SPATIAL AND DEMOGRAPHIC MODELING TECHNIQUES APPLIED TO THE LONGLEAF PINE (*Pinus Palustris*) ECOSYSTEM OF NORTH CENTRAL FLORIDA

By

EVA LOUISE LOUDERMILK

A THESIS PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

UNIVERSITY OF FLORIDA

2005

This document is dedicated to my family and friends.

ACKNOWLEDGMENTS

I foremost thank my two advisors, Wendell Cropper and Loukas Arvanitis, for there support, dedication, and belief in my graduate career. My other committee members, Michael Binford and Jane Southworth, provided invaluable help in all aspects of my research. Jack Putz, Eric Jokela, and Alan Long have given their expertise in various details of my project.

I thank the School of Forest Resources and Conservation for financial support as well as George Blakeslee and Tim White for their dependable guidance. The opportunities and amenities at the Forest Information Systems laboratory have been immeasurable. Mike Rasser, Balaji Ramachandran, and Valentina Boycheva gave me guidance early in my graduate research, while I have been able to confide in my trustworthy peer and lab partner, Doug Shoemaker, throughout the years.

Special thanks go to Libby Zimmerman, Mike Penn, Amy Copeland, and Bobby Cahal of the Goethe State Forest staff and Robert Mitchell and Stephen Pecot from the Joseph W. Jones Ecological Center who have provided valuable data for my research. This experience would not have been complete without the encouragement and support from my family and friends, especially my husband, Erick, and my devoted parents, Eva and Staffan Lundberg.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

page

Abstract of Thesis Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Master of Science

SPATIAL AND DEMOGRAPHIC MODELING TECHNIQUES APPLIED TO THE LONGLEAF PINE (*Pinus Palustris*) ECOSYSTEM OF NORTH CENTRAL FLORIDA

By

Eva Louise Loudermilk

December 2005

Chair: Loukas G. Arvanitis
Cochair: Wendell P. Cropper
Major Department: Forest Resources and Conservation

Modeling longleaf pine (*Pinus palustris)* response to fire requires addressing processes at both the landscape and population scale. The LANDIS (LANdscape DIsturbance and Succession) model simulates tree behavioral traits and stochastic fire disturbances on a large but coarse temporal and spatial scale. A matrix population model simulates growth and survival of a species through transition probabilities. Using specific elements from each model provides an opportunity to examine the population dynamics of *P. palustris* in a large managed forest.

The purpose of this research was to a) spatially model forest successional patterns of a *P. palustris* ecosystem in a north-central Florida forest using LANDIS; b) develop a density dependent matrix population model of *P. palustris*; and c) utilize the linked outputs of LANDIS and the matrix population model to examine individual *P. palustris* populations at the Watermelon Pond Unit (WPU) of the Goethe State Forest, FL. Remote

and ground reference data aggregated with spatial and image analysis techniques were explicit elements used to develop the LANDIS model. An existing four year *P. palustris* transition matrix model was extended to include a seedling size class, fecundity estimates, and a density dependent function to develop the demographic model. Two fire scenarios were applied to both LANDIS and the demographic model, simulating a fire-maintained *P. palustris* ecosystem and a fire suppressed one. The fire regimes simulated in LANDIS were used to determine which one of the two transition matrices was employed for several individual *P. palustris* populations at the WPU through time.

LANDIS simulated certain traits of *P. palustris* dynamics well, but the results were not entirely realistic: Fire frequency was still much lower than what is required in a fire-maintained ecosystem, especially within individual populations. Land managers of the WPU may use LANDIS to visualize the adverse effects that hardwoods may have on *P. palustris*. Further fine-tuning of parameters and smaller time steps may improve this model for visualizing *P. palustris* dynamics. At the scale of individual populations, the matrix model may be used for management of *P. palustris*. Elasticity and model behavior analyses have demonstrated that the matrix population model plausibly represented *P. palustris* dynamics in this ecosystem. A dual transition matrix technique (with and without fire) was used to simulate the response of this conifer to fire scenarios. The hybrid technique provided for the missing elements of one model to be supplied by the other, but comparing outputs from each model was not possible due to their incompatible output formats. Research on *P. palustris* population dynamics, coupled with advanced modeling techniques, provides for opportunities to continue understanding this complex conifer and its habitat.

CHAPTER 1
INTRODUCTION

Seemingly endless longleaf pine (*P. palustris*) savannahs once dominated the southeastern United States. Logging, development, and fire suppression have depleted this ecosystem, and now only a few remaining natural old growth longleaf pine areas are left (Platt et al., 1988; Hartnett and Krofta, 1989; Myers, 1990). One of these areas is found in the Goethe State Forest (Remnants, 2002) located in Levy and Alachua counties of Florida, USA. One portion, known as the Watermelon Pond Unit (WPU), was once predominantly longleaf pine habitat. It has since been severely degraded or has succeeded into other biological communities, such as scrub and hardwood forests (Hardin, 2004). Information on patterns and ecological functions of this system on various scales are increasingly needed for designing sound forest management plans (He et al., 2002), including prescribed burning, which is essential for this ecosystem's maintenance and restoration requirements (Andrews, 1917; Platt et al. 1988; Boyer, 1990; Hardin, 2004). In this research, we intended to model this ecosystem on two different levels; a landscape and population scale, to determine the advantages that each has for long-term land management plans.

Modeling successional patterns and the fire regime on a spatially explicit landscape scale and over long time periods is an effective way to gain knowledge of complex processes utilizing existing ecosystem-level inputs (He et al., 2002). The LANDIS (LANdscape DIsturbance and Succession; Mladenoff et al., 1996) model was used in this study to develop a management tool for visualizing longleaf pine dynamics at the WPU

and the adverse affects that hardwoods have on its community. Two model fire regimes were developed to simulate a fire maintained longleaf pine ecosystem and a fire suppressed one.

Modeling longleaf pine dynamics on a population scale, such as with a density-dependent transition matrix approach, may provide managers with more detailed information about the system, specifically size-class rates of survival, mortality, and fecundity (Caswell, 2001). The population model was parameterized based on literature estimates of this conifer's response to fire occurrence and fire suppression. The model framework included two separate transition matrices representing each fire condition.

These two modeling techniques provide managers with two methods for examining the long-term dynamics of this system on two very different scales. These two models may now be brought together: Information from LANDIS, such as simulated fire frequency, may be used to employ the transition matrix model to analyze the individual longleaf pine populations at the WPU during various fire regimes over time.

CHAPTER 2
SPATIAL MODELING OF FOREST SUCCESSION AND FIRE DISTURBANCE IN A LONGLEAF PINE (*Pinus Palustris*) MANAGED ECOSYSTEM IN NORTH-CENTRAL FLORIDA

Introduction

Modeling Forest Succession

Modeling forest succession is essential in understanding the relatively slow changes of large heterogeneous forests for long-term land management plans. Attempts have been made to physically measure forest succession quantitatively. However, this is limited in practice due to for labor-intensive sampling over long time periods. Individual-based models of tree competition and succession have been a common approach for this issue (e.g., Botkin, 1993). Forest simulation models are effective over various spatial and temporal scales and useful when comparing the affects of different land management practices, predicting land-use, climate change, and forest production over time (Peng, 2000).

Managing fire-dependent ecosystems in Florida, such as longleaf pines (*Pinus palustris*) savannahs, has become increasingly important to reduce wildfire outbreaks and ensure future establishment of this sensitive tree species. Mechanistic and stochastic models of fire and fuel dynamics have aided in this type of management. Mechanistic models include FARSITE (Finney, 1998) and BEHAVE (Andrews, 1986) that require specific physical and chemical properties of the landscape to determine the rate and shape of fire spread. The stochastic model DISPATCH (Baker et al., 1991) simulates the effects of changing climate or shifts in fire disturbance regimes on relatively large

landscapes. LANDIS (LANdscape DIsturbance and Succession, Mladenoff et al., 1996) models landscapes over large spatial and temporal scales requiring relatively coarse input data of dominant tree species and fire characteristics of the land (He and Mladenoff, 1999). This model is spatially interactive, implementing variables such as tree species, seeding characteristics, and cohort-based growth capabilities, as well as fire ignition, spread, and fuel traits. These features enable users to gain insight into the overall dynamics of the forest system visually and quantitatively over decades to several centuries (Mladenoff and He, 1999). The focus of this study was to spatially model long-term forest succession in a longleaf pine (*Pinus palustris*) ecosystem through two fire disturbance regimes utilizing the LANDIS model and assessing its practicality as a management tool in the Goethe State Forest, Florida.

Longleaf Pine Habitat: Sandhill

Description

The sandhill community is found on rolling hills of sandy infertile soils of north-central Florida. Sparse longleaf pines (*Pinus palustris*) dominate the canopy with a low understory of wiregrass (*Aristida stricta*) as well as other grasses and forbs. The mid-canopy consists mainly of turkey oak (*Quercus laevis*) and blue-jack oak (*Quercus incana*) in varying densities (Myers, 1990; Greenberg and Simons, 1999). Some oaks produce “oak domes,” dense thickets of sand-live oaks (*Quercus geminata*) with little or no vegetative ground cover (Guerin, 1993).

History and Current State

Sandhill was once one of the largest forest types in the southeastern coastal plain of the United States, but has diminished by over 98% due to harvesting and fire suppression (Myers, 1990). The highly dispersed pine and low understory provided for an easily

traveled and nicely shaded route for early European settlers (Hall, 1829). Overtime, this ecosystem became fragmented by clear-cutting for timber, development, introduction of livestock, and agricultural practices. Many of these fragments have suffered from fire suppression, resulting in encroachment by faster growing, shade tolerant tree species (Frost, 1993; Rasser, 2003).

Restoration and preservation of *P. palustris* dominated ecosystems has become a well known practice in the southeast which contributes to recreation, aesthetics, reducing the onset of pest infestation, and conservation for endangered and often endemic species that thrive in this habitat (Boyer, 1993; Neel, 1993). Land managers plan for frequent low-intensity fires (~3-5 years) that keep encroaching hardwoods in check (Hartnett and Krofta, 1989; Platt and Rathbun, 1993). These fires also create an environment that supports *P. palustris* recruitment and open savannah like parks for recreation including hunting and easily traveled trails (Myers, 1990). Several endemic species thrive in these habitats, including the Sherman's fox squirrel (*Sciurus niger)*, red-cockaded woodpecker (*Picoides borealis*), brown-headed nuthatch (*Sitta pusilla*), Bachman's sparrow (*Aimophila aestivalis*), and the gopher tortoise (*Gopherus polyphemus*) (Engstrom, 1993).

Unique Traits

P. palustris is the characteristic fire-dependent conifer of sandhill communities. Frequent low-intensity fires remove accumulated leaf litter, overgrown grasses, and encroaching oaks exposing bare-mineral soil required for seed germination and establishment (Croker, 1975; Boyer, 1990; Myers, 1990). Another distinctive feature about this pine is its seedling's slow growing "grass stage." Here it develops a long thick tap root (Myers, 1990), increases in diameter (Platt et al., 1988), and is protected from fire through dense tufts of long, moisture rich needles. It may stay in this stage for 5-15

years. Within one growing season, *P. palustris* can grow over 1m in height avoiding lethal temperatures of fire near the ground surface while protecting the terminal bud. A maturing tree develops fire-resilient scaly plates, which define it as the most fire-resistant pine. Furthermore, the ecosystem has vegetation with pyrogenic traits that facilitate the ignition and spread of fire (Fonda, 2001; Myers, 1990). Without frequent fire, the stable *P. palustris* dominated forest disappears due to failure of seedling establishment and incursion of hardwood upland species (Myers, 1990).

Competitive Oaks

If fire is suppressed on sandhill sites for less than a decade, oaks (*Quercus* spp.) or other hardwood species (*Prunus serotina, P. caroliniana*) from adjacent communities may encroach and often out-compete the shade intolerant *P. palustris* (Myers, 1990). Southern hardwood species often resprout, even if they appear to be killed by fire or other disturbances. Most flourish under dense canopy cover and have chemical and physical traits that reduce the onset of fire (Platt and Schwartz, 1990). Three southeastern United States oak species (*Q. geminata, Q. hemisphaerica, Q. laevis)* are focused on in this study as competitors with *P. palustris*.

Turkey oak (*Q. laevis*) is a deciduous species uniquely adapted to fire-maintained communities of the southeastern U.S. They are found in dry sandy areas and well drained ridges of the coastal plain (Berg and Hamrick, 1994). Sandhill areas are their favored habitat, sometimes out-competing longleaf pines eventually forming “turkey oak barrens.” *Q. laevis* life history traits, such as vegetative propagation, fast growth, and vigorous resprouting subsequent to fire, are important factors in the interaction with *P. palustris*. It does not contend well with other more shade tolerant oaks (e.g., *Q. geminata, Q. hemisphaerica*), which are also examined in this study, increasing the risk

of upland forest encroachment during fire inhibition (McGinty and Christy, 1977; Putz, personal communication, 2005).

The commonly dominant laurel oak (*Q. hemisphaerica*) is found in a diversity of north and central Florida habitats which exhibit a broad range of moisture and fertility gradients (Platt and Schwartz, 1990). The moisture rich environments created by hardwood habitats with *Q. hemisphaerica* decrease the likelihood and intensity of fire, although fires during dry periods may be detrimental to this tree and habitat (Wade et al., 1980). It is frequently considered a facultative seral species on sandhill sites, with a high tolerance of shade, clonal traits and resprouting capabilities subsequent to moderately intense burns (Putz, personal communication, 2005). Boundaries between hardwood forests and sandhills are often kept in check by low-intensity prescribed burns ignited in sandhill areas and allowed to creep into the edges of hardwood forests (Platt and Schwartz, 1990; Hardin, 2004).

Sand-live oak (*Q. geminata*) tolerates highly infertile sandy soils typical of Florida's scrub ecosystem as well as xeric hardwood forests of north-central Florida. Its traits are similar to *Q. virginiana* (live oak), but are smaller in size and produces acorns in pairs. *Q. geminata* is not quite as tolerant of shade as *Q. hemisphaerica* and is slightly more fire tolerant, but thrives as a clonal propagator and strong resprouter after fire. *Q. geminata* form the aforementioned clonal 'oak domes' within sandhill communities that can spread and dominate the landscape as scrub or xeric hammock if not regulated by frequent burning (Guerin, 1993).

Sandhill, scrub, and hardwood forests are mutually exclusive ecosystems that respond very differently to fire. Sandhill habitats have vegetation with pyrogenic traits

that facilitate the ignition and spread of fire. Scrub and sandhill and are closely linked ecologically but the fire-frequency is much lower in scrub and its principal components are invasive (Myers, 1990). Hardwood forests create moisture rich environments containing less flammable leaf litter deterring the onset of fire and reducing its intensity (Platt and Schwartz, 1990).

Objectives

The purpose of this research was to use the LANDIS model to study the spatial relationships of these four species and their habitats in response to various fuel treatments. Two scenarios were developed for this study: (I) the Frequent Fire Model (FFM), simulating a fire-maintained *P. palustris* ecosystem; and (II) the Infrequent Fire Model (IFM), simulating a historically fire suppressed landscape. Following are questions proposed for this research: 1) Can the unique fire regime of the *P. palustris* habitat be modeled using LANDIS? 2) What are the implications of using LANDIS as a long-term management tool for the *P. palustris* habitat? 3) Are the fire and fuel characteristics of LANDIS sufficient to simulate the short and long mean fire return intervals of various habitats in the study site?

LANDIS Model Description

General Characteristics

LANDIS (LANdscape DIsturbance and Succession) was introduced in 1996 and has been used extensively for spatial analysis and modeling of large heterogeneous landscapes and long time frames (Mladenoff et al., 1996, Mladenoff and He, 1999). Originally, LANDIS was designed to simulate the forests of the northern lake states (Mladenoff et al., 1996, He and Mladenoff, 1999). Since then, it has been used for forest succession modeling in many parts of the world. Successional patterns of an undisturbed

boreal forest reserve in northeast China were compared to surrounding disturbed areas using dominant tree species in LANDIS (He et al., 2002). In Finland, Pennanen and Kuuluvainen (2002) manipulated the simulated fire behavior and successional processes of LANDIS to form FIN-LANDIS. Instead of using specific tree species of a forest, Franklin et al. (2001) used plant functional groups. These groups were ascertained from Noble and Slayter's (1980) vital attribute fundamentals describing the successional role of plant species. He et al. (2004) created various fuel treatments to assess the risk of wildfire occurrence in the Missouri Ozark Highlands. Overall, LANDIS is used to simulate large forested areas that have limited inputs. The presence/absence nature and coarse scale of LANDIS avoids the need for precise measurements and prediction of species abundance (Mladenoff and He, 1999). The spatial scale is user defined but is often in 10's to 100's of square meter pixels. The temporal scale is restricted to 10-year time intervals.

LANDIS combines the ability to simulate landscape-sized forest successional patterns while implementing specific tree species attributes and probabilistic disturbance regimes, such as fire, wind, and harvesting. Forest succession is simulated in LANDIS based on seed dispersal, seedling establishment, sprouting traits, competition (fire and shade tolerance), growth, and mortality characteristics of each tree species modeled (Gustafson et al., 2004). For instance, a shade-intolerant species cannot establish easily on a site where shade tolerant species are well established. These species will remain dominant unless other attributes, disturbances or environmental factors alter the conditions throughout the simulation (Mladenoff and He, 1999).

Fire Disturbance Characteristics

Fire disturbance in LANDIS affects tree establishment, mortality, and inter-specific competition. The probability of establishment for each tree species is based on fire tolerance, age, and site characteristics. The stochastic and spatially explicit nature of fire is represented through mathematically defined distributions and various algorithms. Fire disturbance parameters influence the size, probability of fire occurrence on the land, return interval, spread, and severity of the fire regime. The fire tolerance levels (1-5) of each tree species are categorical representations of their relational tolerances to fire.

Fire probability (*P*) in LANDIS follows a negative exponential distribution and is calculated in LANDIS with the following equation:

$$P = b \times If \times MI^{-(e+2)} \qquad (2\text{-}1)$$

MI is the mean fire return interval (years) for each landtype. The parameter *If* represents the year since the last fire on each landtype. A larger *If* represents a higher probability that a fire will occur on that landtype. The fire probability coefficient (*b*) represents the chance a cell randomly selected for ignition check will ignite and is used during the calibration process (He et al., 2003; Mladenoff and He, 1999).

The fire probability function works directly with ignition and spread of fire in LANDIS. Fire is ignited based on the percentage of cells checked for ignition (chosen randomly) and on the probability that a fire will occur. It is also a function of map size (Ignition = ignition coefficient x total number of cells). LANDIS is able to ignite and therefore simulate more than one fire disturbance within an iteration, but the chance is exponentially decreased through time (He and Mladenoff, 1999). Fires spread in LANDIS as a function of fire size, fire probability, species attributes (e.g., fire tolerance and age), and spatial arrangement of adjacent cells. A fire will continue to spread until

the pre-determined maximum fire size is reached, the adjacent cells cannot burn based on probability estimates, or it reaches the edge of 'forested' land (He and Mladenoff, 1999; Mladenoff and He, 1999).

Fuel accumulation for each landtype is established from a conceptual fire curve representing a relationship between fuel quantities, based on detritus accumulation and decomposition characteristics (Gustafson et al., 2004). It is dependent on the time since a burn last occurred (He et al., 2003) and the landtype severity and species susceptibility to fire act together to determine which species and age-cohorts are killed during a fire disturbance (Mladenoff et al.,1996). As such, the fire disturbance in LANDIS is not entirely stochastic as some areas within a landscape may be more susceptible to fire than others (He and Mladenoff, 1999).

The fire disturbance file is exclusively designed for simulating fire size on the entire landscape and is a determining factor of fire spread, fire probability, fire and forest susceptibility, and spatial configuration of forest conditions (Gustafson et al., 2004). Fire size also follows the notion that large disturbances are less frequent than small disturbances through a log-normal distribution (Mladenoff and He, 1999). These fire disturbance parameters and their calculations are described in detail elsewhere (He and Mladenoff, 1999; Mladenoff and He, 1999; He et al., 2003).

Methods

Study Area

The Watermelon Pond Unit (WPU) of the Goethe State Forest is a 1938-ha tract located in Levy and Alachua counties of Florida, USA (latititude 29° 32' 42 ", longitude 82° 36' 20"; Figure 2-1). Its checker-board structure makes management difficult, especially for prescribed burning. Agricultural land owners, state and county roads, and

two small towns divide the forest, further complicating management. Before European settlement, the land was a homogeneous landscape of the sandhill community type dominated by *P. palustris*. During the last century, the area was fragmented by anthropogenic effects, specifically phosphate mining and non-sustainable timber harvesting. Many of these areas were unmanaged causing dramatic successional changes in this ecosystem with few *P. palustris* trees left today (Rasser, 2003).

A main goal of land managers is the immediate implementation of prescribed fire plans for restoration and preservation of sandhill areas (Hardin, 2004). Sandhills of the WPU are classified into four general groups, ranked in order of quality: 1) areas with scattered mature *P. palustris* (>=30 ft^2 basal area) with subdominant *Q. laevis* and abundant natural *P. palustris* regeneration, 2) stands where *Q. laevis* predominate with *P. palustris* being a minor component (10-20 ft^2 ba) and sparse *P. palustris* regeneration, 3) pure *Q. laevis* and scrub oak stands, and 4) areas newly planted with *P. palustris* seedlings. Wiregrass (*Aristata stricta*) and other natural herbaceous groundcover are found in these areas, which are considered strong indicators of community health (Hardin, 2004). Note that *Q. laevis* is an abundant tree species found at the WPU, and is considered a dominant component of some historic sandhill sites (Greenberg and Simons, 1999). As such, it provides a rare opportunity for the WPU staff to manage *Q. laevis* dominated sandhills.

To maintain a level of biodiversity, it is important to keep intact the recently developed scrub and hardwood communities while restraining further encroachment into sandhill sites with prescribed burning plans. Scrub is Florida's most endangered ecosystem with many rare and threatened endemic species. Prescribed fire initiated in

sandhill areas will be allowed to burn into the edges of these scrub and hardwood forests as part of the land management plans (Hardin, 2004).

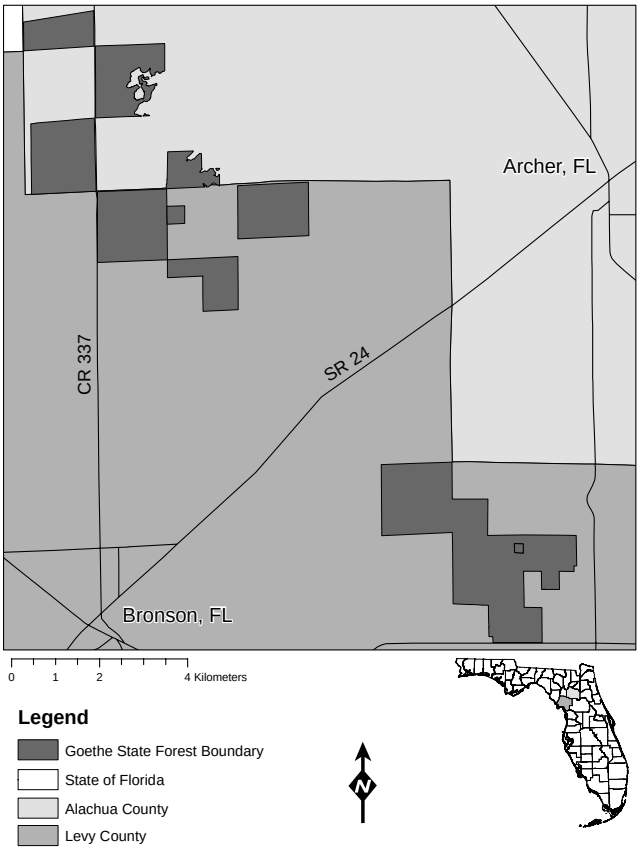

Figure 2-1. Map of the study site: Watermelon Pond Unit of the Goethe State Forest, Florida, USA.

Parameterization of LANDIS

Spatial inputs

Spatial data specific to the WPU used to develop both the landtype and the forest composition map and their attributes are the: a) biological communities delineated from high-resolution digital aerial photography taken in February 2002, b) geo-referenced ground data on tree species from 2002 (Rasser, 2003), c) geo-referenced ground data on biological communities from 2003 and d) temporal aerial photography. The high-resolution digital aerial photography (0.3m ground sampling distance) was donated from

Mpower3/Emerge (Andover, MA). These datasets provided baseline information representing the area's vegetative structure and composition. ArcGIS 8.x, 9.0 and IMAGINE 8.x were used to develop the final Erdas GIS file format datasets with a spatial resolution of 20m. All input parameter files for LANDIS, except the spatial files, are included in the Appendix.

Landtypes. The WPU was stratified into four distinct habitats unique in their fire and fuel traits: a) current *P. palustris* sandhill habitat, b) hardwoods, c) scrub, and d) wet areas. These landtypes were created from digitally delineated biological communities on habitat type and their characteristic tree species. The ground reference data was used to perform an accuracy assessment on the landtype map. The fire accumulation and severity curves for each landtype were qualitatively assessed based on literature and current site conditions of each habitat and used for both fire scenarios (Figure 2-2). Qualities, such as highly flammable longleaf pine needles (Fonda, 2001) and wiregrass, dry sandy soils, and low decomposition rates create the characteristic sandhill environment with highly frequent (<10 years) low-intensity fires. Scrub is considered a pyrogenic community that accumulates fuels slowly and often has a high heat of ignition, but produces catastrophic fires at a rather low MI (50 years) (Myers, 1990). Furthermore, the abundance of the shrub *Ceratiola ericoides*, a highly flammable and characteristic scrub species, contributes to the pyrogenic nature of this habitat. Hardwood forests have rather long MIs (80 years) with a moisture rich environment and fast decomposition rates that greatly reduce the intensity of these periodic fires (Platt and Schwartz, 1990). The wet areas are defined as portions of the WPU with hydric soils, currently abundant with water, and/or prairie type habitat with fluctuating water levels. Since the wet areas have little or no

trees, they were not actively modeled in LANDIS. The approximate areas for each landtype are as follows: current *P. palustris* habitat (1050 ha), scrub (375 ha), hardwoods (400 ha), and wet areas (165 ha). Even though the WPU has distinct habitats, it is small and relatively flat, which does not restrict the establishment of any of these tree species. Therefore, the establishment coefficients were set to one for each tree species on all landtypes in the FFM and instead their successional behavior was purely designed based on their attribute parameters and response to fire. The establishment coefficients in the IFM were also set to one, except *P. palustris* was reduced to 0.25 because of its weak competitive and establishment abilities during fire suppression.

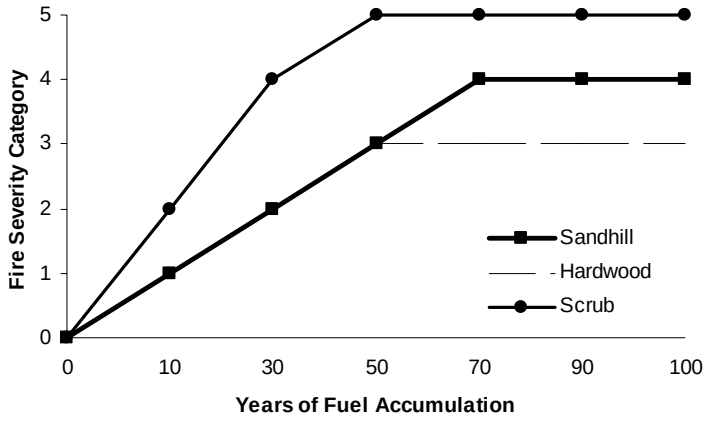

Figure 2-2. Fire fuel accumulation curve for all three active habitats at the WPU.

Forest composition. The forest composition map and associated attributes were derived from ground reference data, temporal aerial photography, and managerial records and correspondence. Forest classes required for LANDIS were distributed using the biological community spatial dataset as a foundation. The vegetative data designated the tree species found in each forest class. The ground reference data was used to perform an accuracy assessment on the forest composition map. For simplification, only the four most abundant tree species at the WPU were used in the LANDIS model, namely

longleaf pine (*P. palustris*), turkey oak (*Q. laevis*), sand-live oak (*Q. geminata*), and laurel oak (*Q. hemisphaerica*). Historic aerial photography and forest management records were used to determine tree age-class distributions. Approximately one set of aerial photographs of the study site per decade back to 1949 were used. The final map consisted of 17 classes with various combinations of species and their age distributions within the study site (see Appendix).

Species attributes

Demographic parameters for the four tree species modeled were obtained from literature (Duncan and Duncan, 1988; Boyer, 1990; Young and Young, 1992; Preston and Braham, 2002) and experts opinion (Long, personal communication, 2004; Jokela, personal communication, 2004; Putz, personal communication, 2005; Table 2-1.). Unlike other studies using LANDIS (Pennanen and Kuuluvainen, 2002; Wimberly, 2004), longevity was input as the typical lifespan of a given species in this geographic region rather than its maximum known lifespan. This creates a more realistic mortality inference of each species. A seeding distance was input to represent the range that a tree species can effectively seed out, with the assumption that other natural effects, e.g., wild animals, influence where a seed may fall and germinate. The *Quercus* spp. modeled are readily able to resprout after a disturbance at a very young age. With a long seeding range and early propagation, some *Quercus* spp. establish and spread effortlessly in LANDIS. The propagation probability coefficient was developed by understanding its sensitivity (see below) within LANDIS and qualitatively shaping this variable for each *Quercus* spp.

Fire Simulation Scenarios and Parameters

Two fire scenarios were created to simulate a fire-maintained *P. palustris* ecosystem (Frequent Fire Model: FFM) and a fire suppressed one (Infrequent Fire Model: IFM), each with unique fire return intervals and fire size parameters. All fire parameters for both models (Table 2-2., Table 2-3.) were obtained from the Goethe State Forest management plans (Hardin, 2004) and communication with management personnel (Cahal, personal communication, 2005; Copeland, personal communication, 2005; Penn, personal communication, 2005; Zimmerman, personal communication, 2005). Because the *P. palustris* ecosystem requires frequent low intensity fires, the mean fire return interval (MI) of this habitat in the FFM was set to <10 years to ensure fires every LANDIS time step. The *P. palustris* ecosystem in the IFM followed historic records noting the fire suppressed period dating back to 1890 with a MI of 45 years (Zimmerman, personal communication, 2005). The scrub and hardwood habitats followed the same landtype parameterization methods mentioned in the 'Spatial Input: Landtypes' section. Fire size variables for both models were estimated from delineated prescribed burns for the WPU, their management plans, and known wildfire outbreaks. The burn size parameters of the FFM followed that of known sizes for prescribed burns and future management plans. The burn size parameters of the IFM were directly related to the only known wildfire that occurred in 1980. Each simulation was run for 50 LANDIS time steps (500 years) to ensure reaching model stabilization. Species abundance was recorded and used to compare the effectiveness of each fire scenario focusing on *P. palustris* and its establishing abilities.

Calibration and Sensitivity Analyses

The fire parameters of LANDIS were calibrated by adjusting the associated fire coefficients interactively to achieve a desired mean fire return interval for all landtypes and mean fire sizes for each of the two fire scenarios within a 500 year simulation. Default values were initially used for the fire size (50) and fire probability [b = MI of each landtype (see Equation 2-1)] coefficients and manipulated in intervals of 10 depending on the scale and direction of error (He et al., 2003). For each treatment, these values were systematically varied until the parameters met the simulated values or until no further improvements could be made.

Many of the tree species attributes were interactively manipulated to develop relational species behavioral traits. For instance, *Q. hemisphaerica* and *Q. geminata* were set to have rather similar dominance traits if no fire was introduced and the former with stronger seeding capabilities, while *P. palustris* thrived and established itself subsequent to a burn. *Q. laevis* was targeted as a transitional species that dominates areas with *P. palustris* if fire is somewhat infrequent or recently ceased, but may be replaced by invading *Q. hemisphaerica* and *Q. geminata*. *P. palustris* was also set to not have the ability to vegetatively propagate or establish well during fire suppression.

The vegetation propagation probability coefficients of the *Q.* spp. were set equal to one another because of their similar re-sprouting abilities after a burn. Only a small (1% to <6%) change in the abundance of any of the four species was recorded from the simultaneously adjusted vegetation propagation coefficients over a range from 0.1 to 0.9 of the three *Q.* spp. To avoid bias, the median coefficient (0.5) was chosen for all three *Q.* spp.

Sensitivity analyses were performed on the mean fire size and mean fire return interval to measure their contribution to the model response. Each parameter was adjusted 20% from the base run and *P. palustris* abundance was recorded during 500 simulation years as well as the simulated mean fire size on the landscape in each interval (Mladenoff and He, 1999). The MI analysis was only performed on the IFM to illustrate the effects of a 20% change in the MI of all landtypes simultaneously, which could not be done with the already minimal fire return interval (<10 yrs.) of the FFM.

Table 2-1. Attributes of the four species studied using LANDIS.

	PIPA	QUGE	QULA	QUHE
Longevity (yrs.)	200	130	100	100
Age of Maturity (yrs.)	20	20	20	20
Shade Tolerance (1-5)	1	4	3	4
Fire Tolerance (1-5)	5	1	4	1
Effective Seeding Distance (m)	30	50	50	70
Maximum Seeding Distance (m)	50	70	70	90
Propagation Probability After Fire (0-1)	0	0.5	0.5	0.5
Minimum Resprout Age (yrs.)	0	5	5	5

PIPA: *Pinus palustris*; QUGE: *Quercus geminata*; QULA: *Quercus laevis*; QUHE: *Quercus hemisphaerica*

Results and Discussion

Calibration and Sensitivity Analyses

Mean fire size was calibrated for both the FFM and IFM, with a -12% and -16% error, respectively (Table 2-2.). Error is calculated by the dividing the difference between observed fire size and the expected fire size by the expected fire size. The simulated MS was accurate to within <0.7% between both models. The IFM was more accurately calibrated than the FFM in terms of expected mean fire return intervals (Table 2-3.). The low MIs of the hardwood and scrub habitats could not be calibrated accurately in the FFM due to the high MI (<10 yrs.) of the *P. palustris* sandhill habitat. This result

appeared realistic as fires may ignite within sandhill areas and spread into adjacent habitats. The total amount of area burned in hardwood and scrub sites were relatively low in the FFM while sandhill areas burned readily (Figure 2-3.). The hardwood sites were the most difficult to correctly calibrate for either scenario because the low intensity fire after long durations of fire suppression increased the probability that fire could occur again in LANDIS. As such, the increase MI of the sandhill areas in the IFM contributed to the decrease in fire frequency of both the hardwood and scrub habitats. The hardwood habitat MI became more accurately simulated while scrub habitat resulted in an exceedingly larger MI. Ultimately, the fire and fuel characteristics in LANDIS were sufficient to simulate the diverse fire regimes of theses three habitats during longer fire return intervals.

Table 2-2. Calibration analysis of mean fire size (MS) in each fire regime scenario.

	Frequent Fire Model	Infrequent Fire Model
Predetermined MS, ha (% area)	120 (5.9%)	106 (5.3%)
Simulated MS, ha (% area)	105 (5.2%)	101 (5.0%)
Standard Deviation (% area)	59 (2.9%)	28 (1.4%)
Error	-12%	-16%

Table 2-3. Calibration analysis of mean fire return intervals (MI) in each fire regime scenario.

	Frequent Fire Model			Infrequent Fire Model		
	Sandhill	Hardwoods	Scrub	Sandhill	Hardwoods	Scrub
Predetermined MI	10	80	50	45	80	50
Simulated MI	13	15	25	38	46	77
Standard Deviation	6	6	16	19	27	71
Error	31%	-81%	-50%	-15%	-43%	53%

The mean fire size (MS) parameters were generally more sensitive in the IFM than the FFM (Figure 2-4.). In the IFM, there was a 17% increase and 7% decrease in MS with the direct 20% change in MS. The strong increase in fire size was directly related to the average increase of 36% in *P. palustris* abundance throughout the simulation. This

simulation reflects a management goal of fire re-introduction at the WPU. The FFM resulted in a 2% and 4% increase in MS with a 20% increase and decrease in the MS, respectively. These small changes correlated with the small average changes in *P. palustris* abundance, ranging from 0.5% to 3%. The lack of change in the simulated MS of the FFM is the direct result of the influence of the time since the last fire in LANDIS. Once a fire has occurred, fire probability and severity diminish on that site. Since the MS showed little change in the FFM, the *P. palustris* population was only slightly influenced.

The MIs, MS, and *P. palustris* abundance changes in the IFM were more sensitive to a 20% increase in MI within all landtypes rather than a decrease (Figure 2-5). There was a 13% increase in overall simulated MI with an increase in overall MI. The increase in MI resulted in two fires dropped in years 90 and 320. MS did not show much change (-2%) with increased MI, but the total amount of area burned increased by 5%. *P. palustris* abundance reacted with a 16% increase in average abundance with increased MI. A large fire on the sandhill habitat in year 400 brought on new *P. palustris* growth and influenced the calculated increase in average abundance greatly. There was no change in simulated MIs, MS, or *P. palustris* abundance throughout the simulation when the MIs were reduced by 20%. These changes are complex (Mladenoff and He, 1999) and largely due to fire probability estimates calculated for each landtype as a function of MI, time since last fire, and a calibrated fire probability coefficient.

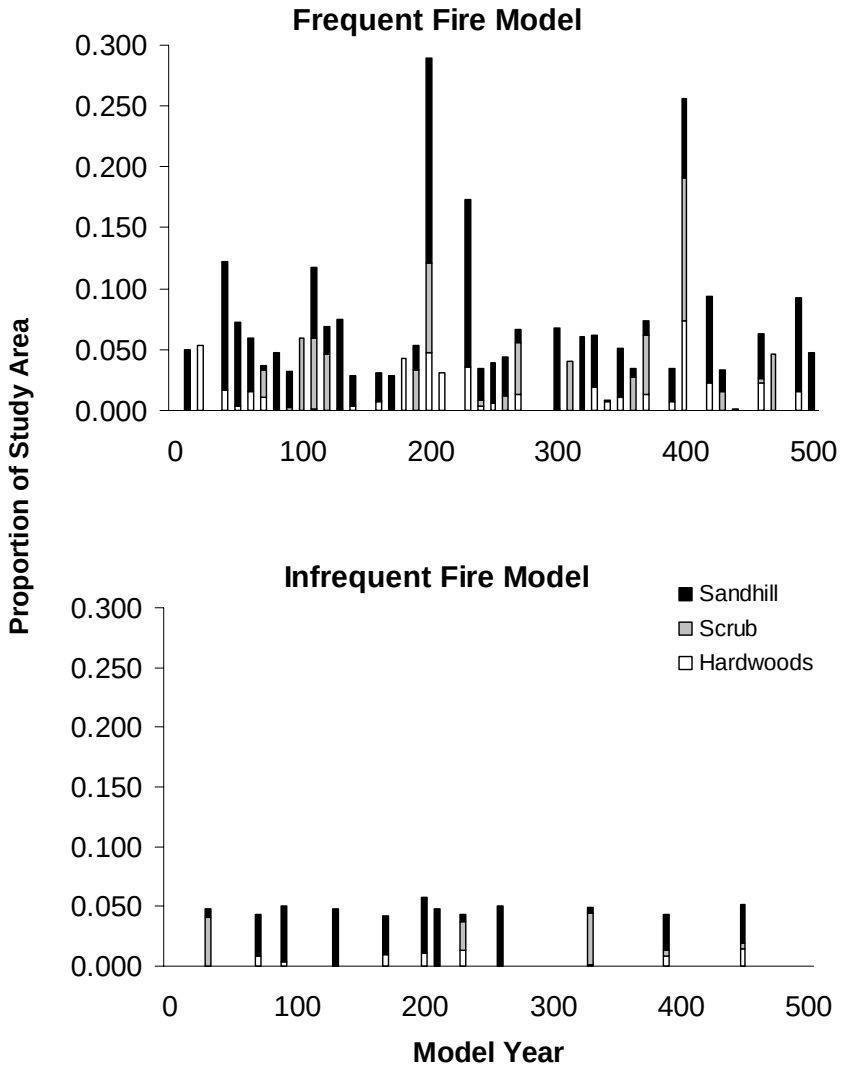

Figure 2-3. Proportion of area damaged by fire and burn frequency in each habitat using both fire scenarios in LANDIS.

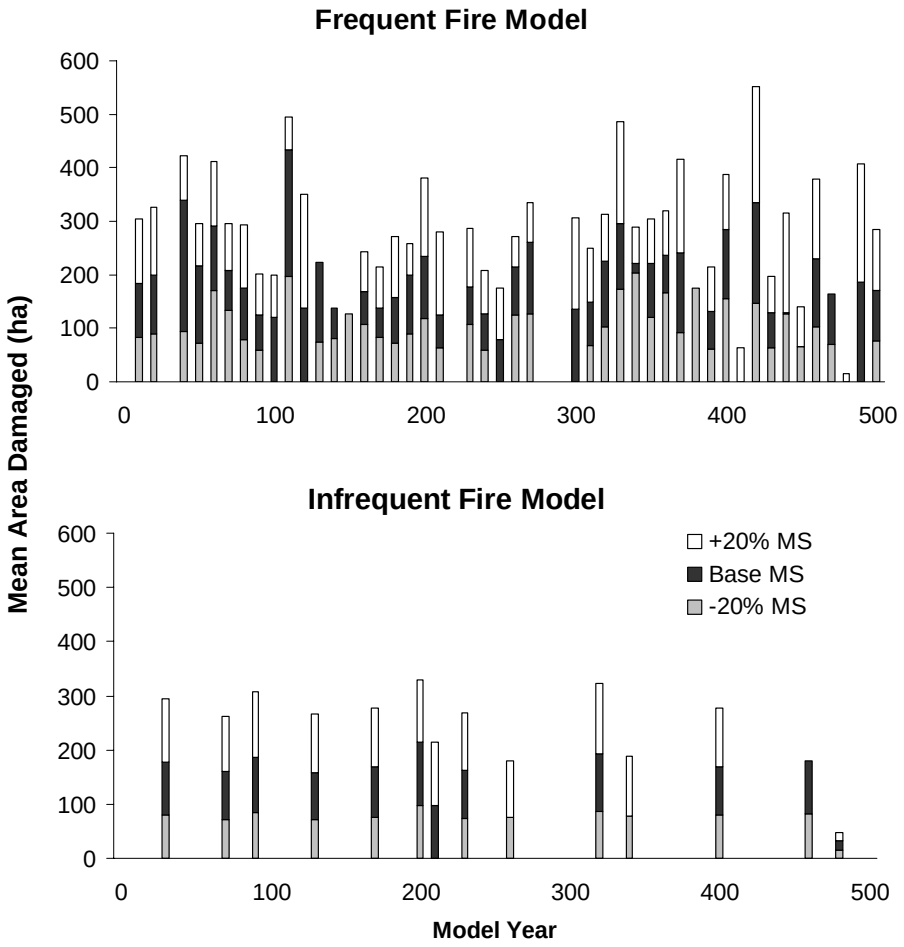

Figure 2-4. Sensitivity analysis: Mean area damaged by fire each model year as the mean fire size (MS) changed by 20% in both fire scenarios.

Fire Scenario Effects on Species Abundance

Species abundance changes throughout the LANDIS simulations illustrate the effects of the two fire regimes on each species. The results were analyzed after model stabilization (~yr. 200), unless otherwise stated. The most dramatic effects between the two fire regimes was the change in abundance of *P. palustris* (Figure 2-6.). In the FFM, the population was able to recover and gradually increase in number through regular recruitment. Gaps were formed from trees that died of old age or killed by fires (Figure 2-7.). As fires occurred, mature *P. palustris* were able to seed into these gaps and within

a few decades become a dominant species. The moderately fire resistant *Q. laevis* becomes more dominant on the land as well during a frequent fire regime, while *Q. hemisphaerica* and *Q. geminata* are suppressed. At year 500, the higher mean population abundance (34%) of *P. palustris* in the FFM demonstrates the ability of this species to thrive in a fire-maintained community (Figure 2-8.). Over 500 years, the mean abundance of *P. palustris* and *Q. laevis*, the two more fire tolerant tree species increased by 28% and 22%, respectively, when using the FFM compared to the IFM. The other two oaks, *Q. hemisphaerica* and *Q. geminata*, only revealed a slight increase in mean abundance (4% and 2%, respectively) in the FFM. Fires do not entirely extirpate any of these three oak populations because of their ability to vegetatively propagate subsequent to fire at a relatively young age (Boyer, 1990; Long, personal communication, 2004, Table 2-1.). Their quick re-establishment capabilities make *P. palustris* ecosystems difficult to restore after long periods of successional changes caused by fire suppression (Hartnett and Krofta, 1989).

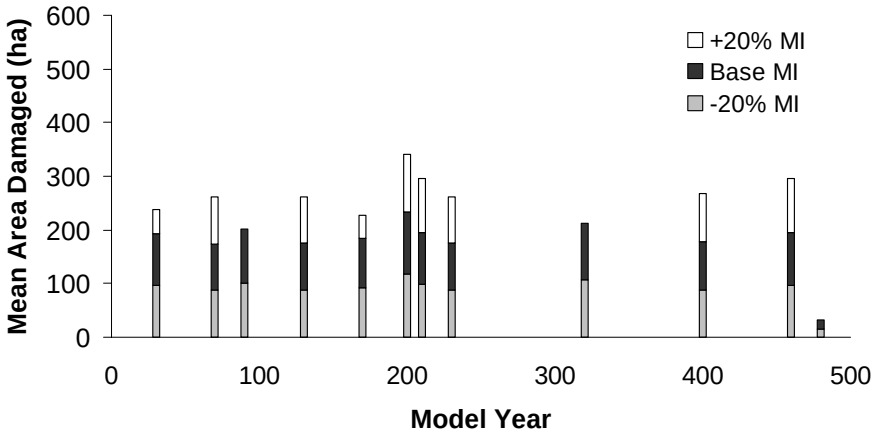

Figure 2-5. Sensitivity analysis: Mean area damaged by fire each model year with change in overall mean fire return interval (MI) in the IFM.

The FFM demonstrated more stability in the tree populations over time than the IFM, illustrated by the overall lower variation of species abundance throughout the 500 year simulations (Table 2-4.) This is caused by the highly intermittent fires in the IFM (Figure 2-3.). Even though the FFM maintained a relatively stable population of *P. palustris*, the outcomes were not entirely realistic. The northern portions of the WPU with *P. palustris* were burned only 1 to 10 times over the 50 LANDIS time steps. A typical sandhill community requires prescribed fires every 3-5 years (Hardin, 2004), or at least a 10 year return time (Platt et al., 1991). As such, the entire community at the WPU should burn every LANDIS time step. The model may have been affected by the fragmented structure of the WPU. Fires burned more readily (20 fires) within the non-restrictive boundaries of the southeastern portion of the WPU (Figure 2-9.) suggesting fire spread constraints in the smaller confined areas of the northern WPU.

Management Implications

Using this LANDIS model as a management tool for the WPU is plausible for understanding the adverse effects that some of Florida's oak species have on *P. palustris* ecosystems within just a few decades. The strong seeding and re-sprouting abilities, shade tolerance, fast growth, and diverse site characteristics of *Q. hemisphaerica* make it a difficult tree to control on fire suppressed sandhill sites and may require other methods of control (Myers, 1990; Putz, personal communication, 2005). *Q. geminata* may also be difficult to control, is tolerant of the typical xeric conditions of the sandhill and scrub communities, and therefore is a strong competitor with *P. palustris* (Myers, 1990). Both of these *Q*. spp. are regularly kept in check by frequent fires that are allowed to creep into their borders (Hardin, 2004), but are opportunistic during fire suppression.

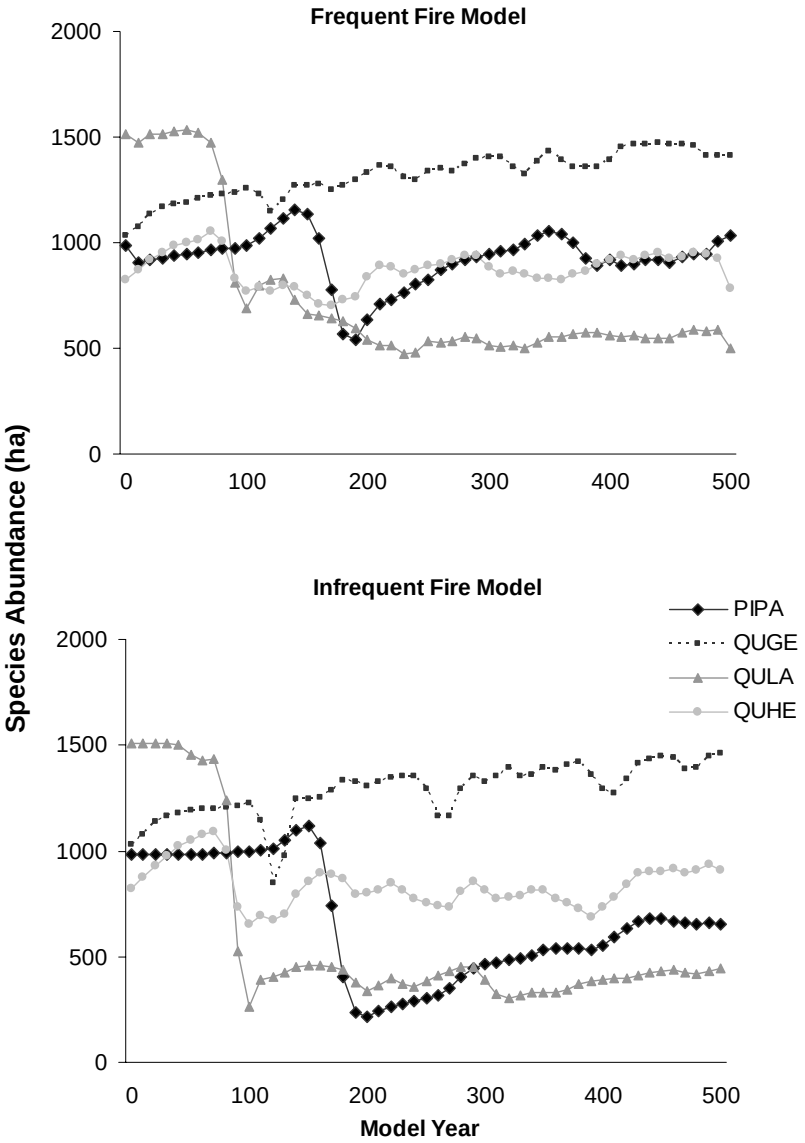

Figure 2-6. Fire scenario effects on species abundance in a single LANDIS model run. PIPA: *Pinus palustris*; QUGE: *Quercus geminata*; QULA: *Quercus laevis*; QUHE: *Quercus hemisphaerica*

Q. laevis tolerates fires well and re-sprouts vigorously following fire (McGinty and Christy, 1977), but was the least abundant species on the landscape during the model runs. In LANDIS, this species was replaced by the other hardwoods due to its lack of shade tolerance and short longevity. *P. palustris* was able to out-compete *Q. laevis* with frequent fire in spite of the oak's re-sprouting abilities. As such, the species is complex

and difficult to model. Otherwise, LANDIS is known to be capable of adequately simulating forest dynamics when only a few species are included (Franklin et al., 2001; Pennanen and Kuulavainen, 2002).

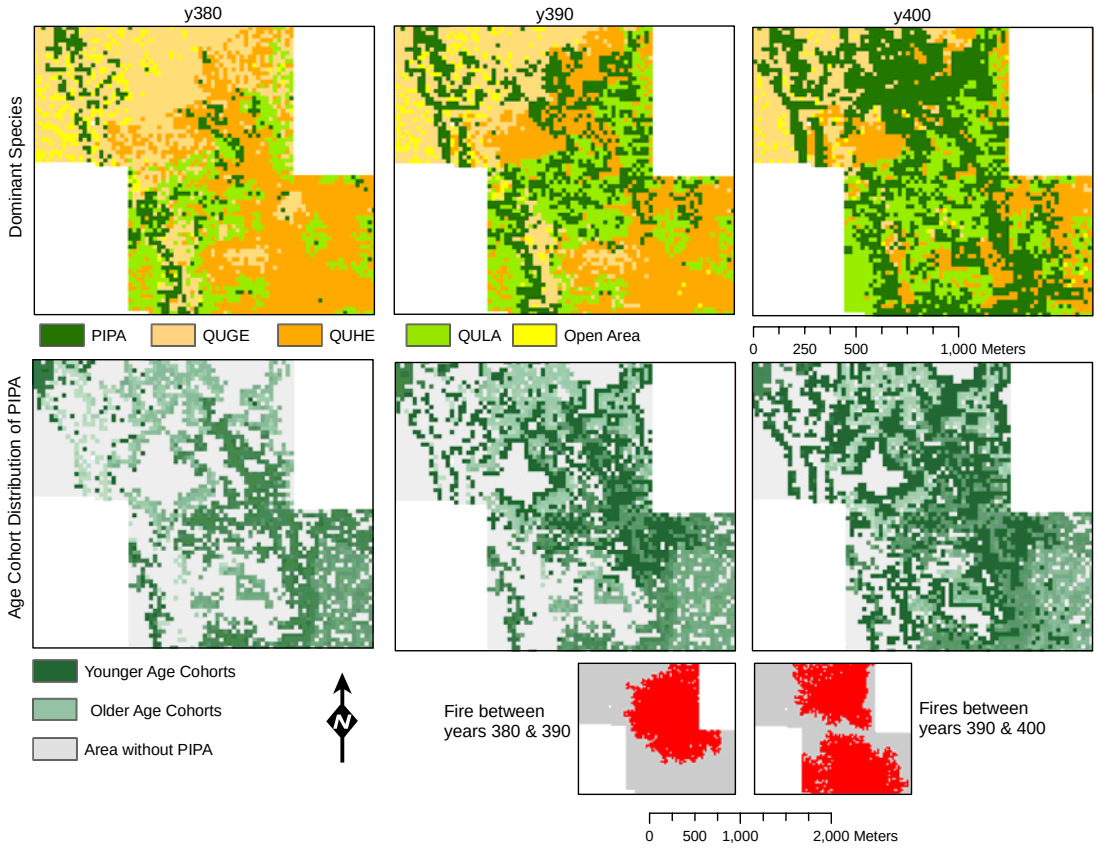

Figure 2-7. *P. palustris* (PIPA) behavior following fire disturbance in a southeastern portion of the WPU. The top row represents the dominant species of each cell. The bottom row illustrates the recruitment of young PIPA in openings created by fire induced tree mortality. PIPA: *Pinus palustris*; QUGE: *Quercus geminata*; QULA: *Quercus laevis*; QUHE: *Quercus hemisphaerica*

Even though the *P. palustris* population did stabilize and continued to increase in abundance in the FFM, this version (3.7) of LANDIS is applicable for only a few of the management plans for the WPU. LANDIS maintained an aesthetically pleasing mosaic type landscape pattern and illustrated the invading capabilities of particular hardwood species. It also provided the spatial and temporal aspects of fire and tree species

behavior with minimal inputs (Mladenoff et al., 1996; Mladenoff and He, 1999). The seeding characteristics of all four species were effectively modeled: They all took advantage of gaps created by fire or age induced mortality and the oaks readily re-sprouted subsequent to fire disturbance. *P. palustris* typically became dominant shortly after a fire through tolerance and recruitment (Figure 2-7.). The short fire return interval of 3-5 years (Hardin, 2004) required to maintain and/or restore sandhill communities could not be modeled with LANDIS 3.7 because of the 10 year time step. Furthermore, the fragmented structure of the WPU restricted fire spread across the landscape.

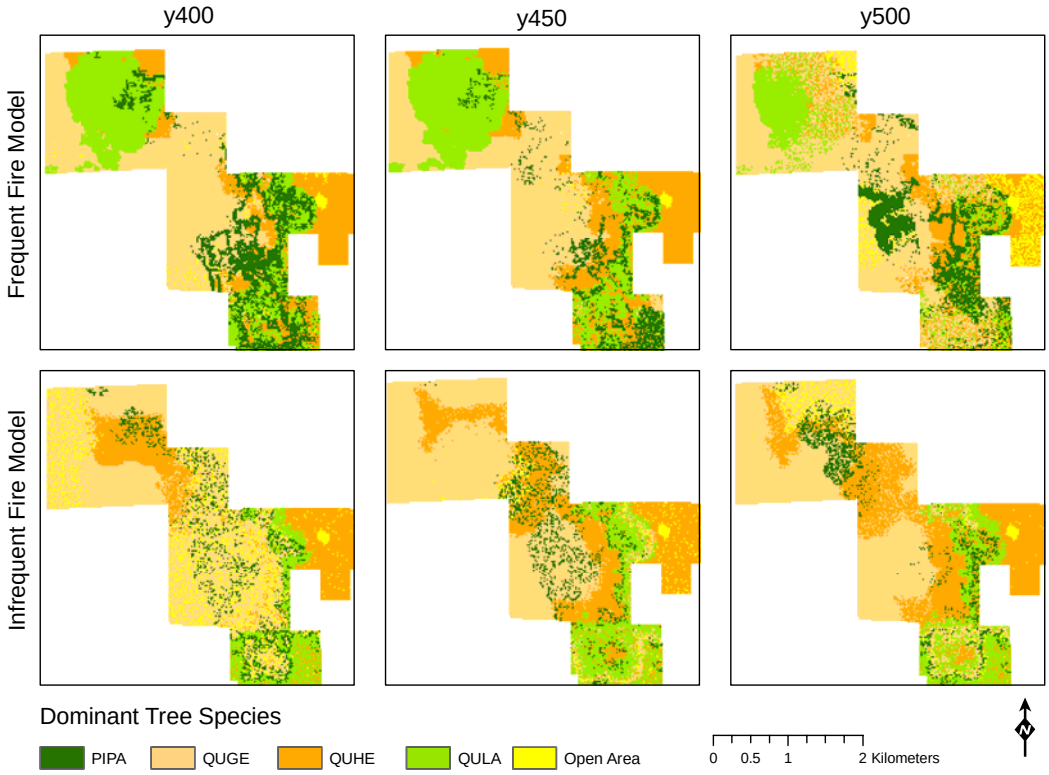

Figure 2-8. Comparison of dynamics of tree species dominance between the two fire scenarios in the east portion of the WPU. PIPA: *Pinus palustris*; QUGE: *Quercus geminata*; QULA: *Quercus laevis*; QUHE: *Quercus hemisphaerica*

Table 2-4. Statistics on species abundance within each fire scenario.

	Frequent Fire Model		Infrequent Fire Model	
	Mean	Std	Mean	Std
PIPA	924	125	664	279
QUGE	1,319	108	1,285	128
QULA	745	357	583	413
QUHE	876	81	837	103

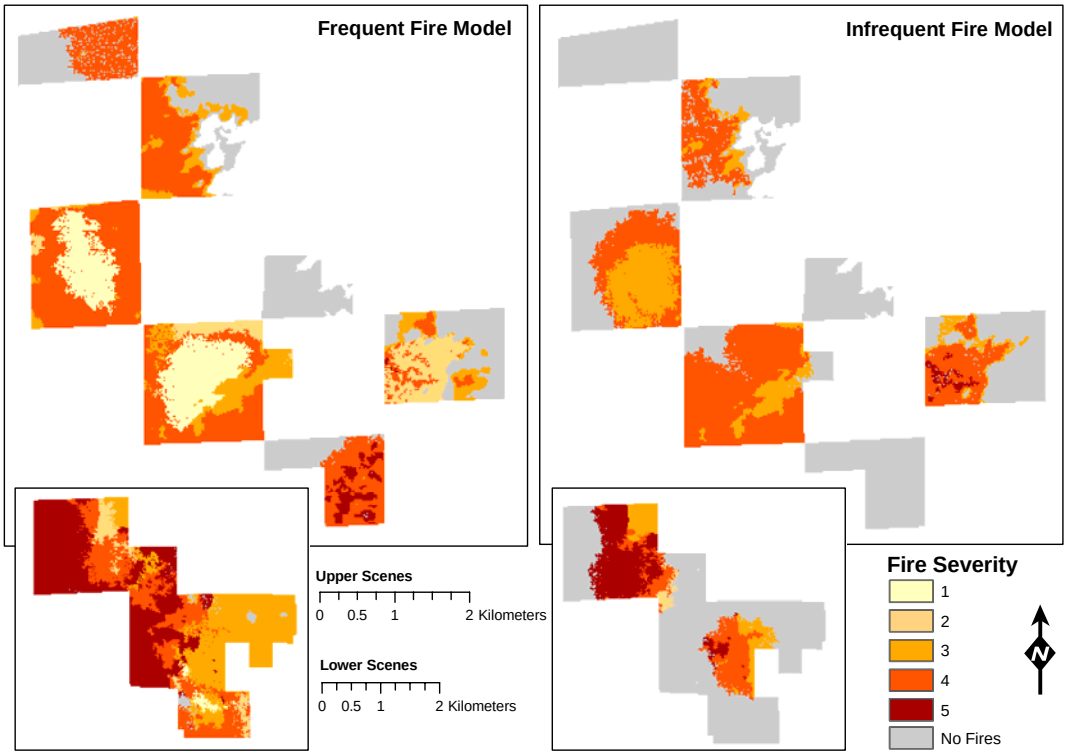

Figure 2-9. Map of all fires, their distribution, and severity at the WPU throughout the 500 year simulation. Darker reds are more severe fires. The most recent fire is displayed on top of older ones.

Future Model Development

Modeling techniques that may further advance this study's use of LANDIS includes implementing smaller time steps, further calibration, and fine-tuning of the spatial inputs. The next version of LANDIS (LANDIS II) will have one to several year time steps, which may enhance the realism of *P. palustris* behavior to fire and its

competitive tree species. Since the fragmented structure of the WPU restricted fire spread in this LANDIS model, simulating each section separately may induce more frequent fires on each individual population of *P. palustris*. The fire and fuel characteristics of LANDIS were sufficient to simulate the various fire regimes desired in this study, especially during higher fire return intervals and severe fires. Although, additional calibration may increase accuracy of the fire disturbance parameters. Other tree species present at the WPU may be added to the model to study more complex interactions within the landscape. Wiregrass (*Aristida Stricta*), a grass species and an indicator of *P. palustris* sandhill community health (Hardin, 2004) may be included as a relational species (Gustafson et al., 2004). Additional historical data or tree cores from the WPU may provide for more accurate age distributions of species. Although long-term validation procedures are difficult to establish, they would support the quality and viability of this model.

Conclusions

Several of this study's objectives were met. Two fire regimes were created to assess the landscape over time in relation to *P. palustris* and its competitive hardwoods in an ideal fire-maintained habitat and a fire suppressed one. Even though this model did demonstrate certain characteristics of *P. palustris* dynamics well, the results were not entirely realistic: Fire frequency was still considerably lower in the FFM, especially within individual populations, than what is required to maintain a viable *P. palustris* ecosystem. *Q. hemisphaerica* and *Q. geminata* were quite accurately depicted on the landscape, while some of the simulated dynamics of *Q. laevis* lacked realism. LANDIS II may provide the details to more precisely simulate the fire regime desired for this study, although the fragmented structure of the WPU may still adversely affect the

model's fire spread processes. The WPU may be able to use LANDIS as a management tool to visualize the adverse effects hardwoods may have on *P. palustris* sandhill communities within just a few decades. With some fine-tuning of parameters and implementation of smaller time steps, this model may dramatically improve and be applicable for management to visualize *P. palustris* population dynamics through time.

CHAPTER 3
DEVELOPMENT OF A DEMOGRAPHIC MATRIX MODEL OF LONGLEAF PINES
(*Pinus Palustris*)

Introduction

Longleaf Pine

P. palustris is a unique fire-dependent tree species of the southeastern United States. Frequent low-intensity fires remove accumulated leaf litter, overgrown grasses, and encroaching oaks exposing bare-mineral soil required for seed germination and establishment (Croker, 1975; Boyer, 1990; Myers, 1990). Another distinctive feature about this pine is its seedling's slow growing 'grass stage'. Here it develops a long thick tap root (Myers, 1990), increases in diameter (Platt et al., 1988), and is protected from fire through dense tuft of long, moisture rich needles. It may stay in this stage for 5-15 years. Within one growing season, *P. palustris* can grow over 1m in height avoiding lethal temperatures of fire near the ground surface while protecting the terminal bud. A maturing tree develops fire-resilient scaly plates, which define it as the most fire-resistant pine. Furthermore, the ecosystem has vegetation with pyrogenic traits that facilitate the ignition and spread of fire (Fonda, 2001; Myers, 1990). Without frequent fire, the stable *P. palustris* dominated forest disappears due to failure of seedling establishment and incursion of hardwood upland species (Myers, 1990).

Sandhill, a *P. palustris* dominated ecosystem, was once one of the largest forest types in the southeastern coastal plain of the United States, but has diminished by over 90% due to harvesting and fire suppression. The highly dispersed pine and low

understory provided for an easily traveled and nicely shaded route for early European settlers (Hall, 1829). The ecosystem became fragmented by clear-cutting for timber, development, introduction of livestock, and agricultural practices. Many of these fragments have suffered from fire suppression resulting in encroachment by more fast growing, shade tolerant tree species (Frost, 1993; Rasser, 2003).

Restoration and preservation of *P. palustris* dominated ecosystems has become a well known practice in the southeast which contributes to recreation, aesthetics, reducing the onset of pest infestation, and conservation for endangered and often endemic species that thrive in this habitat (Boyer, 1993; Neel, 1993). Land managers plan for frequent low-intensity fires (~3-5 years) that keep encroaching hardwoods in check (Hartnett and Krofta, 1989; Platt and Rathbun, 1993). These fires also create an environment that supports *P. palustris* recruitment and open savannah like parks for recreation including hunting and easily traveled trails (Myers, 1990). Several endemic species thrive in these habitats, including the Sherman's fox squirrel (*Sciurus niger)*, red-cockaded woodpecker (*Picoides borealis*), brown-headed nuthatch (*Sitta pusilla*), Bachman's sparrow (*Aimophila aestivalis*), and the gopher tortoise (*Gopherus polyphemus*) (Engstrom, 1993).

Population Matrix Modeling

Population matrix models are an ideal starting point for analyzing tree population dynamics (Escalante et al., 2004; Zuidema and Zagt, 2000). Population matrix models often use size-based classes and transition probabilities developed from individual tree measurements over time. They are mechanistically designed to simulate survival, growth, death, and fecundity in user defined time steps assuming that the environment in which their data was collected is constant over time (Caswell, 2001). The labor required to census and map the data needed to estimate these probabilities is intense (Silvertown et

al., 1996). Estimation of size-specific fecundity is especially difficult because the process of seedling establishment depends on seed production, seed viability, dispersal, and site quality on multiple scales.

Objectives

The purpose of this research was to study *P. palustris* demographics in order to develop comprehensive density-dependent transition matrix models using multiple data sources. Two transition matrices were developed: (I) A *P. palustris* population transition matrix for a fire-maintained ecosystem and; and (II) A *P. palustris* population transition matrix for an ecosystem during fire suppression. These matrices were combined into one model to assess its response to various fire frequencies.

Methods

Data Sources

Data were compiled on longleaf pine demography from several sources for the development of the fire-maintained transition matrix model. A population transition matrix built by Platt et al. (1988) for longleaf pines (*P. palustris*) at the Wade Tract, Thomas County, Georgia was used as a base for our model. Longleaf pine seedling and mature tree growth data recorded by the Joseph W. Jones Ecological Center at the Ichwauy Preserve, Baker County, Georgia (Jones et al., 2003; Palik et al., 2003) were used to extend the Platt model. Longleaf pine seedling survivorship data were extracted from the Jones Center data and a seedbed preparation study performed at the Escambia Experimental Forest in southwest Alabama (Croker, 1975). Simulated fire suppression effects on longleaf pine recruitment were estimated from a study in Chinsegut Hill McCarty-Woods in northern Glades County, Florida (Hartnett and Krofta, 1989).

Transition Matrix Development

We extended an existing four year transition matrix model (Platt et al., 1988) with a new 0-2cm diameter size class (Table 3-1a.). The model was implemented in the python programming language. The transition matrix created by Platt et al. was specifically designed for a frequently burned *P. palustris* population (1-4 years), and therefore an ideal starting point. The four year transition probabilities were in eight size classes, starting with 2-10cm and continuing in 10cm increments (e.g., 10-20cm) until reaching the 70cm+ size class. The Platt model lacked seedling (0-2cm) size class transition probabilities and fecundity estimates for a fire maintained *P. palustris* ecosystem. An intensive gap analysis on *P. palustris* seedling survivorship at the Ichwauy Preserve from 1998 through 2003 provided a complete population state vector (Jones et al., 2003; Palik et al., 2003). In this study, ground measurements were collected on adult longleaf pines [>4cm dbh (diameter at breast height)] and randomly planted plots of seedlings. Seedling survivorship (34%) was estimated in two frequently burned *P. palustris* sites (Croker, 1975; Jones et al., 2003; Palik et al., 2003) which was similar to Boyer's (1963) seedling survival rate (38%). Although the seedling mortality rate (including significant fire scorch) seems high, the effects of fire suppression on seedling establishment are profound (Boyer, 1963; Boyer, 1990; Myers, 1990).

The current population of *P. palustris* at the Ichwauy Preserve is essentially at an ideal maximum density or K (basal area of 11.58 m^2/ha) according to Boyer's (1999) estimates for maintaining a healthy and naturally regenerating *P. palustris* population and therefore applied as such to the model. We assumed that fecundity and seedling survival were functions of tree density. Size-specific relative cone production from Platt et al. (1988) was used to scale fecundity estimates. Fecundity values in the matrix represent

the size-specific per capita number of newly established seedlings that enter the population. Because seedling establishment depends on a complex process that includes cone production, seed viability, seed dispersal, and germination safe sites, these parameters are difficult to estimate. In order to estimate fecundity parameters, we assumed a maximum population growth rate (λ) of 1.05. The maximum growth rate would only occur in a population with no density limitation. Size-specific fecundity values were estimated with an iterative procedure (Cropper and DiResta, 1999) using the Bisection method. We assumed that fecundity scaled with size according to the ratio of 1:1:3:3:5:5:5 for the seven largest size classes. Model behavior is not sensitive to the assumption of how fecundity scales with size (Cropper and DiResta, 1999). This is also consistent with the relatively low elasticity (asymptotic growth rate sensitivity) for fecundity values in the matrix model (see below).

Longleaf pine seedling growth (McGuire et al., 2001; Gagnon et al., 2004) and distribution pattern in gaps (Platt et al., 1988; Brockway and Outcalt, 1998) indicate that seedlings are competitively inhibited by larger trees. Although the functional relationship between adult density and seedling establishment and survival cannot be quantified, long-term simulations require density-dependence for realism. A population characterized by our matrix model growing at $\lambda = 1.05$ could increase from 200 trees per ha to 1,662 trees per ha in 80 years. For comparison, the density of a virgin longleaf pine stand in Louisiana in 1935 was reported to be between 191 and 233 trees per ha (Penfound and Watkins, 1937).

In order to simulate seedling density-dependence, we assumed that the fecundity and seedling survival matrix elements were functions of the number of trees greater than

10cm diameter. We also assumed a local population carrying capacity (K) of 500 trees greater than 10cm diameter (100m radius plot). Calibrating the density function starts with two sets of matrix parameters; one, the matrix for the maximum growth rate (λ = 1.05, or other assumed values); the other being a matrix that represents stable growth at K (λ = 1.00). Fecundity and seedling survival values are calculated as:

$$f(N) = Max * e^{(-kd * N)} \qquad (3\text{-}1)$$

where f(N) is the value of the matrix element at population size N, Max is the value of the matrix element in the maximum growth matrix, and kd is a constant (e.g., a fecundity value of 2.63 for trees greater than 50 cm at λ = 1.05; Figure 3-1.). The value of kd is determined by solving the equation for a value of f(N) equal to the λ = 1 matrix element and a value of N set at K, which is at a stable equilibrium in this model. This density-dependent model has been used to model fisheries (Caswell, 2001) and a Poa population in the UK (Case, 2000) based on measured fecundity and seedling survival at different densities.

A second transition matrix model was created to represent the effects of fire suppression on *P. palustris* establishment (Table 3-1b.). It has been determined that after just 15 years without fire disturbance, *P. palustris* recruitment ceases (Hartnett and Krofta, 1989) due to lack of bare mineral soil, low shade tolerance, and poor competitive abilities of seedlings (Myers, 1990). Even just a few years of fire suppression can dramatically reduce the amount of recruitment and vigorous herbaceous encroachment may adversely affect growth and survival of young longleaf pines (Hartnett and Krofta, 1989; Platt and Rathbun, 1993). As such, we assumed that seedling number would decline exponentially as fires are suppressed (Figure 3-2.). We were able to achieve this

by simply using the same transition probabilities as the first model and setting the size-specific fecundity parameters to zero.

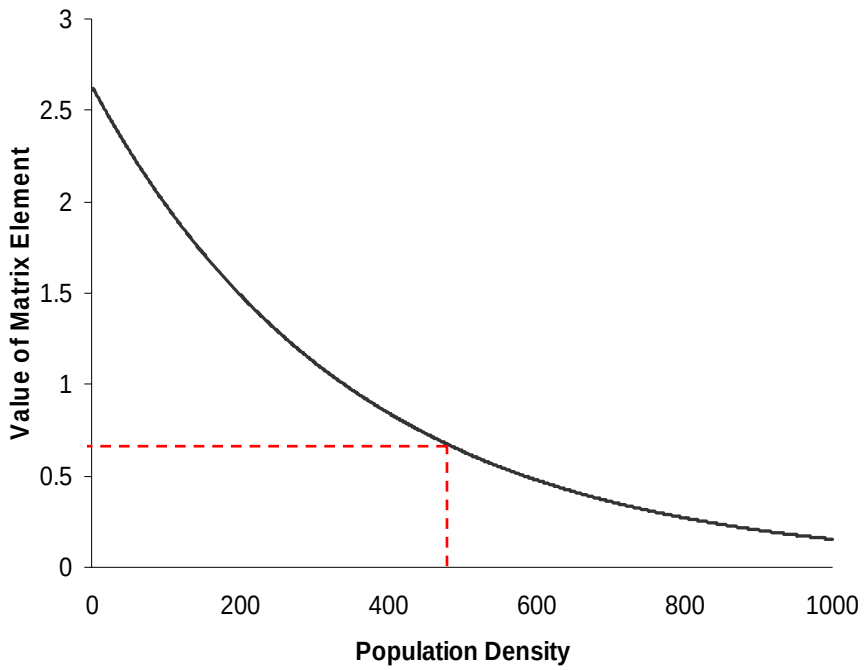

Figure 3-1. Example of the function used to determine the values of the matrix elements (trees >50cm dbh) assuming a maximum growth rate (λ=1.05). The dotted line represents the population at K, which is at a stable equilibrium.

Table 3-1. Transition matrices developed from multiple data sources including the base transition matrix created by Platt et al. (1988). The measurements refer to the diameter of the trees (at breast height for those applicable).

a.) Fire Transition Matrix

	Year 0 (cm)								
Year 4 (cm)	**0 to 2**	**2 to 10**	**10 to 20**	**20 to 30**	**30 to 40**	**40 to 50**	**50 to 60**	**60 to 70**	**70 +**
0 to 2	0.114	0	0.123	0.123	0.369	0.369	0.615	0.615	0.615
2 to 10	0.228	0.756							
10 to 20		0.082	0.834						
20 to 30			0.138	0.865					
30 to 40				0.127	0.834				
40 to 50					0.152	0.899			
50 to 60						0.077	0.875		
60 to 70							0.084	0.891	
70 +								0.054	0.882
Deaths	0.658	0.162	0.028	0.008	0.014	0.024	0.041	0.055	0.118

b.) No Fire Transition Matrix

	Year 0 (cm)								
Year 4 (cm)	**0 to 2**	**2 to 10**	**10 to 20**	**20 to 30**	**30 to 40**	**40 to 50**	**50 to 60**	**60 to 70**	**70 +**
0 to 2	0.114	0	0	0	0	0	0	0	0
2 to 10	0.228	0.756							
10 to 20		0.082	0.834						
20 to 30			0.138	0.865					
30 to 40				0.127	0.834				
40 to 50					0.152	0.899			
50 to 60						0.077	0.875		
60 to 70							0.084	0.891	
70 +								0.054	0.882
Deaths	0.658	0.162	0.028	0.008	0.014	0.024	0.041	0.055	0.118

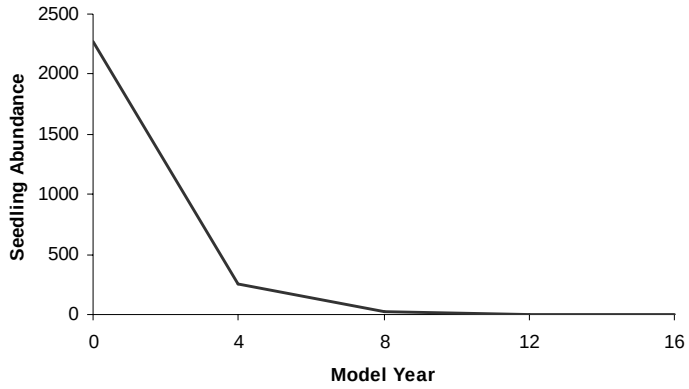

Figure 3-2. Negative exponential function of seedling establishment after the onset of fire suppression. Seedling numbers are below zero by year 16.

Results and Discussion

Error Analysis

A simulated population with one fire in each four year time step was compared to real data from the Ichwauy Preserve collected on a five year time interval (1998-2003) for an error analysis (Table 3-2.). Only the size-classes from 2cm on were used in this analysis because the same individuals were measured in 1998 and 2003. This does not account for additional individuals entering the population, which is otherwise the case in the fire matrix model using fecundity and seedling transition probabilities. As a result, there was a high percentage of error (118%) in the 2-10cm size class. The 60-70cm size classes resulted in the most percentage error (303%) due to the small population and associated changes in that size class. Otherwise, the % error ranged from -11 to 6%.

Determining *P. palustris* growth from diameter measurements within five years is difficult because of the slow and variable growth characteristics of *P. palustris*. As the habitat is burned, the pine's scaly plates protect the tree, but may stunt its growth and allow the bark to slough off causing growth patterns to seem absent or even reversed (e.g., lower dbh) during short periods (Myers,1990; Putz, personal communication,

2005). As such, it is also relatively safe to compare *P. palustris* growth measurements with a one year discrepancy.

Table 3-2. Error analysis comparing one simulated time step of the fire matrix model to real five year growth data from the Ichwauy Preserve, FL.

Size-Class (cm)	% Error	Difference
2 - 10	118	474
10 - 20	-11	-105
20 - 30	6	55
30 - 40	-7	-88
40 - 50	4	32
50 - 60	-5	-7
60 - 70	303	6
70 +	0	0

Elasticity Analysis

An elasticity analysis of the transition matrix was performed to evaluate the relative sensitivity of λ to changes in the matrix elements (Caswell, 2001). Elasticity (e_{ij}) is calculated using the following equation:

$$e_{ij} = \frac{a_{ij}}{\lambda} \bullet \frac{v_i w_j}{< W, V >} \qquad (3\text{-}2)$$

Where a_{ij} are elements of the stage population matrix, W is the right eigenvector of the dominant eigenvalue (λ), V is the left eigenvector, and $<W, V>$ is the scalar product of the two eigenvectors.

The population matrix elements were classified as P, the probability of surviving and remaining in the same size class; G, the probability of growing into the next largest size class; and F, the per capita production of established seedlings. Overall, the elasticity values (Figure 3-3.) demonstrated that *P. palustris* population growth was far more sensitive to P (range: 0.003 – 0.17), while G and F were much less sensitive (range: 0.001 – 0.04). This suggests that accurate estimates for P are necessary for representing the population growth rate (Doak et al., 1994). G values for smaller size class trees were higher, signifying the relative importance of *P. palustris* growth of younger trees. As λ's

increase, G and F begin to play a stronger role in the model as P weakens. In conclusion, this elasticity analysis follows similar analyses of other natural populations by summarizing the comparative effects of small changes in demographic rates (Doak et al., 1994; Escalante et al., 2004).

Fire Frequency Analysis

Simulated fire frequency was varied to assess model behavior (Figure 3-4.; Figure 3-5.). With constant fires (1-4 year fire return interval) the population remained steady and at K. Lower standard deviation and standard error of the total population with frequent fires suggested a more stable population through time (Ott and Longnecker, 2001; Table 3-3.). As the fire return intervals became larger, spikes in species abundance became more dramatic with each onset of fire but the population remained well below K and continued to deplete with proliferation of fire suppression (Figure 3-4.). These spikes in population increase are the direct result of seedling recruitment when fires are brought back into the system (Figure 3-5.). It is not clear how well this simulates reality. A healthy *P. palustris* population that has experienced fire suppression lasting 40 years may not be able to re-establish itself from a newly introduced fire regime due to the large fuel load that has most likely accumulated and other vegetative encroachment (Hartnett and Krofta, 1989; Gilliam and Platt, 1999). However, the model does assume that fire occurs 1-4 times in each time step. As such, some recruitment is likely especially if cone production is in a mast year and conditions are favorable (Platt et al., 1988; Boyer, 1999). The shorter fire return intervals then depict the more realistic behavior of *P. palustris* in a fire maintained community.

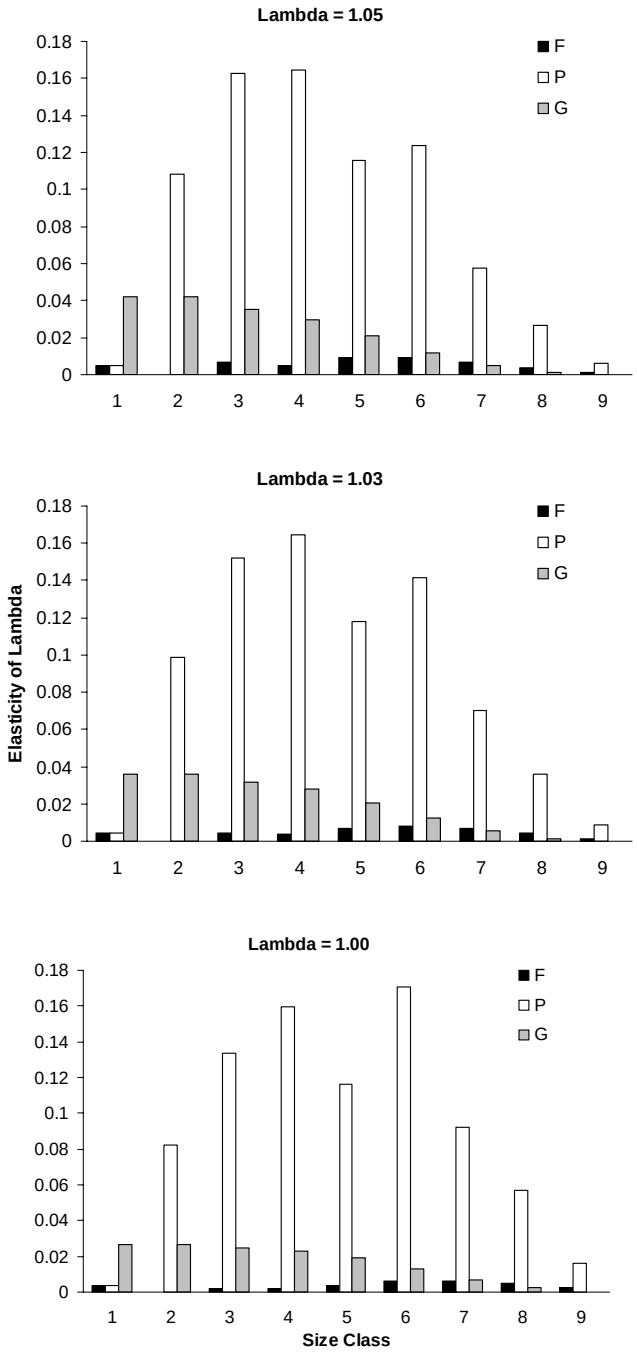

Figure 3-3. Elasticity of various lambda values (λ). F: fecundity; P: probability of remaining in the same size class; G: probability of growing to the next size class. Size classes are in order from smallest to largest.

Table 3-3. Descriptive statistics of the various fire return intervals. Every four year fire return interval represents 1-4 years of low-intensity burns in one matrix time step.

Fire Return Intervals (yrs.)	4	8	12	20	40	No Fire
Mean	5,940	4,994	4,620	4,226	3,957	3,537
Standard Error	35	125	153	181	192	199
Standard Deviation	177	639	779	920	980	1,015
Sample Variance	31,447	407,997	606,372	847,299	960,623	1,029,834
Minimum	5,776	4,027	3,444	2,909	2,715	2,247
Maximum	6,756	6,756	6,756	6,756	6,756	6,756

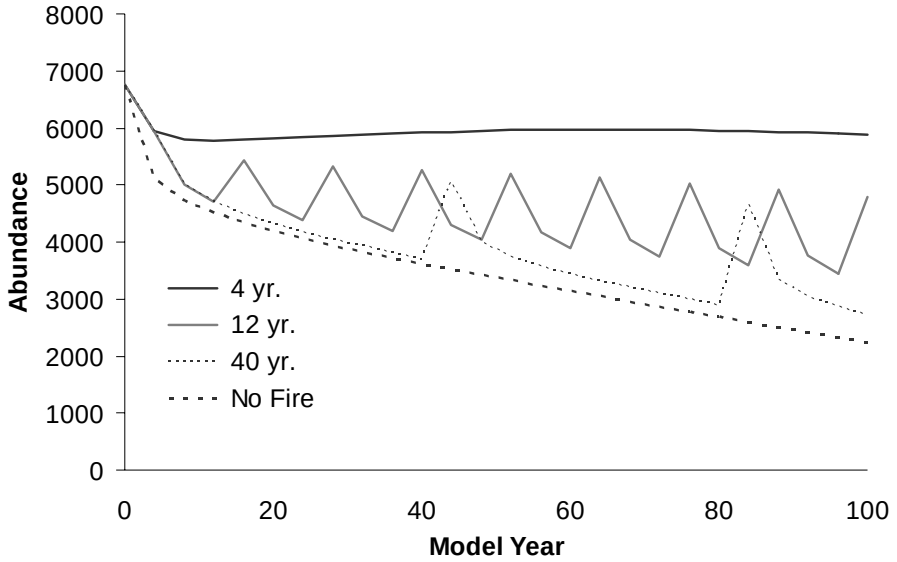

Figure 3-4. Total number of individuals of *P. palustris* during various fire intervals. The peaks in population growth are from seedlings establishing during years of fire occurrence.

When the population was indefinitely subjected to fire suppression, the seedling size class effectively disappears within four time steps (16 years) in a negatively exponential fashion (Figure 3-5.), while the total population continued to decline until it reached below one at year 536. With pines reaching maximum and mean ages of 400-500 (Boyer, 1999) and 200-250 (Putz, personal communication, 2005), respectively, and assuming no anthropogenic (e.g., logging) or catastrophic disturbances (e.g., hurricanes), this estimate of the youngest tree reaching 536 years of age is unlikely. Although, the

population is under 100 by year 316, suggesting a struggling population in route to its demise.

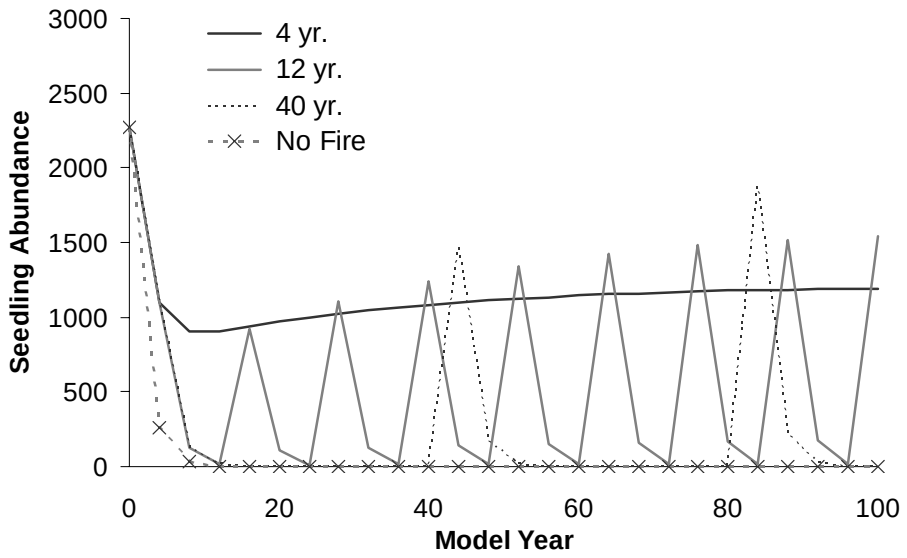

Figure 3-5. Total number of *P. palustris* seedlings during various fire intervals. The peaks coincide with population growth rates in Figure 3-4.

An advantage to the frequent fire regime is the consistent uneven age structure of the population. Infrequent fires that stimulate new *P. palustris* growth tend to create gaps of missing age-classes in the population. This may influence cone production and seed crops with the lack of necessary mature trees at particular periods in time. Gap sizes or densities of adult trees may therefore fluctuate dramatically through time as a result. Unnecessarily large gaps allow some *P. palustris* recruitment, but also allow for faster growing competing vegetation to take over the landscape. If gaps are not large enough, seedling establishment and success may be inadequate for a sustainable population (Grace and Platt, 1995; Palik et al., 2003).

Future Model Development

Several additions to the transition matrix and more in-depth validation procedures may be used to further develop this model. Since most *P. palustris* forests are managed

to some degree and are often in a restoration stage, there are many variations in population structure and composition, understory and site conditions, and fuel traits, which may influence population development. The model should include validation with site specific management strategies, such as burning initiatives, seedbed preparation, and thinning. These managed forests spanning from east Texas to the east coast of Virginia (Frost, 1993) provide for an opportunity to use and compare this model with their *P. palustris* population dynamics. More specifically, K may vary between sites and between size and even age classes within a population. In our model, fecundity estimates were assumed based on a hypothetical growth rate. Applying empirical fecundity values in a stage based distribution may improve these estimates. Seedling parameters are difficult to estimate due to their complex growth and survival patterns related to environmental influences, such as fire and nutrient competition from adult *P. palustris* or encroaching vegetation (Grace and Platt, 1995; Gagnon et al., 2004). Their growth rate in diameter was especially difficult. For instance, Grace and Platt (1995) showed that many *P. palustris* seedlings do not even reach 2cm in diameter in four years. As such, it may be required to separate this size class into smaller size classes for particular *P. palustris* populations.

This modeling technique may be further improved by acquiring more long-term data on this slow growing and long-lived species. Unfortunately, funding and research opportunities are often rather short-term and therefore may influence the model's utility. For instance, the data sources used in this study did not have measurements recorded beyond a six year period. Other studies (e.g., Veno, 1976) used past research and data

collected to continue understanding forest dynamics of a site on a larger temporal scale (>20 years).

Implications of Using Multiple Data Sources

It would have been ideal to collect all of the data for model development and testing within the Goethe State Forest. This was not practical because of the incredible time, money, and effort required to collect and analyze the raw data needed to create such a comprehensive demographic model on *P. palustris*. On the other hand, using multiple data sources may produce large errors associated with environmental and anthropogenic factors. *P. palustris* populations may vary by site condition, such as vegetative structure and composition, landscape history, climatic conditions, soil and available nutrients, and high genetic variation (Boyer, 1990). Management and research objectives impact these populations as well, through variation in the fire regime, physical manipulation of the landscape (e.g., planting, thinning), and having different data collection methods and goals.

Conclusions

This model has the potential to become practical and useful for further understanding of the population dynamics of this long-lived conifer. The essential elements of a complete transition matrix have been estimated from reliable resources. A K was implemented into the model as a spatial restriction or density-dependent function. The unique survivorship characteristics of *P. palustris* seedlings and fecundity estimates were applied to the transition matrix to develop a more comprehensive modeling scheme. Elasticity and model behavior analyses provided for model responsiveness to its inherent elements and validation procedures resulted in relatively low error. Using the dual transition matrix technique applied the behavioral response of this conifer to fire. The

abundant research done on *P. palustris* population dynamics (e.g., Boyer, 1990) coupled with population modeling techniques provide opportunities to continue understanding this complex conifer and its habitat.

CHAPTER 4
HYBRID APPROACH TO SPATIAL AND DEMOGRAPHIC MODELING OF LONGLEAF PINES (*Pinus Palustris*)

Introduction

Longleaf Pine

P. palustris is a unique fire-dependent tree species of the southeastern United States. Frequent low-intensity fires remove accumulated leaf litter, overgrown grasses, and encroaching oaks exposing bare-mineral soil required for seed germination and establishment (Croker, 1975; Boyer, 1990; Myers, 1990). Another distinctive feature about this pine is its seedling's slow growing 'grass stage'. Here it develops a long thick tap root (Myers, 1990), increases in diameter (Platt et al., 1988), and is protected from fire through dense tuft of long, moisture rich needles. It may stay in this stage for 5-15 years. Within one growing season, *P. palustris* can grow over 1m in height avoiding lethal temperatures of fire near the ground surface while protecting the terminal bud. A maturing tree develops fire-resilient scaly plates, which define it as the most fire-resistant pine. Furthermore, the ecosystem has vegetation with pyrogenic traits that facilitate the ignition and spread of fire (Fonda, 2001; Myers, 1990). Without frequent fire, the stable *P. palustris* dominated forest disappears due to failure of seedling establishment and incursion of hardwood upland species (Myers, 1990).

Sandhill, a *P. palustris* dominated ecosystem, was once one of the largest forest types in the southeastern coastal plain of the US, but has diminished by over 98% due to harvesting and fire suppression (Myers, 1990). The highly dispersed pine and low

understory provided for an easily traveled and nicely shaded route for early European settlers (Hall, 1829). The ecosystem became fragmented by clear-cutting for timber, development, introduction of livestock, and agricultural practices. Many of these fragments have suffered from fire suppression resulting in encroachment by more fast growing, shade tolerant tree species (Frost, 1993; Rasser, 2003).

Restoration and preservation of *P. palustris* dominated ecosystems has become a well known practice in the southeast which contributes to recreation, aesthetics, reducing the onset of pest infestation, and conservation for endangered and often endemic species that thrive in this habitat (Boyer, 1993; Neel, 1993). Land managers plan for frequent low-intensity fires (~3-5 years) that keep encroaching hardwoods in check (Hartnett and Krofta, 1989; Platt and Rathbun, 1993). These fires also create an environment that supports *P. palustris* recruitment and open savannah like parks for recreation including hunting and easily traveled trails (Myers, 1990). Several endemic species thrive in these habitats, including the Sherman's fox squirrel (*Sciurus niger)*, red-cockaded woodpecker (*Picoides borealis*), brown-headed nuthatch (*Sitta pusilla*), Bachman's sparrow (*Aimophila aestivalis*), and the gopher tortoise (*Gopherus polyphemus*) (Engstrom, 1993).

Hybrid Modeling

Creating hybrid ecosystem process models provide an opportunity to employ important aspects of two or more models to create a new more robust model. Hybrid models can be constructed with components that include simulation models, statistical models, and empirical spatial models [Geographic Information System (GIS) models]. Robinson and Ek (2003) utilized at least six various empirical and physiological based modules to develop an individual-tree growth and dynamics model. Logofet and Korotkov (2002) incorporated spatially explicit forest inventory data to apply a

geographical component within a Markov chain model measuring natural succession of forest types. Lamar and McGraw (2005) compared two matrix population models of eastern hemlock (*Tsuga canadensis* L.), one created from field data and one created from remote sensing techniques using low elevation aerial photography. Each of these studies used the inherent strengths from each model to establish a more viable model of forest dynamics. In this study, density-dependent matrix population models use particular outputs from the spatially explicit LANDIS (LANdscape DIsturbance and Succession; Mladenoff et al., 1996) model to assess *P. palustris* population dynamics.

Population matrix models are an ideal starting point for analyzing tree population dynamics (Escalante et al., 2004; Zuidema and Zagt, 2000). They have become powerful tools used in the natural sciences and have gone on to be used in hybrid model research (Logofet and Korotkov, 2002; Lamar and McGraw, 2005). Population matrix models often use size-based classes and transition probabilities developed from individual tree measurements over time. They are mechanistically designed to simulate survival, growth, death, and fecundity in user defined time steps assuming that the environment in which their data were collected is constant over time (Caswell, 2001). The labor required to census and map the data needed to estimate these probabilities is intense (Silvertown et al., 1996). Estimation of size-specific fecundity is especially difficult because the process of seedling establishment depends on seed production, seed viability, dispersal, and site quality on multiple scales.

LANDIS on the other hand, models landscapes over large spatial and temporal scales requiring relatively coarse input data of dominant tree species and fire characteristics of the land (He and Mladenoff, 1999). The model is spatially interactive,

implementing variables such as tree species seeding characteristics and cohort-based growth capabilities, as well as fire ignition, spread, and fuel traits. These features enable the user to gain insight into the overall dynamics of the forest system visually and quantitatively over decades to several centuries (Mladenoff and He, 1999).

Objectives

The purpose of this research was to utilize the linked outputs of a spatially explicit forest succession model (LANDIS), and a density dependent transition matrix model to examine *P. palustris* population dynamics over time. Temporal fire data from LANDIS was used to select between two transition matrices: (I) A *P. palustris* population transition matrix for a fire-maintained ecosystem and; (II) A *P. palustris* population transition matrix during fire suppression. The ultimate goal was to tie *P. palustris* population numbers to specific management units or independent populations.

Methods

Study Area

The Watermelon Pond Unit (WPU) of the Goethe State Forest is a 1938-ha tract located in Levy and Alachua counties of Florida, USA (latititude 29° 32’ 42 “, longitude 82° 36’ 20”; Figure 4-1.). It has a checker-board structure that makes land management difficult, especially for prescribed burning. Agricultural land owners, state and county roads, and two small towns divide the forest, further complicating management. Before European settlement, the land was a homogeneous landscape of the sandhill community type dominated by *P. palustris*. During the last century, the area was fragmented by anthropogenic effects, specifically phosphate mining and non-sustainable timber harvesting. Many of these areas were unmanaged causing dramatic successional changes in this ecosystem with few *P. palustris* trees left today (Rasser, 2003). Now, one of the

main management goals is the immediate implementation of prescribed burning initiatives for restoration and preservation of the remaining sandhill areas (Hardin, 2004).

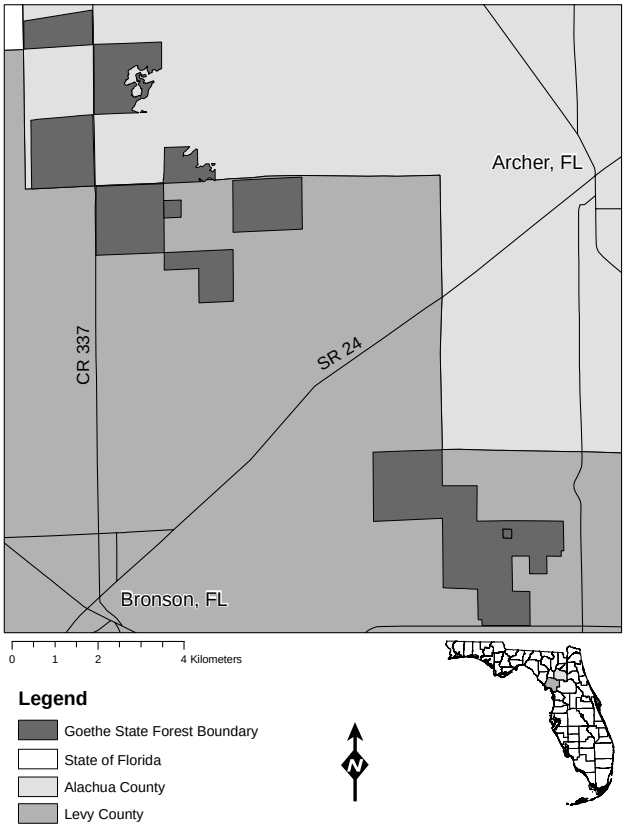

Figure 4-1. Map of the study site: Watermelon Pond Unit of the Goethe State Forest, Florida, USA.

Outside Data Sources

Data were collected on longleaf pine demographics from several outside sources for the development of the fire-maintained transition matrix model used in this study. A population transition matrix built by Platt et al. (1988) for longleaf pines (*Pinus palustris*) at the Wade Tract, Thomas County, Georgia was used as a base for our model. Longleaf pine seedling and mature tree growth data recorded by the Joseph W. Jones Ecological Center at the Ichwauy Preserve, Baker County, Georgia were used for assessing density parameters (Jones et al., 2003; Palik et al., 2003). Longleaf pine seedling survivorship

data were extracted from the Jones Center data and a seedbed preparation study performed at the Escambia Experimental Forest in southwest Alabama (Croker, 1975). Simulated fire suppression effects on longleaf pine recruitment were estimated from a study in Chinsegut Hill McCarty-Woods in northern Glades County, Florida (Hartnett and Krofta, 1989).

Hybrid Modeling Techniques: The Spatial and Demographic Components

Modeling *P. palustris* response to fire requires addressing processes at both the landscape scale and at the population scale. It is certainly possible to construct a single model that simulates the landscape fire regime as well as seedling establishment and tree growth and mortality. A hybrid approach, however, has the advantage of using models that have already been developed (LANDIS, *P. palustris* matrix population model), which are operating at different time steps, to meet the model objective with significantly less model development effort. The principal problem of the hybrid model approach is passing information between the individual models.

LANDIS outputs, and other data sources, were used to estimate the: a) initial *P. palustris* size-classes and fire distributions; b) *P. palustris* carrying capacity; and c) fire disturbance frequencies, all within individual *P. palustris* populations of the WPU. These populations were chosen because of their size and relative fire disturbance frequency and distribution simulated within LANDIS (Figure 4-2.). A small isolated population in the northern territory (270ha) of the WPU was used as well as the much larger southeastern section (WPU East; 792ha). For comparison, the entire population (1874ha) at the WPU was also simulated assuming each fire disturbance in LANDIS affects the entire site's *P. palustris* population. From a graphical analysis of age and size relationships in Platt et al. (1998), the initial age-class distributions created for LANDIS

(see Chapter 1) were used to determine the size-class distributions found in each of the three *P. palustris* populations. The number of individuals within each population was calculated from: a) the known area of *P. palustris* sandhill habitat within each section; b) the size-class distribution within each section; and c) the *P. palustris* population density of the Ichwauy Preserve (basal area of 11.58 m^2/ha). This population was essentially at an ideal maximum density or carrying capacity (K) according to Boyer's (1999) estimates for maintaining a healthy and naturally regenerating *P. palustris* population. We assumed that fecundity and seedling survival were functions of tree density. Size-specific relative cone production from Platt et al. (1988) was used to scale fecundity estimates (see Chapter 2). Fire frequency distributions were purely based on the occurrence of fire within each of the three populations for each model created in LANDIS. The Frequent Fire Model (FFM) simulated fires every one to two LANDIS time steps (10-20 years) and the Infrequent Fire Model (IFM) simulated a more fire suppressed ecosystem with a fire return interval of 1-7 LANDIS time steps (10-70 years). The size, intensity, and frequency of burns varied across the landscape which were influenced by land characteristics and tree species inter- and intra- specific behavior.

Fire was simulated with the matrix population model through application of two size class transition matrices representing population dynamics with fire or with no fire during each ten year time step in LANDIS. The development and analysis of the two matrices are described in detail elsewhere (see Chapter 2). Essentially, one four year transition matrix represents a *P. palustris* population subjected to a regular low-intensity burning regime (1-4 years). The other four year transition matrix represents a *P. palustris* population subjected to fire suppression with fecundity set to zero. When the fire

transition matrix is chosen, fecundity and seedling survival rates are density-dependent, with equilibrium at the carrying capacity (K). Density-dependence is not applied in the fire suppression transition matrix because of the rapid decline in recruitment in the absence of frequent burning (Hartnett and Kofta, 1989).

Figure 4-2. The three areas within the study site with *P. palustris* populations used in the hybrid model analysis: 1) The entire WPU (1874ha); 2) The southeastern portion of the WPU, namely WPU East (792ha); 3) A small isolated population in the northern section of the WPU (270ha). Refer to Figure 4-1. for the layout of the WPU.

Two application methods were proposed to handle the time step discrepancy between LANDIS and the matrix model. The hybrid matrix model runs an alternate of 2 to 3 times per LANDIS time step, so that five 4-year time steps equal two LANDIS time steps (Figure 4-3.). When a fire occurs in LANDIS, it only disturbs an area once and therefore, the fire matrix model should only run once per LANDIS time step. The

positioning of whether the fire matrix runs first, second, or third, is randomly selected. For comparison, a second matrix model was designed to employ the fire transition matrix 2 or 3 times when a fire occurs in LANDIS.

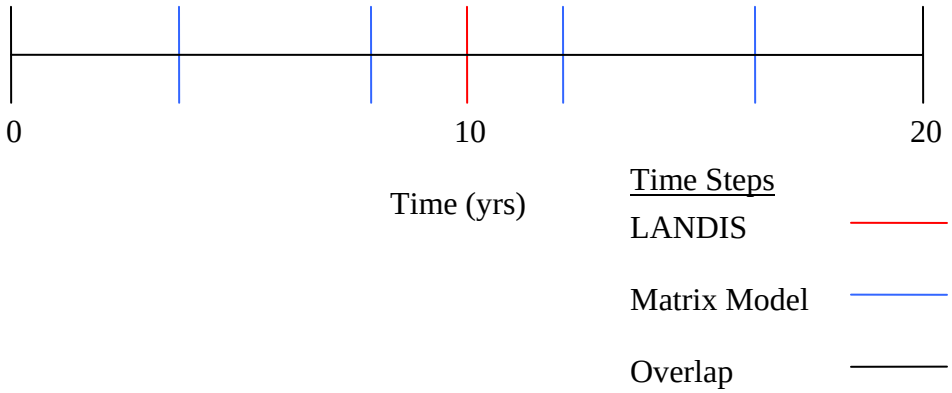

Figure 4-3. Diagram of the time step discrepancy between the matrix population model (4-year) and LANDIS (10-year).

Results and Discussion

Fire Effects on Individual Populations

The overall simulated longleaf pine population abundance changes were a direct result of seedling recruitment fluctuations caused by fire disturbance and fire suppression (Figure 4-4.) As fires occur on the landscape, the accumulated fuel (e.g., leaf litter, herbaceous growth) burns to expose bare mineral soil for the establishment and germination of *P. palustris* seedlings, assuming good seed production and site conditions (Gilliam and Platt, 1999). Without fires, seedling recruitment decreases exponentially until they cease to establish 15 years (~ 4 times steps) from the onset of fire suppression (Hartnett and Krofta, 1989).

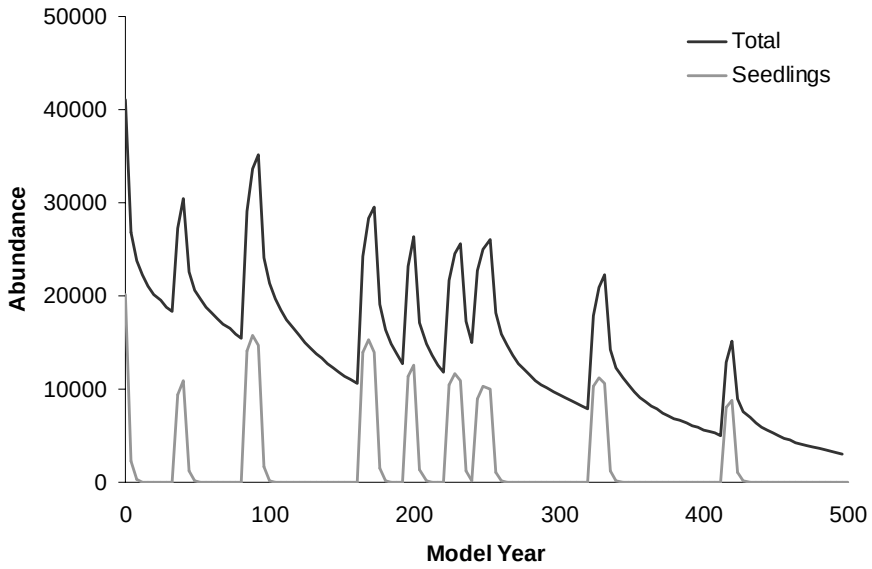

Figure 4-4. Total abundance changes within the small population in relation to the seedling abundance changes. The spikes relate directly between total population numbers and the recruitment of seedlings.

The two application methods for using the fire transition matrix (e.g., 1 or 2/3 times per LANDIS time step) were compared (Figure 4-5.). Having the fire transition matrix run 2 to 3 times more results in a clear percent increase in mean (41-59%) and abundance at year 500 (74-84%) in all three populations. The entire WPU and WPU East had higher variation (31% and 28%, respectively) in population numbers using the transition matrix 2/3 times per LANDIS time step, while the isolated portion of the WPU did not show much difference (0.03%). In the isolated population, there was a time lag that allowed for fire suppression to take effect for both application methods. In the two larger populations, the fires were frequent enough to allow the 2/3 fire method to keep a steady increase or maintained *P. palustris* population (e.g., smooth curve).

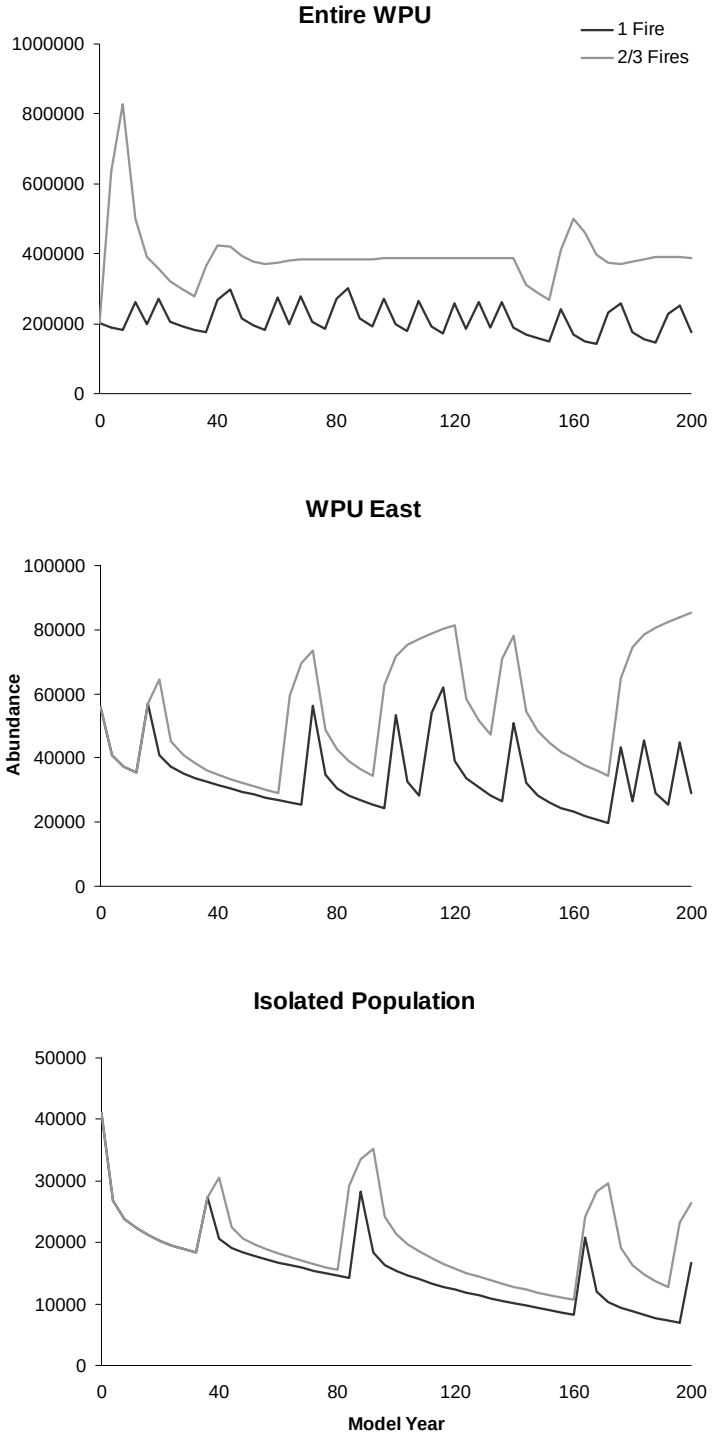

Figure 4-5. Total population changes of the matrix population model assuming fires occur either once or every iteration (2 to 3 times) within a LANDIS time step. Scale may be different between graphs.

P. palustris population dynamics were compared over 500 years assuming fires occurred in all transition matrices (all 2/3 times steps) during fire disturbance in LANDIS (Figure 4-6.). The fire frequencies of the FFM resulted in relatively stable numbers in the two larger populations, while the isolated population continued to decline in both the FFM and the IFM. The 62-80% increase in fire frequency in all populations resulted in 90-96% larger numbers at year 500 using the FFM. The high fluctuations in the WPU East numbers was due to the large number of fires from the FFM that were spaced far enough apart for multiple reactions to fire suppression and seedling recruitment following fires.

Comparing *P. palustris* simulation outputs of LANDIS and the matrix model was not possible due to their incompatible output formats. LANDIS outputs the presence of a species in particular locations (cells) across a landscape and through time, lacking population numbers. The matrix model outputs a species population in size-classes through time, lacking a spatial component. However, utilizing the output fire frequencies of LANDIS in the matrix model to provide *P. palustris* numbers in individual populations at the WPU offered an opportunity for the missing elements of one model to be supplied by the other.

Implications of Hybrid Approach

This modeling approach demonstrates the ability to combine strengths of ecosystem models and compensate for their weaknesses (Kimmins et al., 1999). Here we utilized the *P. palustris* transition probabilities derived from field work done by Platt et al. (1988) and others (Croker, 1975; Hartnett and Krofta, 1989; Jones et al., 2003, Palik et al., 2003) and added a density dependent function (see Chapter 2). A spatial component

was built-in to specifically look at individual populations within the WPU as well as the fire frequencies and distributions created in LANDIS.

Although this was an opportunity to use the elements of two models at two different scales, each model simulates species dynamics quite differently, especially related to fecundity and population changes. LANDIS simulates fecundity from tree age-cohorts reaching maturity and dispersing 'seeds' into adjacent cells (He et al., 2003), while the fire matrix model utilizes fecundity transition probabilities (Caswell, 2001). LANDIS simulates tree growth dynamics through a presence/absence approach with interacting tree age-cohorts and influential disturbances and site conditions (He et al., 2003), while matrix models use size-based transition probabilities of one population of species assuming no competition, disturbance, or site variability (Caswell, 2001).

Future Model Development

The matrix population model approach is not spatially explicit, which may be a major limitation for longleaf pine simulation. Seedling establishment is clearly sensitive to overstory density (Boyer, 1993; Grace and Platt, 1995; McGuire et al,. 2001). The hybrid modeling approach, using LANDIS to provide some of the missing processes, is not a complete solution. Although long-term data is often difficult to obtain, utilizing GIS data may provide the long-term information needed for calibration of such demographic models (Logogfet and Korotkov, 2002). Acquiring and comparing demographic data collected from field-work and remotely sensed imagery (Lamar and McGraw, 2005) may be another calibration and validation option. Obtaining site-specific demographic data is an ideal approach to enhancing this modeling scheme. Since the data sources used to create these models are from a variety of projects and sites, demographic data from the WPU would be critical for model improvement. Other details

that are essential to the integration of these two types of models include understanding size and age relationships of trees such as *P. palustris* (Platt et al., 1988) and measuring fecundity and seedling growth in sites with different fire histories.

The time step discrepancy may be solved by using the next version of LANDIS (LANDIS II), which incorporates one to several year time steps. This may enhance the realism of *P. palustris* behavior to fire and its competitive tree species in LANDIS while providing analogous time steps between the matrix models and LANDIS. As a healthy *P. palustris* population requires frequent (3-5 years) low-intensity fires (Hardin, 2004), the fire return interval may decrease dramatically using LANDIS II, especially in the many isolated populations of *P. palustris* within the WPU.

Conclusions

The hybrid techniques used in this study were successful. The temporal fire frequency and spatial data from LANDIS provided for inputs to simulate the *P. palustris* matrix models using various fire regimes. Individual populations, or management units within the WPU, were simulated and analyzed. The outputs of these two models were not compared because of their incompatible output formats [e.g., presence of species (LANDIS) vs. population numbers (matrix model)]. Using LANDIS II, spatial technologies, such as GIS and remote sensing, and more site-specific long-term ground data on growth and fecundity of *P. palustris* may improve justification procedures. The abundant research done on *P. palustris* population dynamics (e.g., Boyer, 1990) together with demographic and hybrid modeling techniques provide opportunities to continue understanding this complex conifer and its habitat.

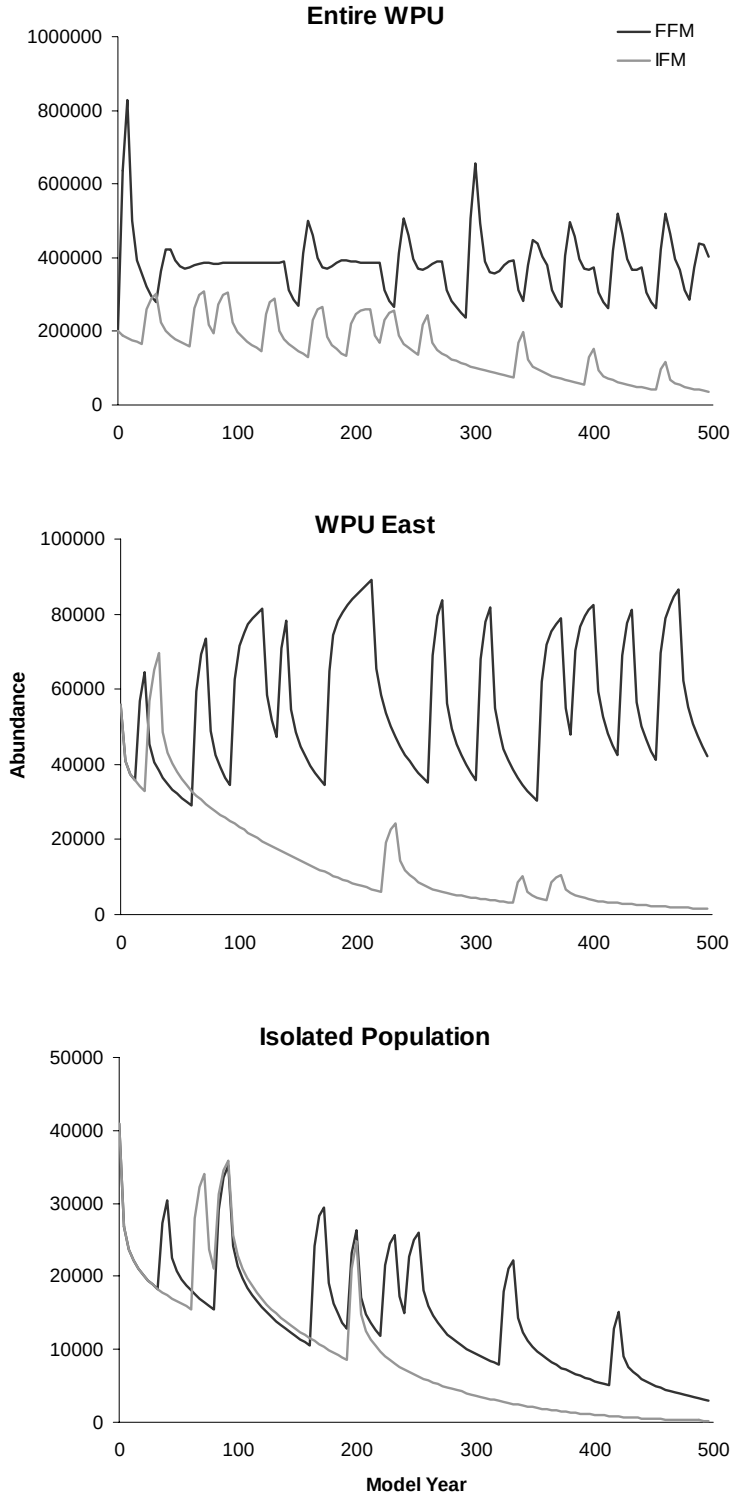

Figure 4-6. Total population changes of the matrix population model assuming fires occur every iteration (2 to 3 times) within a LANDIS time step. Scale is different between graphs. FFM: Frequent Fire Model; IFM: Infrequent Fire Model.

CHAPTER 5
CONCLUSIONS

General Conclusions

Results, conclusions, implications, and overall applicability for each portion of this research are discussed here. Conclusions from the spatial modeling portion of the research include:

- Two fire regimes were created in relation to *P. palustris* and its competitive hardwoods in an ideal fire-maintained habitat and a fire suppressed one.
- LANDIS demonstrated certain characteristics of *P. palustris* dynamics well: recruitment of young after fire, seeding distance, and fire tolerance.
- Results were not entirely realistic: Fire frequency was lower in the FFM than what is required to maintain a viable *P. palustris* ecosystem.
- *Q. hemisphaerica* and *Q. geminata* were accurately depicted, while dynamics of *Q. laevis* lacked realism.

The demographic modeling led to the following conclusions:

- The essential elements of a complete *P. palustris* transition matrix were estimated from data and literature.
- Additions to the *P. palustris* matrix population model developed by Platt et al. (1988) included:
    - A density-dependent function
    - Survivorship and growth rates of *P. palustris* seedlings (<2cm dbh)
    - Fecundity estimates

- Model sensitivity and dynamics were analyzed through elasticity and scenario analyses.
- Validation procedures resulted in relatively low error.
- A dual transition matrix technique (with and without fire) applied the behavioral response of this conifer to fire.

The hybrid modeling approach, consisting of the combined application of LANDIS and the demographic model, led to the following conclusions:

- The temporal fire frequency and spatial data from LANDIS provided inputs to simulate the *P. palustris* matrix models using various fire regimes. General responses to fire suppression were realistic.
- Individual populations within the WPU were simulated and analyzed.
- The incompatible output formats of the two models [e.g., presence of species (LANDIS) vs. population numbers (matrix model)] did not allow for model comparison.

Limitations, Implications, and Future Work

Spatial Modeling

There are several limitations with the spatial model developed using LANDIS. *Q. laevis* tolerates fires well and re-sprouts vigorously following fire (McGinty and Christy, 1977), but was the least abundant species on the landscape during the model runs. The short fire return interval of 3-5 years (Hardin, 2004) required to maintain and/or restore sandhill communities could not be modeled with LANDIS 3.7 because of the 10 year time step. Furthermore, the fragmented structure of the WPU restricted fire spread across the landscape.

With some fine-tuning of parameters and implementation of smaller time steps, this model may dramatically improve and be applicable for management to visualize *P. palustris* population dynamics through time. Species behavior for *Q. laevis* could be improved and additional calibration may fine-tune the model. LANDIS II may provide a superior framework to simulate the fire regime desired for this study, although the fragmented structure of the WPU may still adversely affect the model's fire spread processes. Simulating each section separately may induce more frequent fires on each individual population of *P. palustris*. Future work may also include adding more trees species found at the WPU to LANDIS, obtaining more historical data, collecting tree cores for ground referenced species age distributions, and applying long-term validation procedures to support the quality and viability of the model.

Demographic Modeling

There are several limitations to the development of the *P. palustris* demographic model. The model should include site specific validation where management strategies vary. More specifically, density-dependent dynamics may vary between sites and between size and even age classes within a population. In our model, fecundity estimates were assumed based on a hypothetical growth rate. Applying empirical fecundity values in a stage based distribution may improve these estimates. Obtaining data on seedling growth rates in diameter was difficult and seemed to vary highly within and between sites (Grace and Platt, 1995). It may be required to separate this size class into smaller size classes for particular *P. palustris* populations.

This modeling technique may be further improved by acquiring more long-term data on this slow growing and long-lived species and collecting all of the data for model development and testing within the Goethe State Forest would have been ideal. This

deemed impractical because of the incredible time, money, and effort required to collect and analyze the raw data needed to create such a comprehensive demographic model on *P. palustris*.

Hybrid Modeling Approach

There are several limitations to the hybrid modeling approach. Although this method demonstrates the ability to combine strengths of ecosystem models, each model simulates species dynamics quite differently, especially related to fecundity and population changes. Furthermore, using LANDIS to provide some of the missing processes is not a complete solution. The time step discrepancy may be solved by using LANDIS II which incorporates one to several year time steps. Using LANDIS II, spatial technologies, such as GIS and remote sensing, and more site-specific long-term ground data on growth and fecundity of *P. palustris* may improve justification procedures.

Broad Implications of Research

Forest managers should understand the long-term implications of their management plans on forests as a whole. Using a broad-scaled model, such as LANDIS, provides managers with a glimpse of how their forests are changing over time in respect to tree behaviors and interactions, site conditions, and disturbances without exhaustive input parameters. They may easily change parameters, such as fire disturbances or species attributes in LANDIS using its graphical user interface. To study the finer details of a forest, a comprehensive demographic model aids to assess one species over time within specific populations of a forest. Although these inputs may be difficult to collect, using outside data sources on a commonly researched species may provide for the information needed.

Much of this research and data collected may be used for studies in other natural areas. Although the spatial inputs and site conditions used in LANDIS were specifically designed for the WPU, the attributes for each tree species may be used elsewhere. As the four tree species and their habitats are very common in north-central Florida forests, the methodology may be utilized to study landscape level processes in other managed landscapes. As mentioned earlier, because the *P. palustris* demographic model used multiple data sources, the model may be tested in various areas in the southeast to assess its viability. The site conditions and management regimes within these areas may refine the demographic model for use in a specific area.

APPENDIX
LANDIS PARAMETER FILES

Main Parameter File

```
# Base parameter file  #
#   This file created by Landis Interface version 1.01 #
mySpecies.dat # Species life history attribute file #
myLandTypes.dat # Attributes describing each land type class #
lm_20m_2nd_gis.gis # 8-bit Erdas GIS map of land type or ecoregion #
fcm_20m_gis.gis # 8-bit Erdas GIS maps of species and age cohort classes #
myMapAttrib.dat # Attributes describing each map class #
myMapIndex.dat # Map names for output #
myAgeIndex.dat # Age map names for output #
C:\LANDIS\Project\OutputFFM\ # Path for LANDIS output #
myDisturb.dat # Disturbance input file #
myDefaultPlt.dat # Color information file #
myOutputFreq.dat # Output frequency file #
50 # Number of iterations (10 year time steps) #
1 # Random Seed: 0 - generate randomly; other - fixed seed #
20 # Spatial resolution in meters #
DISPERSAL # Seed dispersal routine #
0 # Wind switch: 0-none; 1-standard; 2-mean; 3-strong; 4-light #
1 # Fire switch: 0-none; 1-standard; 2-mean; 3-strong; 4-light #
0 # Old harvesting switch - currently disabled #
0 # Harvesting: 0-off 1-on #
0 # Adjacency: 0-not considered 1-considered #
0 # Number of decades to consider adjacency #
1.0 # Harvest proportion #
myHarvEvents.dat # Harvest prescription #
fcm_20m_gis.gis # 16-bit Erdas GIS map for stand boundaries #
lm_20m_2nd_gis.gis # 16-bit Erdas GIS map for management areas #
stands.log # Harvest history log summarized by stands #
ma.log # Harvest history log summarized by management area #
```

Species Attribute File

```
# LANDIS species attribute input file::version 3.2 #
# This file created by Landis Interface version 1.01 #
# name longevity maturity shade fire eff_seed max_seed veg_prop sprout reclass #
PIPA 200 20 1 5 30 50 0.0 0 0.5
QUGE 130 20 4 1 50 70 0.5 5 0.5
QULA 100 20 3 4 50 70 0.5 5 0.5
QUHE 100 20 4 1 70 90 0.5 5 0.5
```

Landtype Attribute File: FFM

```
# Landtype file C:\LANDIS\Project\FreqFire\myLandTypes.dat #
#   This file created by Landis Interface version 1.01 #
empty 0 0 0.0 10 0 0
0.0
0.0
0.0
0.0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
CurrentPIPAhabitat 40 5 1.0 5 0 100
1.0
1.0
1.0
1.0
10 30 50 70 90 1 2 3 4 4 0 0 0 0 0 0 0 0 0 0
Hardwood 40 80 0.02 80 0 100
1.0
1.0
1.0
1.0
10 30 50 70 90 1 2 3 3 3 0 0 0 0 0 0 0 0 0 0
Scrub 40 50 0.02 50 0 100
1.0
1.0
1.0
1.0
10 30 50 70 90 2 4 5 5 5 0 0 0 0 0 0 0 0 0 0
Wet 0 0 0.0 10 0 0
0.0
0.0
0.0
0.0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
```

Landtype Attribute File: IFM

```
# Landtype file C:\LANDIS\Project\InFreqFire\myLandTypes.dat #
#   This file created by Landis Interface version 1.01 #
empty 0 0 0.0 10 0 0
0.0
0.0
0.0
0.0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
CurrentPIPAhabitat 40 45 0.02 10 0 22
0.5
1.0
1.0
1.0
10 30 50 70 90 1 2 3 4 4 0 0 0 0 0 0 0 0 0 0
Hardwood 40 80 0.02 20 0 22
0.5
1.0
1.0
1.0
10 30 50 70 90 1 2 3 3 3 0 0 0 0 0 0 0 0 0 0
Scrub 40 50 0.02 10 0 22
0.5
1.0
1.0
1.0
10 30 50 70 90 2 4 5 5 5 0 0 0 0 0 0 0 0 0 0
Wet 0 0 0.0 10 0 0
0.0
0.0
0.0
0.0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
```

Map Attribute File

```
# Map attribute class file C:\LANDIS\Project\FreqFire\myMapAttrib.dat #
#   This file created by Landis Interface version 1.01 #
# Map attribute class 0 #
0 00000000000000000000
0 0000000000000
0 00000000000
0 0000000000
# Map attribute class 1 #
0 00000000000000000000
0 0000000000000
0 00000000000
0 0000000000
# Map attribute class 2 #
0 11100000000000000000
0 0000000000000
1 1110000000
0 0000000000
# Map attribute class 3 #
0 11111100000000000000
0 0000000000000
1 1111110000
0 0000000000
# Map attribute class 4 #
0 00000000000000000000
0 0000000000000
1 1110000000
0 0000000000
# Map attribute class 5 #
0 00000000000000000000
0 0000000000000
1 1111110000
0 0000000000
# Map attribute class 6 #
0 11111100000000000000
1 1111110000000
1 1111110000
1 1000000000
# Map attribute class 7 #
0 11100000000000000000
1 1110000000000
1 1110000000
1 1110000000
# Map attribute class 8 #
0 11100000000000000000
0 0000000000000
1 1110000000
1 1110000000
# Map attribute class 9 #
0 00000000000000000000
1 1111110000000
1 1000000000
1 1000000000
# Map attribute class 10 #
0 00000000000000000000
1 1111110000000
0 0000000000
1 1111110000
# Map attribute class 11 #
0 00000000000000000000
1 1110000000000
0 0000000000
1 1110000000
# Map attribute class 12 #
0 00000000000000000000
0 0000000000000
0 0000000000
1 1111110000
# Map attribute class 13 #
0 00000000000000000000
0 0000000000000
0 0000000000
1 1100000000
# Map attribute class 14 #
0 00000000000000000000
0 0000000000000
0 0000000000
1 1111000000
# Map attribute class 15 #
0 00000000000000000000
1 1110000000000
1 1110000000
0 0000000000
# Map attribute class 16 #
0 00000000000000000000
1 1111110000000
1 1111110000
0 0000000000
```

Map Index File

```
# Map index file C:\LANDIS\Project\FreqFire\myMapIndex.dat #
#   This file created by Landis Interface version 1.01 #
DOM PIPA QUGE QULA QUHE Sandhill Hammock SH-HW
```

Age Index File

```
# Age reclass file C:\LANDIS\Project\FreqFire\myAgeIndex.dat #
#   This file created by Landis Interface version 1.01 #
ypipa yquge yqula yquhe
```

Disturbance File: FFM

```
# Disturbance File C:\LANDIS\Project\FreqFire\myDisturb.dat #
#   This file created by Landis Interface version 1.01 #
[WIND] # default values #
[FIRE]
600000
2600000
1200000
40
3
7
10
10
fire
firefin
fire.log
[HARVEST] # default values #
```

Disturbance File: IFM

```
# Disturbance File C:\LANDIS\Project\InFreqFire\myDisturb.dat #
#   This file created by Landis Interface version 1.01 #
[WIND] # default values #
[FIRE]
883000
1272000
1060000
80
3
7
10
10
fire
firefin
fire.log
[HARVEST] # default values #
```

LIST OF REFERENCES

Andrews, E.F., 1917. Agency of fire in propagation of longleaf pines. Botanical Gazette. 64, 497-508.

Andrews, P.L., 1986. BEHAVE: Fire behavior prediction and fuel modeling system - BURN subsystem, part 1. In: Mladenoff, D.J., Baker, W.L. (Eds.), Spatial Modeling of Forest Landscape Change: Approaches and Applications. Cambridge University Press, Cambridge, UK, pp. 172-174.

Baker, W.L., Egbert, S.L., Frazier, G.F., 1991. A spatial model for studying the effects of climatic change on the structure of landscapes subject to large disturbances. Ecological Modelling. 56, 109-125.

Berg, E.E., Hamrick, J.L., 1994. Spatial and genetic structure of two sandhills oaks: *Quercus laevis* and *Quercus margaretta* (Fagaceae). American Journal of Botany. 81, 7-14.

Botkin, D.B., 1993. Forest Dynamics: An Ecological Model. Oxford University Press, New York, NY, USA, 309 pp.

Boyer, W.D., 1963. Development of Longleaf Pine Seedlings under Parent Trees. USDA Forest Service Research Paper SO-4. Southern Forest Experiment Station, New Orleans, LA, USA, 7 pp.

Boyer, W.D., 1990. *Pinus palustris* Mill. longleaf pine. In: Burns, R, M., Honkala, B.H. (technical coordinators), Silvics of North America, Volume 1, Conifers. USDA Forest Service Agricultural Handbook 654. Washington D.C., USA, pp. 405-412.

Boyer, W.D., 1993. Regenerating longleaf pine with natural seeding. In: Herman, S.M. (Ed.), The Longleaf Pine Ecosystem: Ecology, Restoration, and Management. Proceedings, 18th of the Tall Timbers Fire Ecology Conference. Tall Timbers, Inc., Tallahassee, FL, USA, pp. 299-310.

Boyer, W.D., 1999. Longleaf pine: natural regeneration and management. Alabama Treasured Forests. 18, 7-9.

Brockway, D.G., Outcalt, K.W., 1998. Gap-phase regeneration in longleaf pine wiregrass ecosystems. Forest Ecology and Management. 160, 125-139.

Case, T.D., 2000. An Illustrated Guide to Theoretical Ecology. Oxford press, Oxford, NY, USA, 449 pp.

Caswell, H., 2001. Matrix Population Models: Construction, Analysis, and Interpretation. 2nd Ed. Sinauer Associates, Inc., Sunderland, MA, USA, 722 pp.

Croker, T.C., 1975. Seedbed Preparation Aids Natural Regeneration of Longleaf Pine. USDA Forest Service Research Paper SO-112. Southern Forest Experiment Station, Ashville, NC, USA, 6 pp.

Cropper, Jr. W.P., DiResta, D., 1999. Simulation of a commercial sponge population in Biscayne Bay, Florida: recovery following Hurricane Andrew and management implications. Ecological Modelling. 118, 1-15.

Doak, D., Kareiva, P., Klepetka, B., 1994. Modeling population viability for the desert tortoise in the Western Mojave Desert. Ecological Applications. 4, 446-460.

Duncan, W.H., Duncan, M.B., 1988. Trees of Southeastern United States. University of Georgia Press, Athens, GA, USA, 322 pp.

Engstrom, R.T., 1993. Characteristic mammals and birds of longleaf pine forests. In: Herman, S.M. (Ed.), The Longleaf Pine Ecosystem: Ecology, Restoration, and Management. Proceedings, 18th of the Tall Timbers Fire Ecology Conference. Tall Timbers, Inc., Tallahassee, FL, USA, pp. 127-138.

Escalante, S., Montana, C., Orellana, R., 2004. Demography and potential extractive use of the liana palm, *Desmoncus orthacanthos* Martius (Arecaceae), in southern Quintana Roo, Mexico. Forest Ecology and Management. 187, 3-18.

Finney, M.A., 1998. FARSITE: Fire Area Simulator – Model Development and Evaluation. USDA Forest Service Research Paper RMRS-RP-4. Rocky Mountain Research Station, Ogden, UT, USA, 47 pp.

Fonda, R. W., 2001. Burning characteristics of needles from eight pine species. Forest Science. 47, 390-396.

Franklin, J., Syphard, A.D., Mladenoff, D.J., He, H.S., Simons, D.K., Martin, R.P., Deutschman, D., O'Leary, J.F., 2001. Simulating the effects of different fire regimes on plant functional groups in Southern California. Ecological Modelling. 142, 261-283.

Frost, C.C., 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. In: Herman, S.M. (Ed.), The Longleaf Pine Ecosystem: Ecology, Restoration, and Management. Proceedings, 18th of the Tall Timbers Fire Ecology Conference. Tall Timbers, Inc., Tallahassee, FL, USA, pp. 17-44.

Gagnon, J. L., Jokela, E.J., Moser, W.K., Huber, D. A., 2004. Characteristics of gaps and natural regeneration in mature longleaf pine flatwoods ecosystems. Forest Ecology and Management. 187, 373-380.

Gilliam, F.S., Platt, W.J., 1999. Effects of long-term fire exclusion on tree species composition and stand structure in an old-growth *Pinus palustris* (longleaf pine) forest. Plant Ecology. 140, 15-26.

Grace, S.L., Platt, W.J., 1995. Effects of adult tree density and fire on the demography of pregrass stage juvenile longleaf pine (*Pinus palustris* Mill.). Journal of Ecology. 83, 75-86.

Greenberg, C.H., Simons, R.W., 1999. Age, composition, and stand structure of old-growth oak sites in the Florida High Pine Landscape: implications for ecosystem management and restoration. Natural Areas Journal. 19, 30–40.

Guerin, D.N., 1993. Oak dome clonal structure and fire ecology in a Florida longleaf pine dominated community. Bulletin of the Torrey Botanical Club. 120, 107-144.

Gustafson, E.J., Zollner, P.A., Sturtevant, B.R., He, H.S., Mladenoff, D.J., 2004. Influence of forest management alternatives and land type on susceptibility to fire in northern Wisconsin, USA. Landscape Ecology. 19, 327-341.

Hall, B., 1829. Travels in North America, in the Years 1827 and 1828. In: Myers, R.L., Ewel, J.J. (Eds.), 1990. Ecosystems of Florida. University of Central Florida Press, Orlando, FL, USA, pp. 153.

Hardin, D., 2004. Watermelon Pond Restoration Plan: the First Five Years. Division of Forestry, Forest Management Division, Tallahassee, FL, USA, 27 pp.

Hartnett, D.C., Krofta, D.M., 1989. Fifty-five years of post-fire succession in a southern mixed hardwood forest. Bulletin of the Torrey Botanical Club. 116, 107-113.

He, H.S., Hao, Z., Larsen, D.R., Dai, L., Hu, Y., Chang, Y., 2002. A simulation study of landscape scale forest succession in northeastern China. Ecological Modelling. 156, 153-166.

He, H.S., Mladenoff, D.J., 1999. Spatially explicit and stochastic simulation of forest-landscape fire disturbance and succession. Ecology. 80, 81-99.

He, H.S., Mladenoff, D.J., Nimerfro, K.K., Gustafson, E.J., 2003. LANDIS 3.7 User's Guide. School of Natural Resources, University of Missouri-Columbia, Columbia, MO, USA, 63 pp.

He, H.S., Shang, B.Z., Crow, T.R., Gustafson, E.J., Shifley, S.R., 2004. Simulating forest fuel and fire risk dynamics across landscapes – LANDIS fuel module design. Ecological Modelling. 180, 135-151.

Jones, R.H., Mitchell, R.J., Stevens, G.N., Pecot, S.D., 2003. Controls of fine root dynamics across a gradient of gap sizes in a pine woodland. Oecologia. 134, 132-143.

Kimmins, J.P., Mailly, D., Seel, B., 1999. Modelling forest ecosystem net primary production: the hybrid simulation approach used in FORECAST. Ecological Modelling. 122, 195-224.

Lamar, W.R., McGraw, J.B., 2005. Evaluating the use of remotely sensed data in matrix population modeling for eastern hemlock (*Tsuga canadensis* L.). Forest Ecology and Management. 212, 50-64.

Logofet D.O., Korotkov V.N., 2002. 'Hybrid' optimization: a heuristic solution to the Markov-chain calibration problem. Ecological Modelling. 151, 51-61.

McGinty, D.T., Christy, E.J., 1977. Turkey oak ecology on a Georgia sandhill. American Midland Naturalist. 98, 487-491.

McGuire, J.P., Mithcell, R.J., Moser, E.B., Pecot, S.D., Gjerstad, D.H., Hedman, C.W., 2001. Gaps in a gappy forest: plant resources, longleaf pine regeneration, and understory response to tree removal in longleaf pine savannas. Canadian Journal of Forest Research. 31, 765-778.

Mladenoff, D.J., He, H.S., 1999. Design and behavior of LANDIS, an object-oriented model of forest landscape disturbance and succession. In: Mladenoff, D.J., Baker, W.L. (Eds.), Spatial Modeling of Forest Landscape Change: Approaches and Applications. Cambridge University Press, Cambridge, UK, pp. 125-162.

Mladenoff, D.J., Host, G.E., Boeder, J., Crow, T.R., 1996. LANDIS: A spatial model of forest landscape disturbance, succession, and management. In: Goodchild, M.F., Steyaert, L.T., Parks, B.O. (Eds.), GIS and Environmental Modeling: Progress and Research Issues. GIS World Books, Fort Collins, CO, USA, pp. 175-180.

Myers, R.L., 1990. Scrub and high pine. In: Myers, R.L., Ewel, J.J. (Eds.), Ecosystems of Florida. University of Central Florida Press, Orlando, FL, USA, pp. 150-193.

Neel, W.L., 1993. An ecological approach to longleaf pine forestry. In: Herman, S.M. (Ed.), The Longleaf Pine Ecosystem: Ecology, Restoration, and Management. Proceedings, 18th of the Tall Timbers Fire Ecology Conference. Tall Timbers, Inc., Tallahassee, FL, USA, pp. 337-338.

Noble, I.R., Slayter, R.O., 1980. The use of vital attributes to predict succession changes in plant communities subject to recurrent disturbances. Vegetatio. 43, 5-21.

Ott, R.L., Longnecker, M., 2001. An Introduction to Statistical Methods and Data Analysis. 5th Ed. Duxbury, Pacific Grove, CA, USA, 1152 pp.

Palik, B., Mitchell, R.J., Pecot, S., Battaglia, M., Pu, M., 2003. Spatial distribution of overstory retention influences resources and growth of longleaf pine seedlings. Ecological Applications. 13, 674-686.

Penfound, W.T., Watkins, A.G., 1937. Phytosociological studies in the pinelands of southeastern Louisiana. American Midland Naturalist. 18, 661-682.

Peng C., 2000. Quantitative methods: understanding the role of forest simulation models in sustainable forest management. Environmental Impact Assessment Review. 20, 481-501.

Pennanen, J., Kuuluvainen, T., 2002. A spatial simulation approach to natural forest landscape dynamics in boreal Fennoscandia. Forest Ecology and Management. 164, 157-175.

Platt, W.J., Glitzenstein, J.S., Streng, D. R., 1991. Evaluating pyrogenicity and its effects on vegetation in longleaf pine savannas. In: High Intensity Fire in Wildlands: Management, Challenges, and Options. Proceedings, 17th of the Tall Timbers Fire Ecology Conference. Tall Timbers, Inc., Tallahassee, FL, USA, pp. 143-161.

Platt, W.J., Gregory, W.E., Rathbun, S.L., 1988. The population dynamics of a long-lived conifer (*Pinus palustris*). The American Naturalist. 131, 491-525.

Platt, W.J., Rathbun, S.L., 1993. Dynamics of an old-growth longleaf pine population. In: Herman, S.M. (Ed.), The Longleaf Pine Ecosystem: Ecology, Restoration, and Management. Proceedings, 18th of the Tall Timbers Fire Ecology Conference. Tall Timbers, Inc., Tallahassee, FL, USA, pp. 275-298.

Platt, W.J., Schwartz, M.W., 1990. Temperate hardwood forests. In: Myers, R.L., Ewel, J.J. (Eds.), 1990. Ecosystems of Florida. University of Central Florida Press, Orlando, FL, USA, pp. 150-193.

Preston, R.J., Braham, R.R., 2002. North American Trees. Iowa State Press, Ames, IA, USA, 520 pp.

Rasser, M.K., 2003. Monitoring and Assessing Longleaf Pine Ecosystem Restoration: A Case Study in North-Central Florida [Theses]. University of Florida. University Microfilms, Gainesville, FL. Available from: University library electronic archives or [http://purl.fcla.edu/fcla/etd/UFE0001256]. 60 pp.

Remnants of Florida's Longleaf Forest, 2002. The Longleaf Alliance. <http://www.longleafalliance.org/ecosystem/map/flmap.htm> Data accessed: July, 2005.

Robinson, A.P., Ek, A.R., 2003. Description and validation of a hybrid model of forest growth and stand dynamics for the Great Lakes region. Ecological Modelling. 170, 73-104.

Silvertown, J., Franco, M., Menges, E., 1996. Interpretation of elasticity matrices as an aid to the management of plant populations for conservation. In: Lamar, W.R., McGraw, J.B., Evaluating the use of remotely sensed data in matrix population modeling for eastern hemlock (*Tsuga canadensis* L.). Forest Ecology and Management. pp. 51.

Veno, P.A., 1976. Successional relationships of five Florida plant communities. Ecology. 57, 498-508.

Wade, D., Ewel, J., Hofstetter, R., 1980. Fire in South Florida Ecosystems. USDA Forest Service General Technical Report SE-17. Southeastern Forest Experiment Station, Asheville, NC, USA, 125 pp.

Wimberly, M.C., 2004. Fire and forest landscapes in the Georgia Piedmont: an assessment of spatial modeling assumptions. Ecological Modelling. 180, 41-56.

Young, C.G., Young, J.A., 1992. Seeds of Woody Plants in North America. Dioscorides Press, Portland, OR, USA, 407 pp.

Zuidema, P. A., Zagt, R. J., 2000. Using population matrices for long-lived species: a review of published models for 35 woody plants. In: Zuidema, P.A. Demography of Exploited Tree Species in the Bolivian Amazon [Dissertation]. Utrecht University, Utrecht, NL, pp. 159-182.

BIOGRAPHICAL SKETCH

Eva Louise Loudermilk was born a first generation American in 1976 with a strong Swedish heritage. With a B.S. degree from the University of Florida (UF) in animal science in 2001, she worked as an assistant curator of ornithology at the Florida Museum of Natural History as well as a field assistant monitoring several animal and plant species throughout the state. She became affiliated with the Forest Information Systems Laboratory at the School of Forest Resources and Conservation at UF and began her graduate career in 2003 with an emphasis in Geographical Information Systems. She plans to continue her education within the interdisciplinary ecology PhD program at the School of Natural Resources and Environment at UF.