374	0.269	0.510	0.0030
3	0.366	0.313	0.198	0.435	0.0951

Table 5.16 Intraset correlations indicating influential variables in ordination along T4.

Variable	Axis 1	Axis 2	Axis 3
Fire Temperature	-0.73	0.18	0.66
Duff Consumption	0.86	-0.12	0.50
Bare Soil	-0.63	-0.78	-0.03

Figure 5.1 Plot layout and regeneration methods at the Escambia Experimental Forest, 10 km South of Brewton, AL 31° N, 87 ° W.

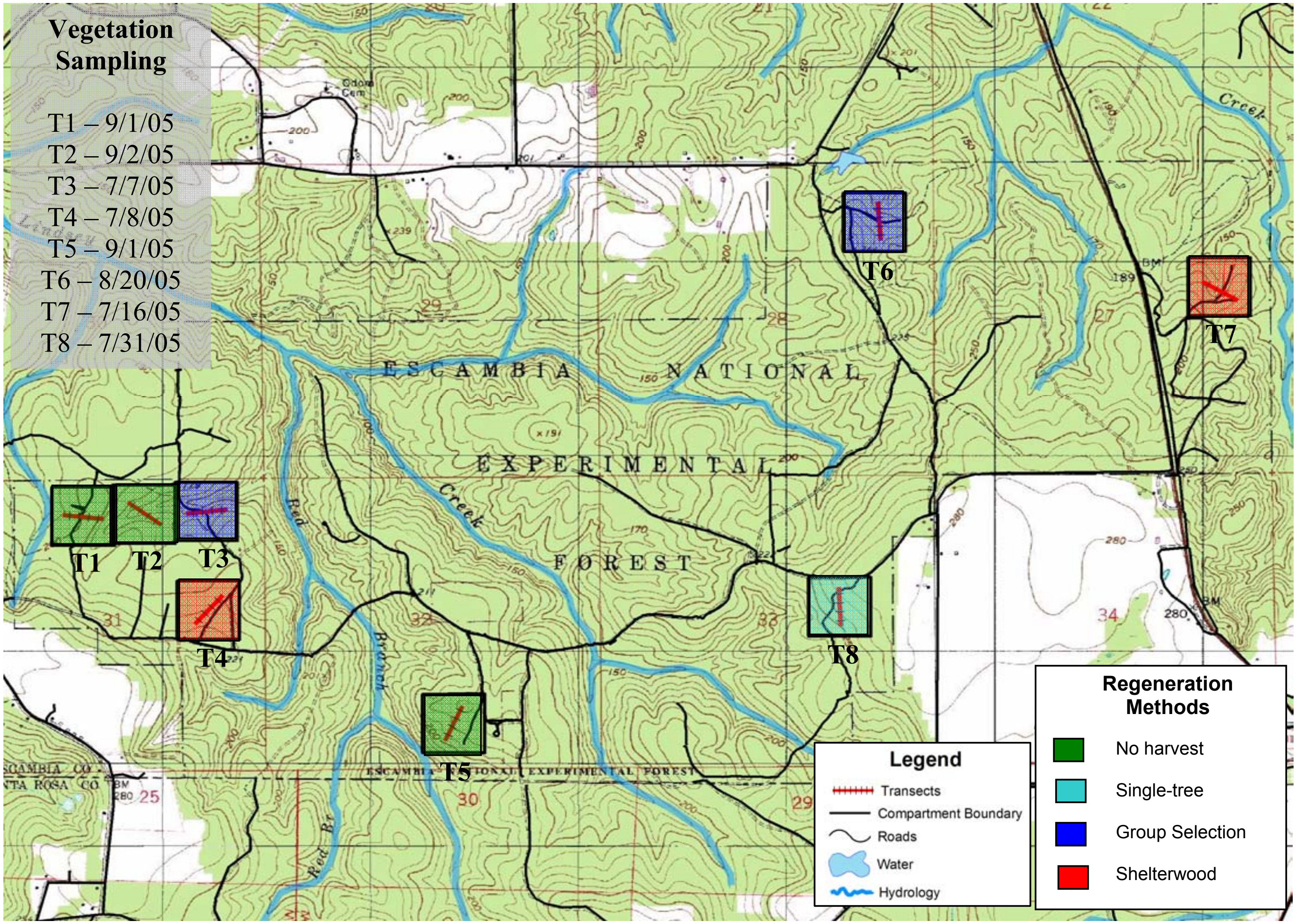


Figure 5.2 Ordination of (a) species and (b) growth form in environmental space along T8 (ST), as defined by CCA using LC scores. The biplot overlay indicates vectors related to the strength of maximum fire temperature, duff consumption, and bare soil. Axes are scaled by standard deviation. Symbols are abbreviations of species encountered and can be found in Appendix 5.8.3.

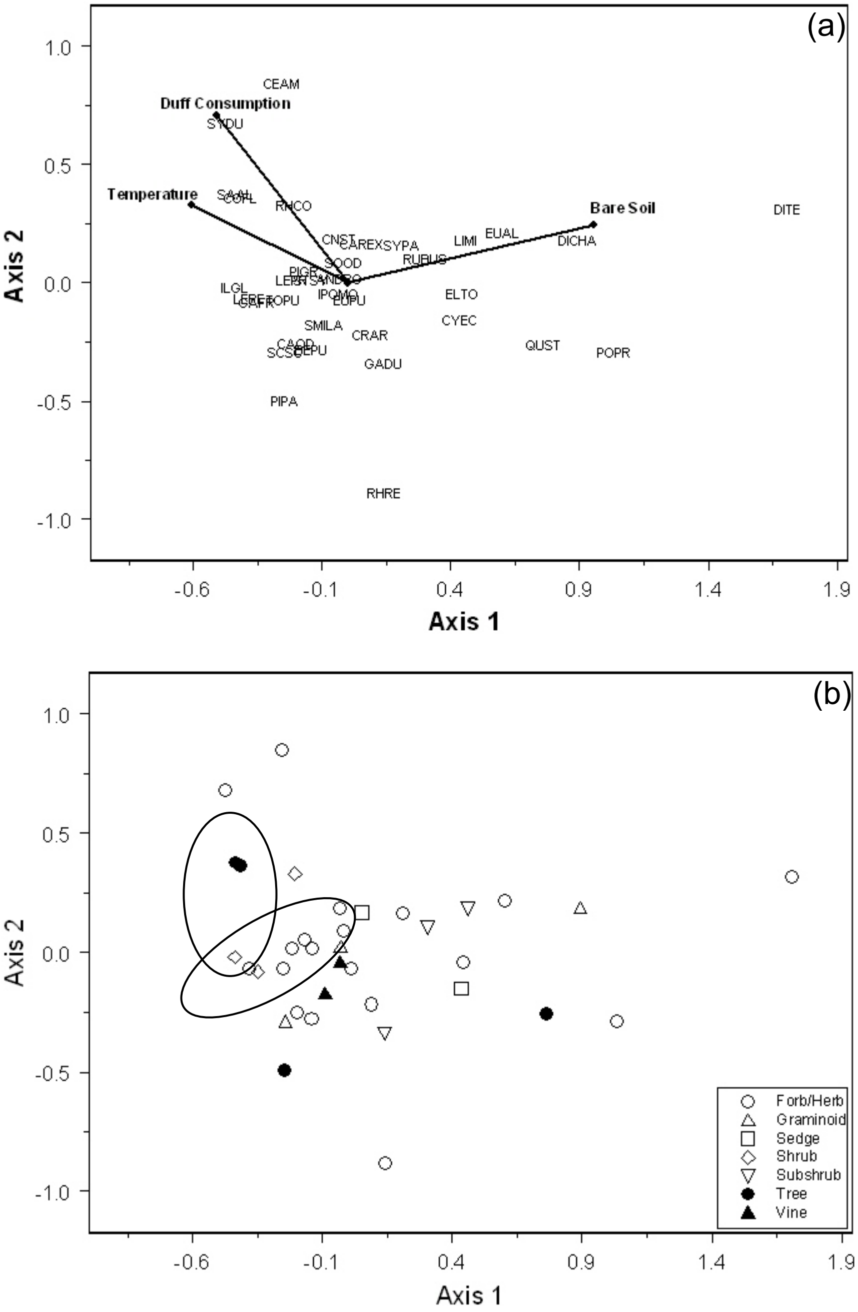


Figure 5.3 Ordination of (a) species and (b) growth form in environmental space along T6 (GS), as defined by CCA using LC scores. The biplot overlay indicates vectors related to the strength of maximum fire temperature, duff consumption, and bare soil. Axes are scaled by standard deviation. Symbols are abbreviations of species encountered and can be found in Appendix 5.8.4.

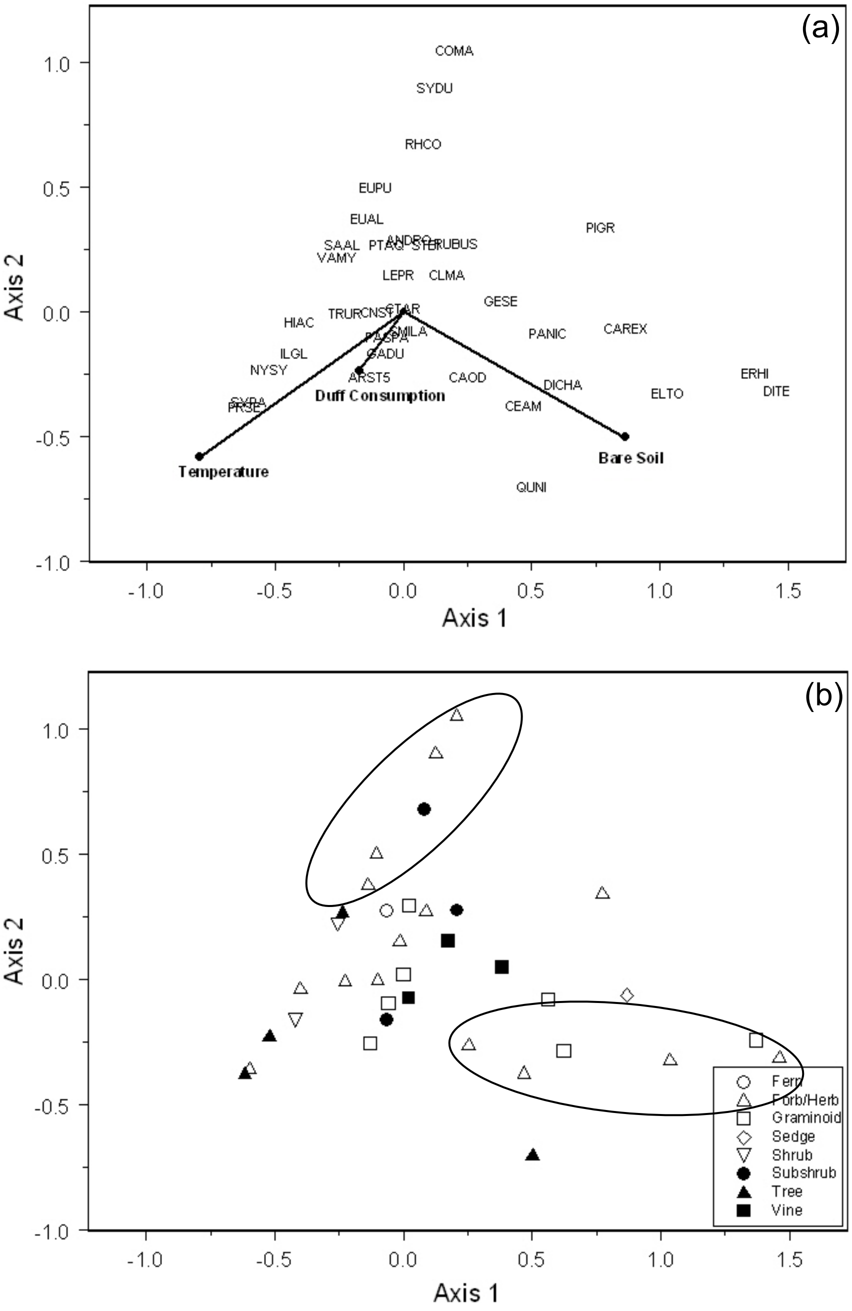


Figure 5.4 Ordination of (a) species and (b) growth form in environmental space along T3 (GS), as defined by CCA using LC scores. The biplot overlay indicates vectors related to the strength of maximum fire temperature, duff consumption, and bare soil. Axes are scaled by standard deviation. Symbols are abbreviations of species encountered and can be found in Appendix 5.8.5.

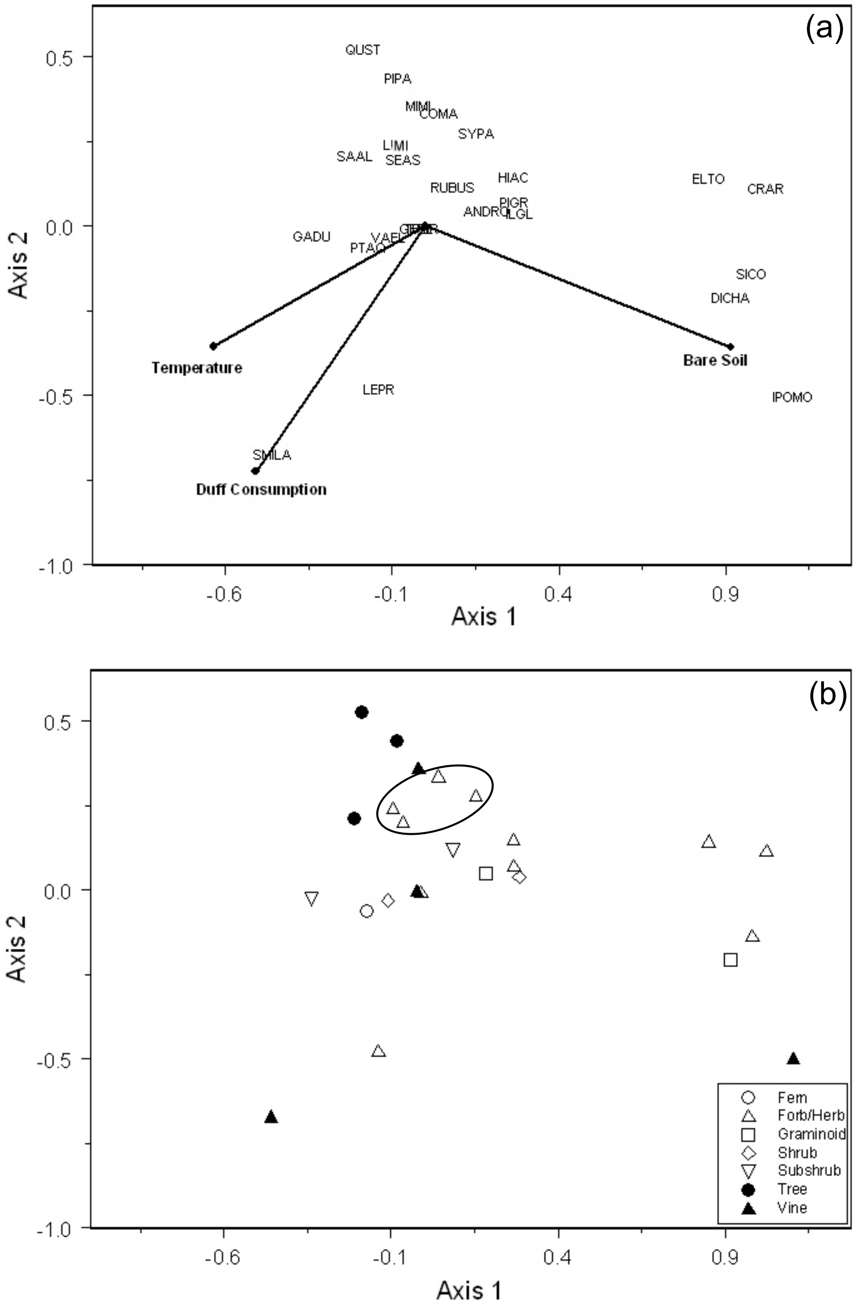
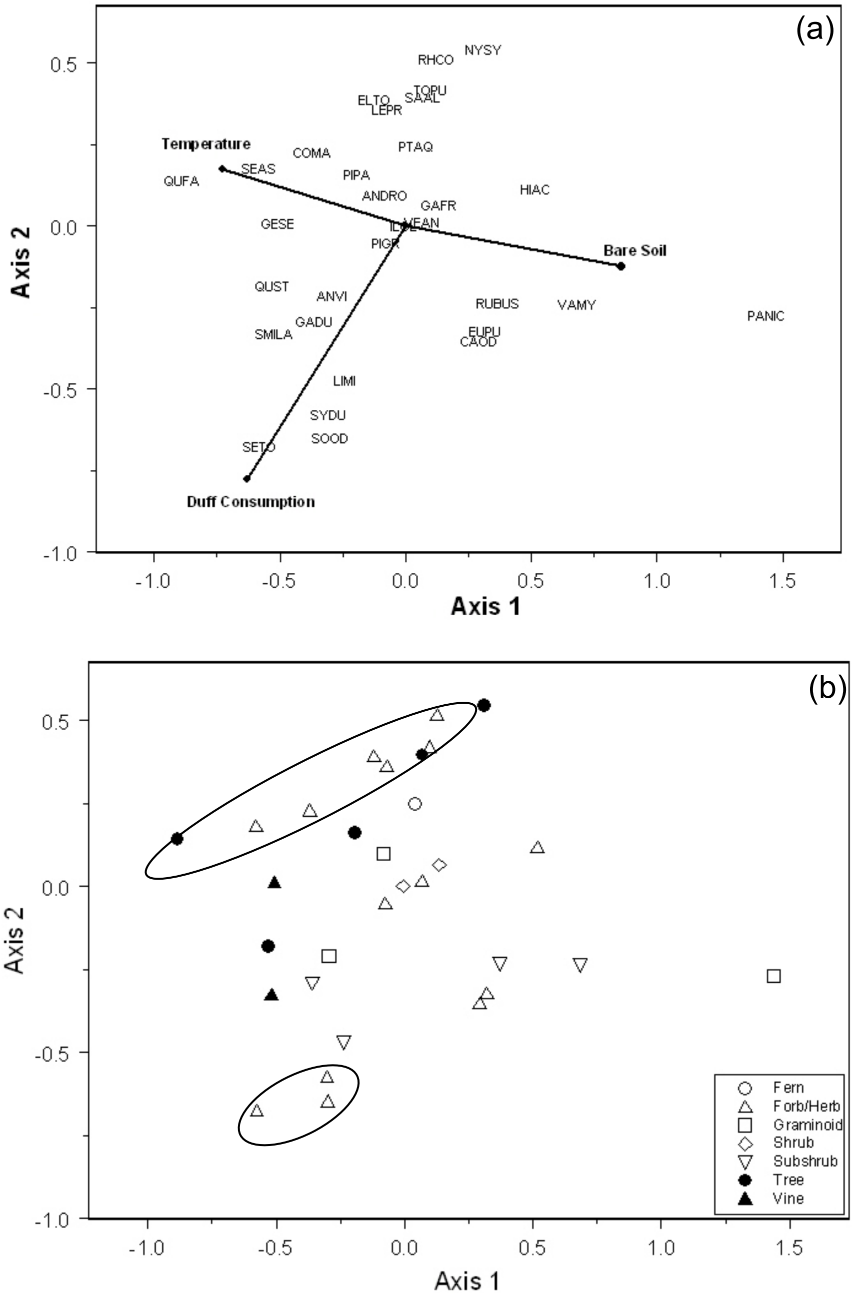


Figure 5.5 Ordination of (a) species and (b) growth form in environmental space along T4 (SW), as defined by CCA using LC scores. The biplot overlay indicates vectors related to the strength of maximum fire temperature, duff consumption, and bare soil. Axes are scaled by standard deviation. Symbols are abbreviations of species encountered and can be found in Appendix 5.8.7.



5.8 Appendices

5.8.1 Post-disturbance average cover, count, and frequency arranged by species code and name along T2 (NH).

Species Code	**Species Name**	**Average Cover**	**Species Count**	**Frequency (%)**
ANDRO	*Andropogon* spp.	12.980	99	50.00
CARYA	*Carya* spp.	2.121	16	8.08
CEAM	*Ceanothus americanus*	0.707	11	5.56
CLMA	*Clitoria mariana*	1.364	21	10.61
COMA	*Coreopsis major*	0.556	9	4.55
DICHA	*Dichanthelium* spp.	2.424	27	13.64
ELTO	*Elephantopus tomentosus*	1.919	22	11.11
GADU	*Gaylussacia dumosa*	3.939	53	26.77
GAFR	*Gaylussacia frondosa*	1.515	20	10.10
GESE	*Gelsemium sempervirens*	14.444	86	43.43
GYAM	*Gymnopogon ambiguus*	0.909	10	5.05
HIAC	*Hibiscus aculeatus*	4.545	40	20.20
LEPR	*Lespedeza procumbens*	3.586	42	21.21
LIMI	*Licania michauxii*	1.111	9	4.55
PIGR	*Pityopsis graminifolia*	2.828	38	19.19
PIPA	*Pinus palustris*	0.859	9	4.55
QUFA	*Quercus falcata*	2.273	19	9.60
QUIN	*Quercus incana*	2.121	13	6.57
QULA2	*Quercus laevis*	1.364	9	4.55
QUNI	*Quercus nigra*	3.434	29	14.65
QUST	*Quercus stellata*	4.343	29	14.65
RUBUS	*Rubus* spp.	3.182	44	22.22
SAAL	*Sassafras albidum*	2.475	31	15.66
SMILA	*Smilax* spp.	2.424	28	14.14
SOOD	*Solidago odora*	0.606	9	4.55
SYDU	*Symphyotrichum dumosum*	1.869	24	12.12
TOPU	*Toxicodendron pubescens*	2.374	37	18.69
TRUR	*Tragia urticifolia*	0.455	9	4.55
VAMY	*Vaccinium myrsinites*	0.909	11	5.56
VITIS	*Vitis* spp.	2.475	20	10.10

5.8.2 Post-disturbance average cover, count, and frequency arranged by species code and name along T5 (NH).

Species Code	**Species Name**	**Average Cover**	**Species Count**	**Frequency (%)**
ANDRO	*Andropogon* spp.	17.121	115	58.08
CAOD	*Carphephorus odoratissimus*	0.455	8	4.04
CEAM	*Ceanothus americanus*	0.808	14	7.07
CRAR	*Croton argyranthemus*	0.657	11	5.56
DICHA	*Dichanthelium* spp.	2.475	36	18.18
ELTO	*Elephantopus tomentosus*	1.162	19	9.60
EUPU	*Euphorbia pubentissima*	0.960	13	6.57
GADU	*Gaylussacia dumosa*	3.434	41	20.71
GAFR	*Gaylussacia frondosa*	3.485	31	15.66
HIAC	*Hibiscus aculeatus*	3.081	23	11.62
ILGL	*Ilex glabra*	2.626	16	8.08
KUST	*Kummerowia striata*	1.566	15	7.58
LEPR	*Lespedeza procumbens*	5.000	51	25.76
LIMI	*Licania michauxii*	0.859	12	6.06
PIGR	*Pityopsis graminifolia*	1.869	25	12.63
PIPA	*Pinus palustris*	0.909	9	4.55
PTAQ	*Pteridium aquilinum*	11.768	65	32.83
QUFA	*Quercus falcata*	2.323	18	9.09
QUIN	*Quercus incana*	1.919	16	8.08
QUST	*Quercus stellata*	2.172	19	9.60
RUBUS	*Rubus* spp.	0.758	10	5.05
SAAL	*Sassafras albidum*	8.081	61	30.81
SETO	*Sericocarpus tortifolius*	1.010	20	10.10
SMILA	*Smilax* spp.	6.364	60	30.30
STSY	*Stillingia sylvactica*	0.707	9	4.55
TOPU	*Toxicodendron pubescens*	2.374	30	15.15
VAMY	*Vaccinium myrsinites*	2.222	15	7.58
VITIS	*Vitis* spp.	2.222	20	10.10

5.8.3 Post-disturbance average cover, count, and frequency arranged by species code and name along T8 (SS).

Species Code	**Species Name**	**Average Cover**	**Species Count**	**Frequency (%)**
ANDRO	*Andropogon* spp.	15.174	96	55.81
BEPU	*Berlandiera pumila*	0.930	12	6.98
CAOD	*Carphephorus odoratissimus*	1.512	20	11.63
CAREX	*Carex* spp.	1.453	13	7.56
CEAM	*Ceanothus americanus*	0.640	10	5.81
CNST	*Cnidoscolus stimulosus*	0.872	14	8.14
COFL	*Cornus florida*	0.988	9	5.23
CRAR	*Croton argyranthemus*	1.047	14	8.14
CYEC	*Cyperus echinatus*	1.570	16	9.30
DICHA	*Dichanthelium* spp.	2.674	33	19.19
DITE	*Diodia teres*	1.221	11	6.40
ELTO	*Elephantopus tomentosus*	4.651	44	25.58
EUAL	*Eupatorium album*	0.988	9	5.23
EUPU	*Euphorbia pubentissima*	1.047	14	8.14
GADU	*Gaylussacia dumosa*	2.035	27	15.70
GAFR	*Gaylussacia frondosa*	3.953	35	20.35
ILGL	*Ilex glabra*	4.012	24	13.95
IPOMO	*Ipomoea* spp.	2.151	33	19.19
LEPR	*Lespedeza procumbens*	10.581	68	39.53
LERE	*Lespedeza repens*	1.163	13	7.56
LIMI	*Licania michauxii*	3.605	27	15.70
PIGR	*Pityopsis graminifolia*	6.337	61	35.47
PIPA	*Pinus palustris*	3.895	22	12.79
POPR	*Polypremum procumbens*	1.977	17	9.88
QUST	*Quercus stellata*	1.628	10	5.81
RHCO	*Rhus copallinum*	4.884	38	22.09
RHRE	*Rhynchosia reniformis*	0.465	7	4.07
RUBUS	*Rubus* spp.	1.395	18	10.47
SAAL	*Sassafras albidum*	2.209	21	12.21
SCSC	*Schizachyrium scoparium*	1.686	12	6.98
SMILA	*Smilax* spp.	6.047	63	36.63
SOOD	*Solidago odora*	3.837	51	29.65
STSY	*Stillingia sylvactica*	0.872	13	7.56
SYDU	*Symphyotrichum dumosum*	0.988	10	5.81
SYPA	*Symphyotrichum patens*	1.686	23	13.37
TOPU	*Toxicodendron pubescens*	4.302	47	27.33

5.8.4 Post-disturbance average cover, count, and frequency arranged by species code and name along T6 (GS).

Species Code	**Species Name**	**Average Cover**	**Species Count**	**Frequency (%)**
ANDRO	*Andropogon* spp.	5.294	42	22.46
ARIST	*Aristida* spp.	1.283	11	5.88
CAOD	*Carphephorus odoratissimus*	2.353	25	13.37
CAREX	*Carex* spp.	0.481	5	2.67
CEAM	*Ceanothus americanus*	2.995	37	19.79
CLMA	*Clitoria mariana*	0.642	8	4.28
CNST	*Cnidoscolus stimulosus*	0.321	6	3.21
COMA	*Coreopsis major*	0.374	6	3.21
CTAR	*Ctenium aromaticum*	0.481	5	2.67
DICHA	*Dichanthelium* spp.	6.043	60	32.09
DITE	*Diodia teres*	0.802	9	4.81
ELTO	*Elephantopus tomentosus*	0.909	10	5.35
ERHI	*Eragrostis hirsuta*	0.428	7	3.74
EUAL	*Eupatorium album*	1.604	18	9.63
EUPU	*Euphorbia pubentissima*	0.963	11	5.88
GADU	*Gaylussacia dumosa*	0.481	8	4.28
GESE	*Gelsemium sempervirens*	3.797	31	16.58
HIAC	*Hibiscus aculeatus*	3.529	18	9.63
ILGL	*Ilex glabra*	26.203	131	70.05
LEPR	*Lespedeza procumbens*	0.428	8	4.28
NYSY	*Nyssa sylvatica*	1.070	8	4.28
PANIC	*Panicum* spp.	2.353	9	4.81
PASPA	*Paspalum* spp.	2.032	13	6.95
PIGR	*Pityopsis graminifolia*	1.283	10	5.35
PRSE	*Prunus serotina*	0.374	6	3.21
PTAQ	*Pteridium aquilinum*	7.647	58	31.02
QUNI	*Quercus nigra*	1.016	9	4.81
RHCO	*Rhus copallinum*	1.337	12	6.42
RUBUS	*Rubus* spp.	7.807	66	35.29
SAAL	*Sassafras albidum*	0.374	5	2.67
SMILA	*Smilax* spp.	7.754	94	50.27
STBI	*Stylosanthes biflora*	0.374	7	3.74
SYDU	*Symphyotrichum dumosum*	1.711	18	9.63
SYPA	*Symphyotrichum patens*	0.428	6	3.21
TRUR	*Tragia urticifolia*	2.193	39	20.86
VAMY	*Vaccinium myrsinites*	1.711	22	11.76

5.8.5 Post-disturbance average cover, count, and frequency arranged by species code and name along T3 (GS).

Species Code	**Species Name**	**Average Cover**	**Species Count**	**Frequency (%)**
ANDRO	*Andropogon* spp.	6.237	59	30.41
COMA	*Coreopsis major*	1.443	23	11.86
CRAR	*Croton argyranthemus*	0.773	13	6.70
DICHA	*Dichanthelium* spp.	3.041	37	19.07
ELTO	*Elephantopus tomentosus*	0.825	10	5.15
GADU	*Gaylussacia dumosa*	4.691	53	27.32
GESE	*Gelsemium sempervirens*	3.454	31	15.98
HIAC	*Hibiscus aculeatus*	3.814	30	15.46
ILGL	*Ilex glabra*	1.082	13	6.70
IPOMO	*Ipomoea* spp.	1.082	17	8.76
LEPR	*Lespedeza procumbens*	0.773	14	7.22
LIMI	*Licania michauxii*	1.340	20	10.31
MIMI	*Mimosa microphylla*	1.031	10	5.15
PIGR	*Pityopsis graminifolia*	2.062	26	13.40
PIPA	*Pinus palustris*	1.237	11	5.67
PTAQ	*Pteridium aquilinum*	38.918	151	77.84
QUST	*Quercus stellata*	2.268	17	8.76
RUBUS	*Rubus* spp.	6.392	84	43.30
SAAL	*Sassafras albidum*	0.979	14	7.22
SEAS	*Sericocarpus asteroides*	1.495	25	12.89
SICO	*Silphium compositum*	1.392	12	6.19
SMILA	*Smilax* spp.	2.062	17	8.76
SYPA	*Symphyotrichum patens*	1.237	20	10.31
TRUR	*Tragia urticifolia*	1.907	34	17.53
VAEL	*Vaccinium elliottii*	2.784	21	10.82

5.8.6 Post-disturbance average cover, count, and frequency arranged by species code and name along T7 (SW).

Species Code	**Species Name**	**Average Cover**	**Species Count**	**Frequency (%)**
ANDRO	*Andropogon* spp.	11.128	89	45.64
CAOD	*Carphephorus odoratissimus*	1.538	20	10.26
COFL	*Cornus florida*	2.769	28	14.36
COMA	*Coreopsis major*	0.615	11	5.64
COSE	*Collinsonia serotina*	3.436	33	16.92
DASE	*Danthonia sericea*	0.667	11	5.64
DICHA	*Dichanthelium* spp.	2.821	40	20.51
ELTO	*Elephantopus tomentosus*	1.692	24	12.31
ERHI2	*Erechtites hieracifolia*	0.769	13	6.67
EUAL	*Eupatorium album*	2.051	25	12.82
EUPU	*Euphorbia pubentissima*	1.487	21	10.77
GAFR	*Gaylussacia frondosa*	0.872	13	6.67
GESE	*Gelsemium sempervirens*	1.282	18	9.23
HEAN	*Helianthus angustifolius*	5.487	39	20.00
HIAC	*Hibiscus aculeatus*	8.103	61	31.28
ILGL	*Ilex glabra*	23.026	154	78.97
MIMI	*Mimosa microphylla*	0.974	14	7.18
MOCE	*Morella cerifera*	3.077	43	22.05
PASPA	*Paspalum* spp.	1.692	19	9.74
PIGR	*Pityopsis graminifolia*	1.897	25	12.82
PTAQ	*Pteridium aquilinum*	6.923	68	34.87
RHCO	*Rhus copallinum*	1.897	15	7.69
RUBUS	*Rubus* spp.	5.231	69	35.38
SCSC	*Schizachyrium scoparium*	1.744	14	7.18
SETO	*Sericocarpus tortifolius*	1.231	20	10.26
SMILA	*Smilax* spp.	3.333	52	26.67
SOOD	*Solidago odora*	1.590	19	9.74
SYDU	*Symphyotrichum dumosum*	5.282	68	34.87
SYPA	*Symphyotrichum patens*	2.205	29	14.87
VAMY	*Vaccinium myrsinites*	2.410	33	16.92
VEAN	*Vernonia angustifolia*	0.667	10	5.13
VITIS	*Vitis* spp.	1.744	14	7.18

5.8.7 Post-disturbance average cover, count, and frequency arranged by species code and name along T4 (SW).

Species Code	**Genus and Species**	**Average Cover**	**Species Count**	**Frequency (%)**
ANDRO	*Andropogon* spp.	2.857	33	18.86
ANVI	*Andropogon virginicus*	3.200	28	16.00
CAOD	*Carphephorus odoratissimus*	1.429	21	12.00
COMA	*Coreopsis major*	0.857	12	6.86
ELTO	*Elephantopus tomentosus*	1.600	19	10.86
EUPU	*Euphorbia pubentissima*	0.971	10	5.71
GADU	*Gaylussacia dumosa*	5.029	47	26.86
GAFR	*Gaylussacia frondosa*	0.686	10	5.71
GESE	*Gelsemium sempervirens*	3.829	39	22.29
HIAC	*Hibiscus aculeatus*	2.686	22	12.57
ILGL	*Ilex glabra*	10.629	50	28.57
LEPR	*Lespedeza procumbens*	0.800	12	6.86
LIMI	*Licania michauxii*	1.200	14	8.00
NYSY	*Nyssa sylvatica*	1.314	11	6.29
PANIC	*Panicum* spp.	2.286	20	11.43
PIGR	*Pityopsis graminifolia*	4.514	50	28.57
PIPA	*Pinus palustris*	1.200	13	7.43
PTAQ	*Pteridium aquilinum*	18.229	84	48.00
QUFA	*Quercus falcata*	2.057	13	7.43
QUST	*Quercus stellata*	2.971	19	10.86
RHCO	*Rhus copallinum*	1.086	11	6.29
RUBUS	*Rubus* spp.	11.200	101	57.71
SAAL	*Sassafras albidum*	2.914	31	17.71
SEAS	*Sericocarpus asteroides*	0.971	12	6.86
SETO	*Sericocarpus tortifolius*	0.800	10	5.71
SMILA	*Smilax* spp.	1.886	19	10.86
SOOD	*Solidago odora*	0.571	8	4.57
SYDU	*Symphyotrichum dumosum*	1.371	15	8.57
TOPU	*Toxicodendron pubescens*	1.829	20	11.43
VAMY	*Vaccinium myrsinites*	1.429	18	10.29
VEAN	*Vernonia angustifolia*	0.971	13	7.43

5.8.8 Axis summary statistics.

	Axis 1	Axis 2	Axis 3
T2			
Eigenvalue	0.091	0.038	0.029
Variance in species data			
% of variance explained	1.3	0.5	0.4
Cumulative % explained	1.3	1.8	2.2
Pearson Correlation, Species-Environment *	0.486	0.339	0.352
Kendall (Rank) Correlation., Species-Environment	0.31	0.176	0.189
T5			
Eigenvalue	0.09	0.065	0.033
Variance in species data			
% of variance explained	1.3	1	0.5
Cumulative % explained	1.3	2.3	2.8
Pearson Correlation, Species-Environment *	0.445	0.444	0.295
Kendall (Rank) Correlation., Species-Environment	0.3	0.286	0.154
T8			
Eigenvalue	0.147	0.047	0.044
Variance in species data			
% of variance explained	2.2	0.7	0.7
Cumulative % explained	2.4	2.9	3.6
Pearson Correlation, Species-Environment *	0.616	0.439	0.411
Kendall (Rank) Correlation., Species-Environment	0.406	0.294	0.225
T6			
Eigenvalue	0.161	0.077	0.042
Variance in species data			
% of variance explained	2.2	1.1	0.6
Cumulative % explained	2.2	3.3	3.9
Pearson Correlation, Species-Environment *	0.61	0.508	0.379
Kendall (Rank) Correlation., Species-Environment	0.362	0.308	0.239
T3			
Eigenvalue	0.106	0.036	0.032
Variance in species data			
% of variance explained	2.1	0.7	0.6
Cumulative % explained	2.1	2.8	3.4
Pearson Correlation, Species-Environment *	0.566	0.566	0.343
Kendall (Rank) Correlation., Species-Environment	0.273	0.273	0.236

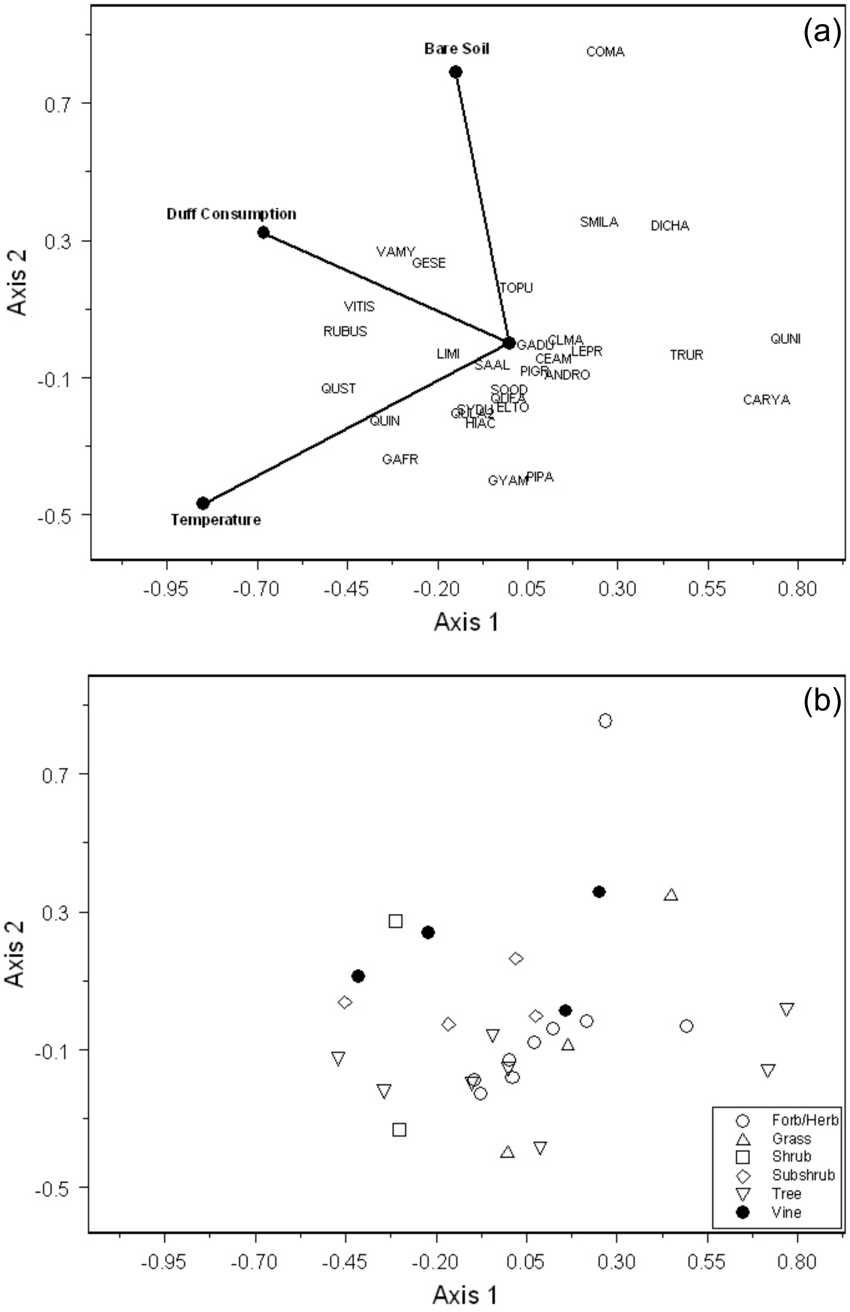
5.8.8 Axis summary statistics (cont.).

	Axis 1	Axis 2	Axis 3
T7			
Eigenvalue	0.076	0.076	0.035
Variance in species data			
% of variance explained	1.5	1.5	1.5
Cumulative % explained	1.5	1.5	1.5
Pearson Correlation, Species-Environment *	0.497	0.497	0.497
Kendall (Rank) Correlation., Species-Environment	0.349	0.349	0.349
T4			
Eigenvalue	0.15	0.07	0.039
Variance in species data			
% of variance explained	2.4	1.1	0.6
Cumulative % explained	2.4	3.6	4.2
Pearson Correlation, Species-Environment *	0.593	0.499	0.366
Kendall (Rank) Correlation., Species-Environment	0.361	0.305	0.274

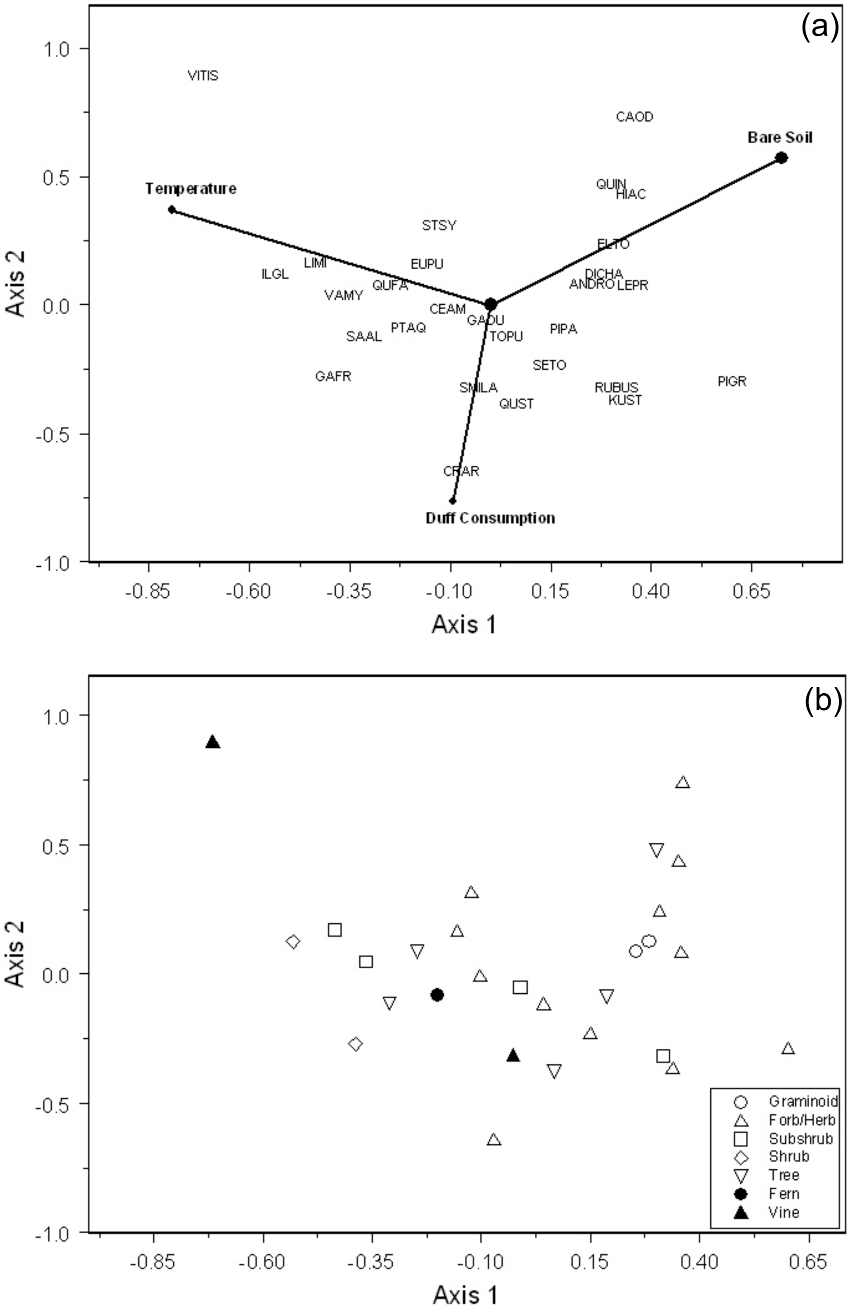
5.8.9 Multiple regression results representing species in site space on environmental variables.

	Canonical Coefficients						
	Standardized			Original Units			
Variable	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3	Stand. Dev.
T2							
Temperature	-0.745	-0.527	0.515	-3.748	-2.651	2.59	0.199
Duff Consumption	-0.481	0.494	-0.781	-2.905	2.984	-4.712	0.166
Bare Soil	-0.251	0.748	0.625	-2.792	8.326	6.957	0.090
T5							
Temperature	-0.695	0.525	0.526	-3.389	2.557	2.564	0.205
Duff Consumption	0.638	0.485	0.674	3.607	2.741	3.808	0.177
Bare Soil	0.14	-0.693	0.758	1.022	-5.05	5.525	0.137
T8							
Temperature	-0.278	0.452	-0.942	-1.334	2.17	-4.527	0.208
Duff Consumption	0.793	0.783	-0.305	3.066	3.026	-1.179	0.259
Bare Soil	-0.146	0.931	0.546	-0.706	4.504	2.644	0.207
T6							
Temperature	-0.521	-0.912	-0.318	-2.14	-3.744	-1.307	0.244
Duff Consumption	0.656	-0.867	-0.096	3.334	-4.411	-0.49	0.197
Bare Soil	-0.109	-0.15	0.989	-0.822	-1.138	7.482	0.132
T3							
Temperature	-0.334	-0.379	-0.954	-1.543	-1.755	-4.41	0.216
Duff Consumption	0.746	-0.727	-0.315	4.107	-4.004	-1.736	0.182
Bare Soil	-0.205	-0.835	0.625	-0.958	-3.905	2.919	0.214
T7							
Temperature	-0.818	-0.64	-0.21	3.122	2.443	0.803	0.262
Duff Consumption	-0.163	0.608	-0.843	-1.142	4.245	-5.886	0.143
Bare Soil	-0.286	0.611	0.865	1.778	-3.795	-5.37	0.161
T4							
Temperature	-0.47	0.344	0.901	-2.112	1.544	4.045	0.223
Duff Consumption	0.616	-0.535	0.815	2.48	-2.154	3.284	0.248
Bare Soil	-0.204	-1.126	0.072	-0.724	-3.988	0.256	0.282

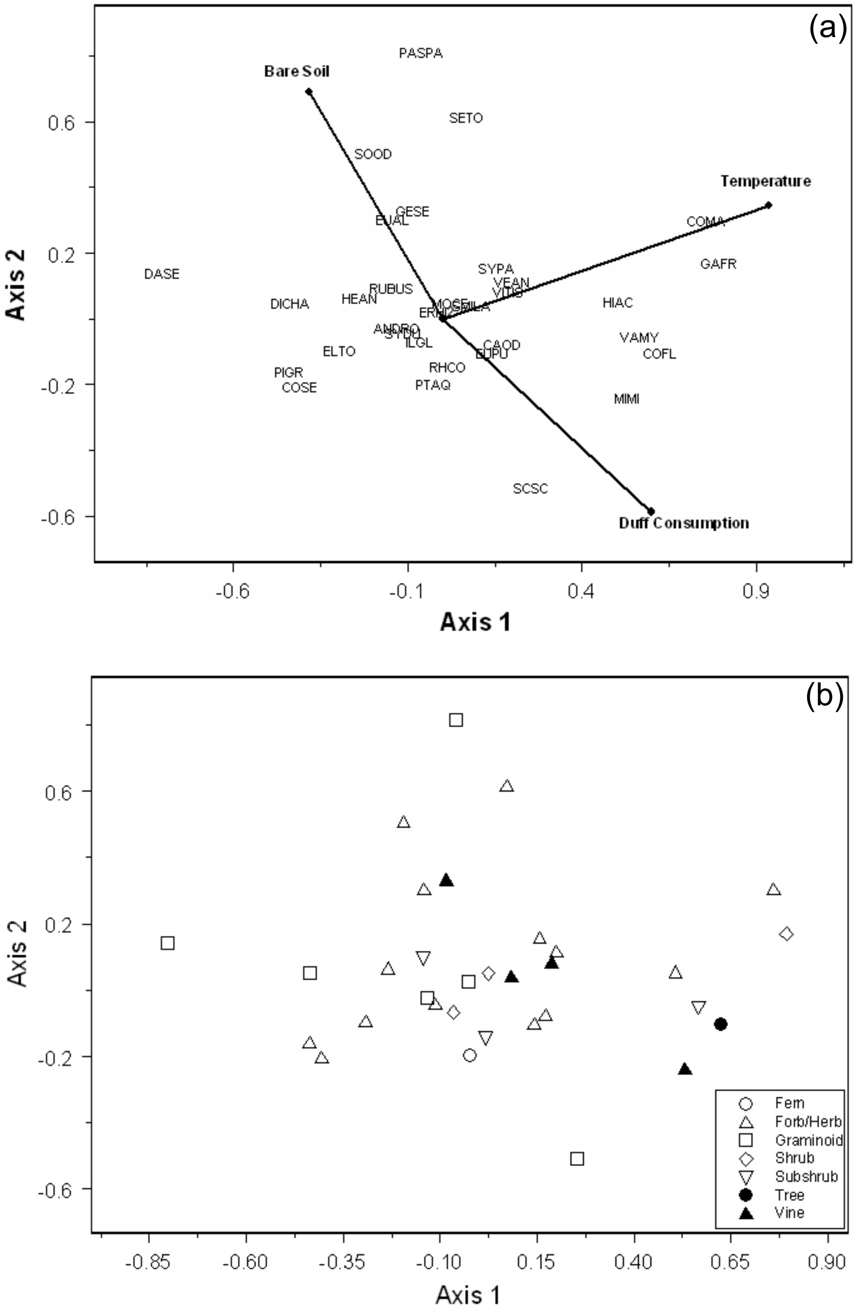
5.8.10 Ordination of (a) species and (b) growth form in environmental space along T2 (NH), as defined by CCA using LC scores. The biplot overlay indicates vectors related to the strength of maximum fire temperature, duff consumption, and bare soil. Axes are scaled by standard deviation. Symbols are abbreviations of species encountered and can be found in Appendix 5.8.1.



5.8.11 Ordination of (a) species and (b) growth form in environmental space along T5 (NH), as defined by CCA using LC scores. The biplot overlay indicates vectors related to the strength of maximum fire temperature, duff consumption, and bare soil. Axes are scaled by standard deviation. Symbols are abbreviations of species encountered and can be found in Appendix 5.8.2.



5.8.12 Ordination of (a) species and (b) growth form in environmental space along T7 (SW), as defined by CCA using LC scores. The biplot overlay indicates vectors related to the strength of maximum fire temperature, duff consumption, and bare soil. Axes are scaled by standard deviation. Symbols are abbreviations of species encountered and can be found in Appendix 5.8.6.



6. CONCLUSIONS

6.1 Summary of Findings

Past and present disturbance interacts to shape the structure of the longleaf pine overstory and regeneration, alter the fuel complex, and transform plant species composition.

6.1.1 Heterogeneity and species diversity as a result of past management

- Heterogeneity (HI) was reduced along transects with low canopy cover, low basal area, and a reduced litter layer, while higher heterogeneity was observed at moderate levels of canopy cover with a deep litter layer.
- Species diversity (H') reached a maximum at intermediate levels of canopy cover and a reduced litter layer.
- The HI increased with a longer Fire Return Interval and decreased as the number of fires increased.
- The H' had trends similar to HI, except for one transect that had high levels of diversity at the maximum Fire Return Interval.

6.1.2 Fire Intensity

- Winter prescribed fires had maximum flame temperatures greater than the range of 232-259°C in more than 50% of the pyrometers.
- Peak variance of maximum fire temperature, according to Three Term Local Quadrat Variance (3TTLQV), occurred at a block size 33-34 along T2 and T5 in the No Harvest compartments, with T5 having several peaks. Along the remaining transects in the harvesting compartments, peak variance of maximum fire temperature occurred at a block range of 34-55.
- Along T2 and T5 in the no harvest compartments, where fire intensity was dependent on small scales, litter depth explained 20% of the variability, while along transects with larger mean patch and gap sizes located in the harvest compartments variation in 10 and 100-hr fuels (28-33%) explained the variability in maximum fire temperature.

6.1.3 Post-Disturbance Vegetation Patterns

- Community species composition in each plot was altered by multiple interacting disturbances (overstory harvest, hurricane, salvage, and prescribed fire).
- A number of understory species, that recover from fire utilizing different growth mechanisms were correlated with maximum fire temperature.

- Other species, such as *Dichanthelium* spp., *Smilax* spp., *Ceanothus americanus, Carphephorus odoratissimus, Rubus* spp., and *Panicum* spp. required bare soil to re-colonize areas in the longleaf pine understory.
- Small-scale variation, common in recovery following disturbance, has a variable impact on species composition across the landscape.

6.2 Synthesis

The results presented in this study reflect the variability of multiple interacting disturbances and how they modify the structure and composition of the longleaf pine communities. The disturbance regimes have been modified from their natural occurrence in several ways: harvesting, prescribed fire, and indirect changes in climate that may alter hurricane frequency and intensity.

The Escambia Experimental Forest is a managed second growth longleaf pine forest that has been the focus of various research objectives: 1) assessment of uneven-and even-aged stand management, 2) growth and yield studies considering effects of site, density, and age, and 3) extensive comparison of fire frequency and fire season on longleaf pine, hardwoods, and the understory species (Boyer et al., 1997). Disturbance has produced variable effects on heterogeneity and diversity across the landscape. Conclusions indicate retention of a spatially variable overstory and maintenance of a variable fire regime enrich habitat heterogeneity, resulting in a more complex landscape.

Recent hurricane disturbance and salvage operations impacted the fuel complex and influenced the spatial patterning of fire intensity, resulting in variable scale patterns across the disturbance gradient. The post-burn heterogeneity that is characteristic in longleaf pine forests structured plant species composition along a fire and ground disturbance gradient. The resultant community was a mix of species that were present on the site prior to the prescribed burns and those that had persisted in the seed bank (Whelan, 1995). All forms of growth common in species found in fire-dependent communities (sprouters, dormant buds, clonal growth, and persistent seed) were observed post-disturbance. As the disturbance gradient shifted from low to high intensity, the understory composition and structure of the longleaf pine forests was differentially impacted, favoring development of different communities.

6.3 Future Directions

This dissertation began with the initial task of documenting spatial heterogeneity before, during, and following prescribed fires in a longleaf pine forest with variable overstory retention. The longleaf pine ecosystem is fraught with events of stochastic disturbance and is in a constant state of natural flux. The Escambia Experimental Forest was a host to two major Atlantic hurricanes that altered not only my study plan, but also the longleaf pine communities.

The hurricanes brought about abrupt changes in the residual overstory community, especially in management compartments that had been previously reduced to 7 m^2/ha. The residual overstory longleaf pines had a short window to adjust to the enlarged growing space. This could have exacerbated injury and mortality from strong winds as windthrow, tree snappage midway along the trunks, and considerable loss of branches in the canopy was common. In contrast, the compartments that remained unharvested or harvested by selection showed less overstory tree mortality. The creation of gaps in longleaf pine forests is crucial to its sustainability through natural regeneration. It is impossible to plan overstory removal around hurricane landfall due to the unpredictable nature of hurricane trajectory and intensity. However, if future hurricanes increase in occurrence and intensity along the Gulf Coast region, timing of harvest and regeneration method may become an important consideration for sustainable management of current longleaf pine forests. The Escambia Experimental Forest could prove to be useful in exploration of the interactions between various management techniques and hurricane disturbance.

Determining fire intensity could be important in prescribing fires following overstory and ground disturbance. As we rely less on natural fire regimes in such ecosystems as longleaf pine, ponderosa pine (*Pinus ponderosa*), giant Sequoia (*Sequoiadendron giganteum*), as well as other fire-dependent communities, it is important to understand the difference in spatial variability that results from both prescribed fire and wildfire. This knowledge could be important in maintaining viable overstory and understory populations of native species. Continued observation of herbaceous communities in the longleaf pine forest at the Escambia Experimental Forest may provide long-term insights concerning interactive impacts of multiple disturbances.

6.4 References

Boyer, W.D., Ward, G.A., Kush, J.S., 1997. The Escambia Experimental Forest marks fifty years of research on the ecology and management of longleaf pine. South. J. Appl. For. 21, 47.

Whelan, R.J., 1995. The Ecology of Fire. Cambridge University Press, New York.