RESTORATION OF FIRE-DEPENDENT DEPRESSION WETLANDS

by

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(Under the direction of L. Katherine Kirkman)

ABSTRACT

Determination of reference conditions for small herb-dominated wetland depressions within the fire-maintained longleaf pine-wiregrass ecosystem is challenging. Most sites have been altered by legacies of fire suppression, which results in the development of an alternative hardwood-dominated community. To reestablish species-rich, herbaceous-dominated communities, we began with restoration of the open community structure and reintroduction of the historic disturbance regime. Specifically, we addressed the following questions: 1. What is the rate and pattern of hardwood succession? 2. Does hardwood canopy removal promote the reestablishment of a species-rich herbaceous wetland plant community? 3. Do depression wetland species form a persistent soil seedbank that provides a source for reestablishment of groundcover species following hardwood removal?

In 2000, we selected ten wetland depressions and randomly assigned five a canopy harvest treatment. We identified a hardwood encroachment pattern that begins as a central nucleus and expands outward. The hardwood species tolerate a range of hydrologic conditions and expand across the moisture gradient, creating homogeneous vegetation across wetlands-upland ecotones. Five years post canopy removal, percent total vegetative cover, species-area curves, and non-metric multi-dimensional scaling analyses of the treatment communities indicated significant increases in species-richness and a shift in the community composition toward herbaceous domination. This rapid recovery of the vegetation and, therefore, of the fine fuels necessary for the reintroduction of frequent fire, was possible largely through initial recruitment from the persistent soil seedbank. We conclude that in certain cases, restoration goals may be guided by vegetation dynamics and defined by priorities to conserve biodiversity and promote the maintenance of rare communities.

Key words: reference sites, depression wetlands, longleaf pine ecosystem, fire

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PROJECT OVERVIEW

Fire suppression is a major cause of decline of the longleaf pine ecosystem. In the absence of fire, a dense canopy of hardwoods encroaches and results in loss of the species-rich herbaceous ground cover, as well as fine fuels. Even within the remaining longleaf pine forests managed with frequent prescribed fire, land use legacies have created fire-suppressed patches embedded within the landscape matrix. To restore and sustain biodiversity within the remaining longleaf pine forests, a landscape scale approach is required that includes reconnecting associated fire-dependent communities such as seasonal wetlands with surrounding uplands (Ware et al. 1993, Sutter and Kral 1994). As part of such an effort, we examine the vegetation recovery of small wetland depressions within a high-quality longleaf pine site fragmented by areas of fire suppression and hardwood encroachment.

The purpose of the study is to characterize the historical successional pattern of hardwood encroachment and to determine the natural regeneration potential of the fire-dependent, species-rich herbaceous groundcover flora of temporarily flooded karst depressions following hardwood canopy removal. Exact reference community compositions were unclear. Small, herb-dominated depression wetlands are increasingly rare due to extensive hardwood encroachment, which spans ecotone-upland connections and homogenizes vegetation gradients. Therefore, we developed a broad framework guided by site data from soils and hydrology (Palik et al. 2000) and land use histories (Goolsby 2006).

Our restoration approach included hardwood canopy harvest, promotion of fine fuels in the development of the ground cover, and connection to the frequent fire regime necessary to sustain the habitat. Specifically, we addressed the following questions: 1. What is the rate and pattern of hardwood succession? 2. Does hardwood canopy removal promote the reestablishment of a species-rich herbaceous wetland plant community? 3. Do depression wetland species form a persistent soil seedbank that provides a source for reestablishment of groundcover species following hardwood removal? This thesis has been written in manuscript format. Chapter 1 includes an overall introduction to the study and a literature review. Chapter 2 is a manuscript that addresses all major study questions and advocates an experimental approach to setting restoration targets. Finally, an overview of study conclusions and suggestions for future research is summarized in Chapter 3.

LITERATURE REVIEW

Reference site selection

Identification of reference sites to guide and gauge ecological restoration success has been an important tool that is widely employed by restorationists. Similar to an experimental control, reference conditions provide clear goals and allow for measurements of the trajectory of changes in the community (Aronson et al. 1995, Moore et al. 1999). Comparisons of restoration and reference sites using metrics such as species-richness or diversity, vegetation structure, and ecosystem processes allow evaluation of restoration progress and provide a basis for adaptive management decisions (White and Walker 1997, Ruiz-Jaen and Aide 2005).

Reference sites can be defined in several ways, including comparisons of current and historic conditions or through utilization of contemporary benchmark locations (White and Walker 1997). Historical property records and maps and series of aerial photographs identify changes in land cover and successional state over time (Archer 1989, 1990, McCay 2000, Goolsby 2006). For example, Kirkman et al. (1996) were able to track 41 years of successional changes in depression wetlands of the coastal plain of South Carolina by interpretation of aerial photography. Within the longleaf pine system, Goolsby (2006) utilized both historic aerial photography and archival land use records to reconstruct patterns of hardwood invasion on upland sites.

Reference information is important as a measure of restoration progress, but selection of appropriate reference communities is often challenging and has led to contentious debates in restoration ecology (Simberloff 1990, Pickett and Parker 1994, Aronson et al. 1995). Historical data from a site can set guidelines for restoration, but original community compositions may be difficult to determine. Valuable data, including groundcover species composition, may be missing from historical land surveys (Asbjornsen et al. 2005) and impossible to determine on fine scales from aerial photography. Therefore, contemporary regional benchmark communities contribute valuable data and measures of success (White and Walker 1997). Contemporary sites have been subjected to stochastic processes, including climate variability and disease outbreaks, and, therefore, may provide more accurate predictions of restoration outcomes (Stephens and Fulé 2005). Such references may be difficult or impossible to locate, however, particularly in rare ecosystems (Dibble and Rees 2005). Only 0.02% of the original tall-grass oak-savanna ecosystem of the Midwestern U.S. remains in small, fragmented patches; therefore, benchmark communities may no longer exist (Asbjornsen et al. 2005). Benchmark selection is further complicated in disturbance-maintained ecosystems whose natural disturbance regimes have been modified (Fulé et al. 1997, Choi 2004, Goebel et al. 2005, Stephens and Fulé 2005). For example, Moore et al. (1999) illustrate major alteration of fire regimes across western ponderosa pine forests following European settlement, and Stephens and Fulé (2005) indicate that remaining sites with intact disturbance regimes are rare.

Historic community composition may be unclear, particularly due to the heterogeneous nature of ecosystems. Reference selection must, therefore, allow flexibility and include a range of conditions (Choi 2004, Goebel et al. 2005, Stephens and Fulé 2005, Laughlin et al. 2006) and new approaches incorporate landscape hierarchies and ecological classification systems (Palik et al. 2000, Goebel et al. 2005). In cases where exact reference identification is not available and multiple vegetation endpoints may be appropriate, goals may be further refined as a part of adaptive management (Laughlin et al. 2006, Manning et al. 2006).

The longleaf pine ecosystem

The longleaf pine-wiregrass (*Pinus palustris-Aristida stricta)* ecosystem is simultaneously one of the most diverse and most threatened ecosystems in North America. Once spanning the southeastern coastal plain from Virginia to northern Florida and Texas, it has been eliminated from 97% of its original range (Ware et al. 1993). Even more critically, only a fraction of the remaining longleaf sites are in pristine condition with an intact, species-rich herbaceous understory (Frost 1993). This drastic decline in longleaf can be attributed to almost four centuries of logging, exploitation for naval stores, development for agriculture, grazing, plantation forestry, and fire suppression (Bridges and Orzell 1989, Clewell 1989, Frost 1993, Peet and Allard 1993, Ware et al. 1993).

Fire is an integral part of the longleaf pine-wiregrass system. Frequent, low-intensity burns create a canopy of widely spaced *Pinus palustris* and occasional *P. elliotii* in wet-mesic sites. This open structure allows sufficient light to support a highly diverse layer of grasses and forbs. Within the herb-dominated understory, longleaf pine savannas harbor the highest small-scale species-richness in North America, with recorded values of 40-50 species per m^2 (Walker and Peet 1983, Bridges and Orzell 1989, Clewell 1989, Peet and Allard 1993, Kirkman et al. 2001). Frequently burned sites consistently exhibit the highest diversity (Lemon 1949, Walker and Peet 1983, Bridges and Orzell 1989, Peet and Allard 1993, Kirkman et al. 2004), and fire suppression causes a shift in community structure from an herbaceous understory to one dominated by shrubs and trees (Lemon 1949, Maliakal et al. 2000). As hardwoods assume dominance, the increased canopy cover almost eliminates the rich herbaceous flora (Walker and Peet 1983, Clewell 1989, Kirkman et al. 2004).

Depression wetlands

Within the wider longleaf system, a complex interaction of environmental factors drives the development of an array of distinctive communities. Among abiotic influences, soil moisture is an especially strong determinant of vegetation dynamics (Peet and Allard 1993, De Steven and Toner 2004, Kirkman et al. 2000, Kirkman et al. 2004). Mesic sites have very high species richness, and fire-maintained upland-wetland ecotones and shallow depression wetlands potentially harbor the highest diversity within longleaf pine savannas (Sutter and Kral 1994, Kirkman et al. 1998).

Ranging in size from less than one to hundreds of hectares, depression wetlands are common throughout the southeastern coastal plain landscape and include a suite of communities, from Carolina bays in more northern sections to cypress domes in Florida. In some cases, depression wetlands form when landscape features create a perched water table and, consequently, precipitation is the driving hydrological determinant. These depressions have little or no connection to groundwater and experience periods of drawdown which can extend for over a year, particularly during droughts. Although depression wetlands have experienced historic declines, largely due to conversion for agricultural and plantation forestry, such hydrologically isolated wetlands no longer receive federal protection.

In southwestern Georgia, Kirkman et al. (2000) define three main groups of coastal plain depression wetlands based on vegetation, including grass-sedge marshes, cypress savannas and cypress-gum swamps. Community development in these wetlands is determined largely by the interaction of hydrology and fire regime (Kirkman 1995, Kirkman et al. 2000, De Steven and Toner 2004). Whereas prolonged or semi-permanent inundation may exclude establishment of woody species in these communities (Kirkman et al. 1996), smaller, shallow depressions with shorter hydroperiods may remain dry for extended periods, creating an opportunity for hardwood encroachment (Bridges and Orzell 1989, Sutter and Kral 1994, Kirkman et al. 2000, De Steven and Toner 2004). Thus, dry-end herbaceous ponds may be particularly dependent on fire to maintain an open canopy. Pre-settlement frequent, but stochastic, fire regimes presumably would have maintained the rich herbaceous dominance of at least some small, seasonally ponded sites (Bridges and Orzell 1989, Kirkman et al. 1998, Kirkman et al. 2000, Kirkman et al. 2004). All coastal plain wetlands have suffered historic declines, but graminoid-dominated ponds are particularly rare. Short inundation periods create pockets of moist soil that are optimal for agricultural conversion (Bennet and Nelson 1991). Furthermore, remaining herbaceous depressions were separated from regular fire, resulting in hardwood succession (Bridges and Orzell 1989, Peet and Allard 1993, Sutter and Kral 1994, Kirkman et al. 1998).

Nearly one-third of the species associated with the longleaf system depend on temporarily inundated depressions including rare plants, amphibians and invertebrates (Sutter and Kral 1994, Kirkman et al. 1996, Drew et al. 1998, Semlitsch and Bodie 1998, Kirkman et al. 1999). In addition to species listed by the Georgia Natural Heritage Program, seasonal ponds provide habitat for two federally endangered plants, pondberry (*Lindera melissifolia*) and American chaffseed (*Schwalbea americana*), as well as the federally threatened flatwoods salamander (*Ambystoma cingulatum*). Beyond simply maintaining rare species, depression wetland communities enhance regional, or gamma diversity with unique assemblages adapted to cyclic conditions of flooding and drought (Semlitsch and Bodie 1998, Kirkman et al. 1998, Kirkman et al. 1999, De Steven and Toner 2004). Amphibian species may be particularly dependent on smaller ponds whose prolonged dry periods exclude predatory fish (Semlitsch and Bodie 1998, Kirkman et al. 1999, Liner 2006). Therefore, conservation and restoration of the range of depression wetlands, including small, seasonally flooded sites, is vital to regional diversity within the longleaf system.

Hardwood succession process

Within the longleaf system, mesic sites exhibit higher productivity compared to more xeric sites, making them especially vulnerable to rapid hardwood encroachment (Gilliam and Platt 1999, Mitchell et al. 1999, Kirkman et al. 2001). Hardwood invasion is a positive feedback process and, once established, fire-resistant oak litter and absence of herbaceous groundcover further suppresses burns (Figure 1.1). Thus, over time, hardwood encroachment accelerates. Invasion by hardwoods, particularly oaks, has been further encouraged in depression wetlands by land management practices. Traditionally, prescribed burns for grazing and game management occur in winter, when depressions are most likely to be flooded and, therefore, fire-resistant. Furthermore, managers often created “bird rings” to maximize the edge habitat favored by northern bobwhite quail (*Colinus virginianus*) by plowing fire breaks around landscape features including wetlands to exclude them from burns (Lemon 1949, Clewell 1989, Goolsby 2006). Even in the absence of fire breaks, large portions of the upland-wetland ecotone have been converted for agriculture and wildlife food plots which prevent the spread of fire from adjacent uplands into depressions (Kirkman 1995, Kirkman et al. 1998, Kirkman et al. 2000, Goolsby 2006).

Details of the hardwood succession process within wet-mesic depressions are not well understood, but observations of historic aerial photos of Ichauway illustrate the transition of herbaceous ponds to dense hardwood stands over a 70-year period. Hardwood establishment is determined primarily by the hydroperiod of the individual depression in conjunction with fire suppression. The pattern and rate of encroachment, therefore, varies considerably among wetlands. In sites subject to frequent or extended inundation, encroachment may follow the hydrarch succession pattern, beginning from the edges and moving inward. In this case, the substrate on the outer edge of the depression is dry enough for hardwood establishment, yet mesic enough to exclude fire. Conversely, in drier sites, depression interiors may provide a fire shadow, allowing succession of a central nucleus of hardwoods. As fire-resistant litter accumulates and increasingly retards the spread of fire, these hardwoods may move further into the adjacent ecotone and upland areas. The increased evapotranspiration rates created by established hardwood species may also alter the hydrologic regime of the depression, resulting in drier conditions and decreased periods of inundation, which would further encourage hardwood establishment (Sun et al. 2001, W. Hicks, personal communication). Restoration of temporarily flooded karst depressions to herbaceous-dominated habitat is an important part of the preservation of regional biodiversity and of habitat for numerous rare plant and animal species (Kirkman et al. 2000). Removal of hardwoods and reinstatement of fire regimes are vital to this goal. Moreover, long-term conservation strategies must prioritize restoration sites and species for active reintroduction. Before such a ranking can be established, important questions including the role of the persistent seedbank remain to be answered (Sutter and Kral 1994, Bakker et al. 1996, Schott and Hamburg 1997, Cox et al. 2004).

Soil Seedbanks

Soil seedbanks potentially play a key function in the restoration of native flora (Bakker et al. 1996, Middleton 2003, Cohen et al. 2004, Cox et al. 2004) and targeted restoration and rare species may be present in the seedbank, even if they are not represented in the standing vegetation (Rabinowitz 1981, Wisheu and Keddy 1991, Kirkman and Sharitz 1994, Sutter and Kral 1994, Lunt 1997, Schott and Hamburg 1997, Cohen et al. 2004). Therefore, seedbank species compositions can be used to infer former community composition and germination from the seed pools in the soil may permit rapid reestablishment of much of the former vegetation without intensive reintroduction efforts (Willems 1988, Bakker et al. 1996, Cohen et al. 2004, Cox et al. 2004). In fact, seedbank germination may provide the only source of natural regeneration for many species, especially as corridors between isolated wetlands continue to be lost, inhibiting seed dispersal (Semlitsch and Bodie 1998, Cohen et al. 2004). Recent studies provide evidence of a limited persistent seedbank in longleaf pine uplands (Cohen et al. 2004, Cox et al. 2004, Coffey and Kirkman 2006), and seedbanks may be particularly well developed in temporary wetlands that are subjected to cycles of wetting and drying (Wisheu and Keddy 1991, Thompson et al. 1998, Hölzel and Otte 2004). Kirkman and Sharitz (1994) recorded more than 100 species of predominantly wetland-specific perennial grasses and forbs in Carolina bay wetland seedbanks, which are similar depression wetland communities of the southeastern coastal plain.

Within the soil, viable seeds remain buried until specific germination requirements are met, sometimes for extended periods (Gerristen and Greening 1989, Matlack and Good 1990, Maliakal et al. 2000) until recruitment is stimulated by species-specific environmental cues (van der Valk and Davis 1978, Smith and Kadlec 1983, Gerristen and Greening 1989, Leck 1989, Kirkman and Sharitz 1994, Bliss and Zedler 1998, Maliakal et al. 2000, Coffey and Kirkman 2006). For example, many wetland species require a period of drawdown for successful germination (van der Valk and Davis 1978, Gerristen and Greening 1989, Kirkman and Sharitz 1994). Others may require increased sunlight or soil moisture from disturbances such as fire or flooding to break dormancy (van der Valk and Davis 1978, Smith and Kadlec 1983, Bliss and Zedler 1998). Hardwood succession causes a structural shift in seasonal wetland communities, creating a closed canopy with minimal light penetration to the ground. The specific germination requirements or conditions for establishment of many species may, therefore, no longer be met; nevertheless, viable seeds of herbaceous wetland species may persist in the soil (Lunt 1997, Middleton 2003). It is unclear, however, if seeds remain viable during decades of hardwood dominance. Through restoration of the open canopy and reintroduction of fire, recruitment from the seedbank may be possible. An investigation into the role of the seedbank will help clarify which target species may reestablish naturally (Wisheu and Keddy 1991, MacDonald et al. 1996, Cox et al. 2004, DeSteven et al. 2006).

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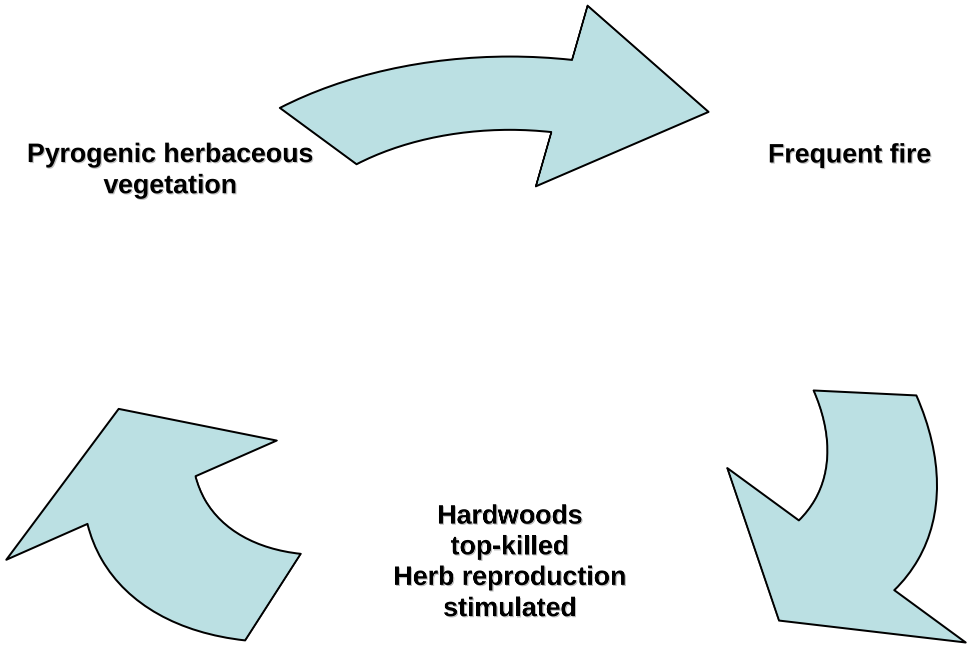

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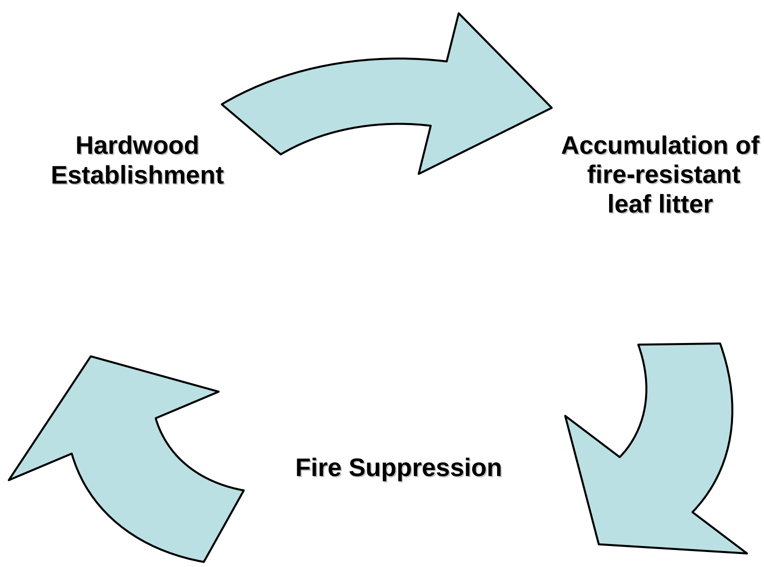

b.

Figure 1.1 Fire-dependent vegetation-fire and hardwood encroachment feedback loops within the longleaf pine ecosystem a. Fire-dependent groundcover serves as fine fuels, perpetuating fire and reinforcing herbaceous dominance b. Following a period of fire suppression, hardwoods establish, fire-resistant leaf litter accumulates, suppressing fire and reinforcing hardwood dominance and expansion

CHAPTER 2

RESTORATION OF FIRE-DEPENDENT DEPRESSION WETLANDS[1]

[1] Martin, K.L. and L.K. Kirkman. To be submitted to ***Restoration Ecology.***

ABSTRACT

Determination of reference conditions for small herb-dominated wetland depressions within the fire-maintained longleaf pine-wiregrass ecosystem is challenging. Most sites have been altered by legacies of fire suppression, which results in the development of an alternative hardwood-dominated community. To reestablish species-rich, herbaceous-dominated communities, we began with restoration of the open community structure and reintroduction of the historic disturbance regime. Specifically, we addressed the following questions: 1. What is the rate and pattern of hardwood succession? 2. Does hardwood canopy removal promote the reestablishment of a species-rich herbaceous wetland plant community? 3. Do depression wetland species form a persistent soil seedbank that provides a source for reestablishment of groundcover species following hardwood removal?

In 2000, we selected ten wetland depressions and randomly assigned five a canopy harvest treatment. We identified a hardwood encroachment pattern that begins as a central nucleus and expands outward. The hardwood species tolerate a range of hydrologic conditions and expand across the moisture gradient, creating homogeneous vegetation across wetlands-upland ecotones. Five years post canopy removal, percent total vegetative cover, species-area curves, and non-metric multi-dimensional scaling analyses of the treatment communities indicated significant increases in species-richness and a shift in the community composition toward herbaceous domination. This rapid recovery of the vegetation and, therefore, of the fine fuels necessary for the reintroduction of frequent fire, was possible largely through initial recruitment from the persistent soil seedbank. We conclude that, in certain cases, restoration goals may be

guided by vegetation dynamics and defined by priorities to conserve biodiversity and promote the maintenance of rare communities.

Key words: reference sites, depression wetlands, longleaf pine ecosystem, fire

INTRODUCTION

Historically, restoration ecology has relied on identification of reference sites to set endpoint goals. Evaluation of restoration progress has typically been guided by comparing restoration and reference site similarities using measures such as species-richness or diversity, vegetation structure, and ecosystem processes (White and Walker 1997, Ruiz-Jaen and Aide 2005). While methodologies to identify appropriate reference conditions have been refined over time (White and Walker 1997, Choi 2004), they remain a significant topic of discussion in restoration literature. Original community composition may be difficult to determine as historical data are often incomplete, particularly at finer scales. Historic community compositions may be particularly challenging to define in disturbance-maintained ecosystems whose natural disturbance regimes have been modified (Choi 2004, Goebel et al. 2005, Stevens and Fulé 2005). Furthermore, pristine sites with intact disturbance regimes are often scarce (Goebel et al. 2005, Stevens and Fulé 2005), especially in ecosystems that remain only as small, isolated patches in their original range. For example, in the remaining 0.02% of the original tall-grass oak-savannas of the midwestern USA, Asbjornsen et al. (2005) advocated an experimental approach using newly obtained data to refine restoration as it proceeds. We suggest that, in some cases, goals for restoration endpoints may be guided by vegetation dynamics and defined in terms of increased biodiversity and habitat heterogeneity.

This restoration approach is particularly appropriate in hardwood-encroached, mesic, depressions in the longleaf pine-wiregrass (*Pinus palustris* P. Mill.-*Aristida stricta* Michx.) ecosystem. In the absence of fire, hardwood species tolerant of a range of environmental conditions gain dominance and may homogenize vegetation across gradients important to herbaceous plant community development. As a result, wetland-ecotone transitions may be obscured, hindering the selection of appropriate reference conditions. Encroachment by fire-resistant species has implications for landscape-scale restoration, necessitating the reestablishment of fire corridors because, once established, fire-resistant litter accumulates and creates a surrounding fire shadow. Clusters of hardwoods then transition into expanding patches of a self-sustaining alternative community and are unaffected by reinstatement of fire, necessitating active intervention to restore herbaceous dominance. To reestablish species-rich herbaceous depression wetland communities, we began by mechanically reinstating the open habitat structure. From there, our management goals were to promote fine fuel development for reintroduction of the frequent fire regime necessary to maintain herbaceous domination.

Longleaf pine ecosystem and associated depression wetlands

Fire is an integral part of the longleaf pine-wiregrass system and regular, low-intensity burns with return intervals of 2-4 years create a canopy of widely spaced longleaf and occasional slash pines (*P. elliotii* Engelm.*)* in wet-mesic sites. This open structure allows sufficient light to support an herb-dominated groundcover, and frequently burned sites consistently exhibit the highest diversity (Lemon 1949, Walker and Peet 1983, Bridges and Orzell 1989, Peet and Allard 1993, Kirkman et al. 2004). Mesic sites, particularly fire-maintained upland-wetland ecotones and shallow depression wetlands, are floristically rich and potentially harbor the highest diversity within longleaf pine savannas (Sutter and Kral 1994, Kirkman et al. 1998). Fire suppression results in hardwood succession and a dramatic shift in community structure (Lemon 1949, Maliakal et al. 2000). As hardwood stems assume dominance, the increased canopy cover reduces and eventually eliminates the species-rich groundcover flora (Walker and Peet 1983, Clewell 1989, Kirkman et al. 2004). Mesic sites are especially vulnerable to rapid hardwood encroachment because of higher productivity when compared to more xeric sites (Gilliam and Platt 1999, Mitchell et al. 1999, Kirkman et al. 2001).

Even within the few remaining high quality examples of the longleaf pine-wiregrass ecosystem managed with frequent fire, legacies of past land use and management practices may result in patches of fire-resistant vegetation. This situation may arise following the widespread use of low-intensity fires conducted during the cool season for grazing and game management. Winter burning promotes herbaceous species-richness (Brockway and Lewis 1997), but cool season fires are less intense and more heterogeneous than historic lighting-ignited burns. Patchy fires resulted in microsites that were favorable for hardwood establishment (Jacqmain et al. 1999), particularly during dormant season fires, as hardwood survival is greater prior to, rather than following leaf out (Waldrop et al. 1992, Glitzenstein et al. 1995). Moreover, game managers often created “bird rings” of successional edge habitat favored by quail by plowing fire breaks around landscape features, including wetlands, to exclude them from burns (Lemon 1949, Clewell 1989, Goolsby 2006). Once oak canopies become established, shade and fire-resistant oak leaf litter inhibit the fire-dependent groundcover vegetation and further suppress fire (Platt et al. 1991). Oak sprouts taller than 2 m are able to survive low-intensity burns, and from small, fire-resistant clusters these patches of trees expand (Guerin 1993).

The practice of winter burning also coincided with periods during which seasonal wetland depressions were most likely inundated. Consequently, such sites would have provided fire-resistant refugia for species such as live oak (*Quercus virginiana* P. Mill.), water oak (*Q. nigra* L.) and laurel oak (*Q. laurifolia* Michx.) that can tolerate periodically saturated soil conditions (Menges et al. 1993, Jacqmain et al. 1999). With establishment of closed canopies of hardwoods, the increased evapotranspiration rates may have resulted in drier conditions and decreased duration of inundation, further promoting woody establishment (Sun et al. 2001, W. Hicks, personal communication). Thus, wet depressions were separated from the landscape-scale disturbance processes, even within intact fire-managed longleaf pine forests.   In depressions with prolonged or semi-permanent inundation, hydrology alone may have excluded woody establishment (Kirkman et al. 1996), although, fire is thought to be an important factor in the maintenance of open canopy herbaceous ponds. Presumably, pre-settlement frequent, but stochastic, fire regimes would have maintained the rich herbaceous dominance of at least some small, seasonally ponded sites. Such sites are increasingly rare in the current landscape (Bridges and Orzell 1989, Kirkman et al. 1998, Kirkman et al. 2000, Kirkman et al. 2004), and many sites that have escaped direct anthropogenic alteration have transitioned into an alternative community dominated by hardwoods.

As part of a landscape-scale restoration effort of a high-quality longleaf pine site fragmented by areas of fire suppression and hardwood encroachment, we examined the revegetation potential of small depression wetlands following removal of the hardwood canopy. Specifically, we addressed the following questions: 1. What is the rate and pattern of hardwood succession? 2. Does hardwood canopy removal promote the reestablishment of a species-rich herbaceous wetland plant community? 3. Do depression wetland species form a persistent soil seedbank that provides a source for reestablishment of groundcover species following hardwood removal?

METHODS

Site description

All of the depression wetlands that we studied were located on Ichauway, a private property of the Joseph W. Jones Ecological Research Center encompassing 11,300 ha of Baker County on the Lower Coastal Plain and Flatwoods (LCPF) Province of southwestern Georgia (McNab and Avers 1994). The climate is humid sub-tropical with annual average rainfall of 131 cm evenly distributed throughout the year and temperatures ranging from 21-34º C in summer and 5-17 º C in winter. Currently, 7500 ha of longleaf pine-dominated forest span the property with at least 211 ha of interspersed depression wetlands, ranging from 1 to 63 ha. These sites have extended hydroperiods and have been classified as cypress savannas, marshes or swamps (Kirkman et al. 2004). Wetlands smaller than 1 ha are difficult to quantify because many have probably been converted for agriculture or cannot be differentiated from surrounding uplands because of hardwood encroachment that extends across upland-wetland soil moisture gradients.

Prescribed fire was integrated into land management at Ichauway when the property was consolidated in the 1920s. Annual cool season burning was used for quail management until 1992, when Ichauway was designated an ecological research center and a greater emphasis was placed on ecosystem maintenance and hardwood control (Goolsby 2006). Sites are burned on a two-year rotation, often during the growing season, to kill hardwood sprouts and to encourage reproduction in many of the fire-dependent groundcover species, including wiregrass. Currently, prescribed fire is encouraged to spread from uplands through ecotones and into depression wetlands. Nevertheless, fire-resistant patches of vegetation remain, requiring active management to restore fuels and frequent fire regimes.

Experimental design and analyses

We selected ten small, oak-dominated depressions for a hardwood removal study. Sites were chosen based on the following criteria: (1) similar size (0.34-1.05 ha) and circular shape; (2) evidence of inundation, particularly high water marks on trees; (3) soil profile traits, particularly the presence of redoximorphic features indicative of hydric soils; and (4) the presence of wiregrass in the adjacent ecotone, indicating potential connectivity with undisturbed and fire-maintained groundcover. Characteristic soils include aquic paleudults, grossarenic paleaquults, aquic arenic paleudults, and typic and arenic paleudults (Goebel et al. 1997). These shallow depressions have a mean (±SE) elevation change of 0.91 (± 0.17) m and slope of 1.01 (±0.14) % from the upland to the lowest point in the depressions. These sites typically flood for a few weeks in the late winter to early spring and draw down shortly after leaf-out. Hydrology is precipitation-driven and, consequently, hydroperiod varies both among years and between sites (Kirkman and Sharitz 1994, Lide et al. 1995).

Characterization of hardwood encroachment

We used aerial photographic interpretations (1:20,000 1948 black and white, USDA 1W4E 82, 83, 113 & 150; 1:20,000 1957 black and white, USDA 1W-4T-47 & 81, 1W-5T-30) and historic maps (Special Collections & Archives, Robert W. Woodruff

Library, Emory University) to confirm evidence of hardwood succession. As an initial overview of the hardwood succession trajectory, we compared hand-drawn property maps from 1929 to current GIS landcover data, which identified sites once labeled as an "open grassy pond" that are currently mapped as hardwood areas. We then used aerial photography to examine historic canopy structures in our study sites. For field verification, we established 20-m wide transects with the length spanning each wetland from opposite upland anchor points that were identified by the presence of wiregrass. Within each transect, we established successive 20 x 20 m vegetation sampling plots, the total number of plots varying from 3-7, depending on the size of the depression. Prior to hardwood removal, each tree was identified to species and diameter at breast height (dbh) was recorded within each 400-m^2 plot. To estimate rate and spatial patterns of encroachment, we examined the age distribution of the two dominant canopy oaks, laurel oak and live oak. Both species are native to the southeastern coastal plain and tolerate short periods of inundation (Menges et al. 1993, Jacqmain et al. 1999). We categorized each plot as either interior or ecotone and compared the mean diameter of the three largest trees in the two zones using analysis of variance with the individual depressions as a block factor (PROC GLM, SAS version 9.0). Data conformed to model assumptions of normality and homoscedasticity.

To establish a timeline of hardwood encroachment, we used a linear regression of age and size of each species using tree ring analysis data collected from 25 stems of each species (PROC REG, SAS version 9.0). We selected stems that represented the range of size classes present within the hardwood depressions at five hardwood-dominated sites with seasonally wet soils, identified by evidence of inundation, particularly by high water marks on trees and redoximorphic soil features (Goebel et al. 1997). We harvested boles using a feller-buncher and removed dbh cross sections (at approximately 1.4 m from the ground) using a chainsaw. The surface of each cross section was sanded with progressively finer sandpaper and annual growth rings were counted. Trees with hollow centers, fused trunks or a significant degree of rot were excluded.

Description of hardwood removal treatment

In the summer of 2000, we randomly assigned five of the ten depressions to the hardwood canopy removal treatment and the remaining five were left as controls. To harvest the hardwoods, an industrial mower was used to remove small saplings, trees up to 43.2 cm dbh were removed with a feller-buncher, and any larger trees were girdled and sprayed with the herbicide Pathway (5.4% picloram, 20.9% 2,4 D-Amine). We also treated stumps with Pathway to prevent resprouting.

Following hardwood removal, the treatment sites have been monitored and further treated for hardwood control. Adjacent upland areas are burned on an approximate two-year rotation and depressions are not excluded from burns. Due to an initial lack of fine fuel accumulation and some invasion by woody saplings and vines, sites have been treated as needed with mowing, additional burning and herbicide applications (Appendix A).

Vegetation Surveys

Herbaceous vegetation was sampled prior to treatments in 2000 and again in 2005. Vegetation surveys were conducted according to a nested plot design adapted from Peet et al. (1998). Within each transect, each 400-m^2 plot was then further divided into four 100-m^2 modules (10 x 10 m) and vegetation was sampled at multiple scales in three of the modules to examine patterns of species packing over time. We used plots nested in the corners to determine presence of all species at the 0.1-m^2, 1-m^2, 10-m^2, 100-m^2 and 400-m^2, levels (Figure 2.1). Species were assigned cover scale values as follows: 1: >1%; 2: 1-5%; 3: 5-15%; 4: 15-25%; 5: 25-50%; 6: 50-75%; 7: > 75%. These values were converted to midpoints of the cover classes. Total percent cover was calculated for each plot from the sum of all species cover values and, due to the multilayered canopy, values > 100% were possible.

Identification of soil seedbank

We used the seedling emergence technique to examine species-richness of the persistent soil seedbank (Poiani and Johnson 1988, Gross 1990, Brown 1992). We collected soil samples from the five oak-dominated control depression wetlands in March 2005. Five soil cores (10 cm in diameter, 6 cm deep) were collected adjacent to the midpoint of each vegetation sampling plot and combined into a single sample per plot. Soil samples were stored at 4º C for two months before we sieved them to remove large rhizomes and debris. Sieved soil was spread over potting soil mix in tubs with holes drilled in the bottom to allow drainage and tubs were placed randomly on greenhouse benches. Moist soil conditions were maintained by daily watering with reverse osmosis purified (RO) water. The greenhouse temperature fluctuated with ambient conditions, but was buffered to remain between 7.2-26.7^{o}C. Light conditions in the greenhouse were modified by shade cloth to 27% of external full sun conditions. From May 2005 to September 2006, each emergent seedling was identified, recorded and discarded. Unknown seedlings were removed, potted and grown until identification was possible.

Vegetation Analyses

Paired t-tests were used to compare mean cover values between treatments and years (PROC TTEST, SAS version 9.0). To examine the change in species-richness due to treatment, a general linear mixed-models analysis was used to test for difference in species-richness at all sampling scales, from 0.1-m^2 to 400-m^2. For the scales repeated within the large plots, we obtained an average of all possible combinations of the nested corners. The mixed-models analysis was used to allow for testing of fixed effects as well as covariant components (Littell et al. 1996). First-order ante-dependence covariance structure (Macchiavelli and Arnold 1994) and Kenward-Roger (Kenward and Roger 1997) adjustment to the denominator degrees of freedom were used in the mixed-models analyses to account for correlations generated by repeated sampling through time and the use of a hierarchical sampling design (see also Kirkman et al. in review). Mean species-richness values were then used to generate species-area curves to illustrate graphically the differences between treatments for each scale of observation.

To explore the changes in the vegetation community composition, presence-absence and abundance data for specified plot sizes were calculated through aggregation of the hierarchical groundcover sampling. Abundance is defined for these analyses as number of scale-specific plots in which the species was present. Plot-level data sets were then subjected to non-metric multidimensional scaling (NMDS) to explore differences between the community compositions in 2000 and 2005. The NMDS was based on the distances between plot communities using a Jaccard index of dissimilarity (one minus the Jaccard index: McCune and Grace 2002). NMDS depicts objects in space such that distances represent the dissimiliarity while minimizing stress, or the discrepancy between the rank-order dissimilarity calculations and ordination distances (Kruskal 1964). Therefore, points farther apart in space represent increasingly dissimilar communities. NMDS is a useful tool for data reduction as well as graphical illustration. To quantify treatment effects, dimension coefficients from the NMDS were treated as response variables in a multivariate response, general linear mixed-models analysis (Wright 1998, Schabenberger and Pierce 2002). Multivariate contrasts were then used to test for significant interactions. Finally, Pearson correlations of changes in species presence-absence were used to identify whether species appeared on an increased or decreased number of plots after treatment. All analyses were preformed using the SAS System 9.0 (SAS On-line Documentation: http://support.sas.com/onlinedoc/913/docMainpage.jsp).

To determine the presence of wetland perennial species in the seedbank, all species were assigned a wetland indicator status based on the USDA Plants database (USDA and NRCS 2006) and consolidated into three categories as in DeSteven et al. (2006). Wetland species included the OBL and FACW categories (67-100% probability of occurrence in wetlands), facultative included FAC and FAC+ species, which are equally likely to be found in wetlands or uplands, and remaining species (FAC-, FACU and UPL) were classified as upland. To infer the contribution of the seedbank to the standing vegetation, Jaccard indices were calculated to examine the similarities between the seedbank and the standing vegetation within each treatment.

Species nomenclature follows Wunderlin and Hansen (2003) with the exception of *Dicanthelium*, which follows Freckmann and Lelong (1993).

RESULTS

Hardwood Encroachment Pattern

A consistent pattern of hardwood establishment was evident from the aerial photographs. Between 1968 and 1998, all depressions were identified as small clusters of hardwood canopy. Earlier photographs (1948 and 1957) revealed, however, these sites had an open canopy, punctuated by some initial hardwood establishment toward the center of the wetland.

The age class distributions of canopy oak trees also indicated a pattern of succession from an initial central nucleus of establishment. For both species, dbh and age were strongly correlated (Figure 2.2). The age estimation is a relative indication of establishment because growth had occurred for several years prior to achieving the height of the measurement. The largest trees in the interior of the depressions were established around 1960; these trees were significantly older than trees in the adjacent ecotones ($p < 0.0001$). Establishment of laurel oak in the ecotone occurred approximately ten years later, and live oaks followed around 1980.

Vegetation Composition

Prior to hardwood removal, bare ground exceeded 75% in all depression interiors and average species-richness did not differ significantly between sites at any of the sampling scales. After five years, total vegetative cover increased significantly at treatment sites when compared to controls ($p<0.001$, Figure 2.3). Post-treatment species-richness also increased significantly in treatment sites at all sampling scales ($p < 0.001$) (Table 2.1). Within hardwood removal sites, woody species declined from 30.4 ±2.3% to 10.2 ±1.0% of the groundcover vegetation.

Greater compositional change occurred over time in the interior of treatment sites than in ecotonal treatment sites or control sites based on distance separations in ordination space within the NMDS analysis. Dissimilarities between treatment communities in 2000 and 2005 were similar at all spatial scales (Figure 2.4). At the same time, ecotone-anchor plot points exhibited a clustered distribution, indicating little dissimilarity between 2000 and 2005. All NMDS analyses used four-dimensional solutions. Distribution of the ordination points in space were similar for species presence-absence and abundance data.

The graphical separation of the vegetation composition in depression interiors over time was reflected in a significant treatment effect, as well as significant higher-order interactions in the mixed-models analysis of NMDS dimension coefficients. Four degree of freedom multivariate contrasts performed on the mixed-models results indicated that depression interiors were significantly different ($p < 0.001$) (Table 2.2), but the uplands were unchanged. Finally, Pearson correlations based on species presence-absence changes from 2000 to 2005 support evidence of a shift toward herbaceous domination, as wetland forbs and graminoids occurred on more plots in 2005 hardwood species occurred on fewer plots (Table 2.3).

Seedbank

Seedling emergence from soil samples totaled 10,615 seedlings and included 67 species (Appendix B). The seedbank was characterized by a mean (± SE) seedling density of 104.6 (± 10.3) /m^2 and mean (± SE) species-richness of 34.6 (± 3.0) per site and was dominated by herbaceous species (92 %), most of which were perennial. Nearly 70% of the species were classified as obligate wetland or facultative species, including three of the four most abundant species, *Oldenlandia boscii, Rhexia mariana* and *Juncus elliottii*. Of the 66 species in the seedbank, nearly half were found exclusively at hardwood removal sites. While many of the species in the post-treatment vegetation were not found in the soil samples we collected (Appendix B), the seedbank species composition had greater similarity with the treatment sites (12.2%) and than with control sites (0.9%) based on Jaccard indices. Many of the species found on at least 20% more plots in the post-treatment standing vegetation were also present in the seedbank (Table 2.3).

DISCUSSION

This study demonstrates how ecosystem management driven by objectives to promote biological diversity and preservation of rare communities can help define endpoint goals for restoration. Guided by knowledge of community development and land use legacies, we prioritized a strategy to reintroduce fire management in a fire-suppressed wetland habitat through reconnection of fire corridors with the surrounding upland.

Management for an alternative community state

We have developed a conceptual model to guide understanding of important thresholds in the hardwood succession process (Figure 2.5). Within depression wetlands, community structure begins to shift from a species-rich understory of graminoids and forbs toward woody dominance after a period of fire suppression that allows oaks to reach a fire-tolerant stage (Guerin 1993). Once established, fire-resistant litter accumulates and creates a surrounding fire shadow. Clusters of hardwoods then transition into expanding patches of a self-sustaining alternative community and are unaffected by reinstatement of fire, necessitating active intervention to restore herbaceous dominance.

The dramatic increase in percent cover and species-richness of the groundcover following hardwood removal indicates that attaining herbaceous dominance in depressions is possible. Beginning with virtually no groundcover, herbaceous species have colonized the sites without reintroduction of seed or plants and our management focus on reintroduction of the natural, community-sustaining, disturbance has allowed the communities to develop through self-design (Mitsch and Wilson 1996). The high percentage of native, perennial, herbaceous wetland species in the treatment sites is an important indication of a shift toward an herbaceous-dominated condition and the resulting community is a unique assemblage. Inclusion of this fire-maintained, species-rich herbaceous state enhances the overall regional, or gamma, diversity of the ecosystem.

The rapid reestablishment groundcover provided fine fuels necessary to carry fire and, therefore, allowed for reintroduction of the frequent disturbance regime necessary to maintain the herbaceous community state. The reconnection of feedback loops between the vegetation and disturbance dynamics is a necessary first step to cross an alternative state threshold and encourage development of a self-sustaining herbaceous community (Suding et al. 2004). Once fuel accumulates and allows fire to spread through the depressions, the community is pushed back across an important functional and structural threshold; however, the initial lack of fuels necessitated a period of management for hardwood control. In the absence of management, hardwoods would likely have reestablished dominance.

The particular restoration trajectory that we observed in these wetlands depended on the surrounding frequently burned upland landscape. Fire management in the depressions relies upon an intact ecotone as an upland-wetland fire corridor. In our case, the wiregrass-dominated upland anchor plots showed little change over the five year period and this undisturbed ecotone connection should allow future fires to burn completely through depressions. The direction of community development may also have been influenced by climatic conditions immediately following hardwood removal. If extreme periods of inundation or drought had ensued, a different species composition may have been favored or the rate of change in fuel conditions and ability to reintroduce fire may have been altered. Consequently, a range of conditions might be predicted as potential responses to such treatments that would require alternative post-treatment management actions.

Legacy of persistent seedbank

The seedbank species composition provides further evidence of an alternative, herbaceous dominated community state. Composed of mainly wetland specific species, the persistent seedbank likely contributed to the rapid increase in groundcover. Evidence from similar southeastern coastal plain depression wetlands, such as Carolina bays (Kirkman and Sharitz 1994, Singer 2001, Mulhouse et al. 2005) and more mesic longleaf sites (Cohen et. al 2004), suggested that native perennial wetland forbs and graminoids form persistent soil seedbanks, yet it was unclear how decades of hardwood dominance would affect seed viabilities. Differences in post-treatment species composition and seedbank composition may be explained by the spatial heterogeneity of seedbanks relative to sampling effort, greenhouse conditions that did not provide the germination requirements for certain species, and/or the introduction of species from outside the seedbank over the five year period. Additional studies are needed to determine the role of seed dispersal in the initial establishment of vegetation as well as the influence of the landuse of the surrounding uplands.

Our goal of increased habitat heterogeneity and biodiversity may provide a new approach to restoration, particularly in rare ecosystems where reference information is limited. We adopted an approach to manage for an alternative, species-rich community state that included a period of passive revegetation, allowing for self-design. Our approach will probably be best realized in systems that harbor legacies of an alternative state such a persistent seedbank, and in situations that permit flexibility in post-treatment actions.

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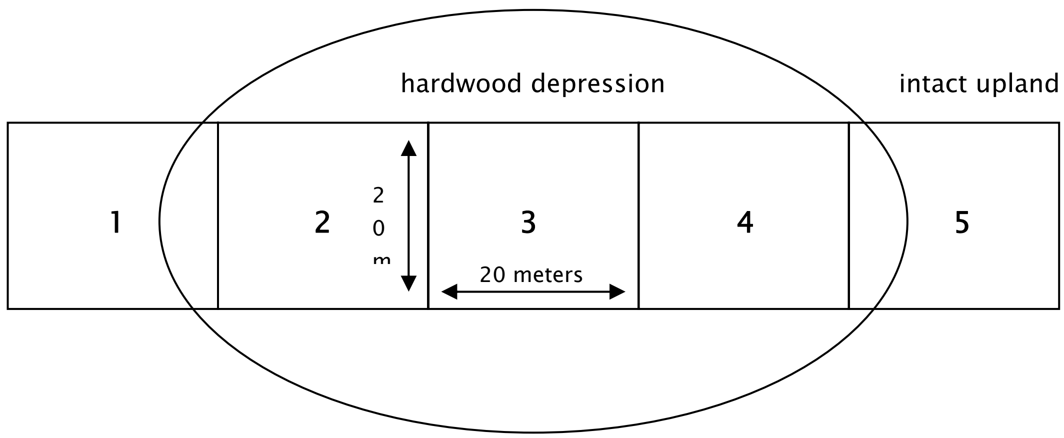

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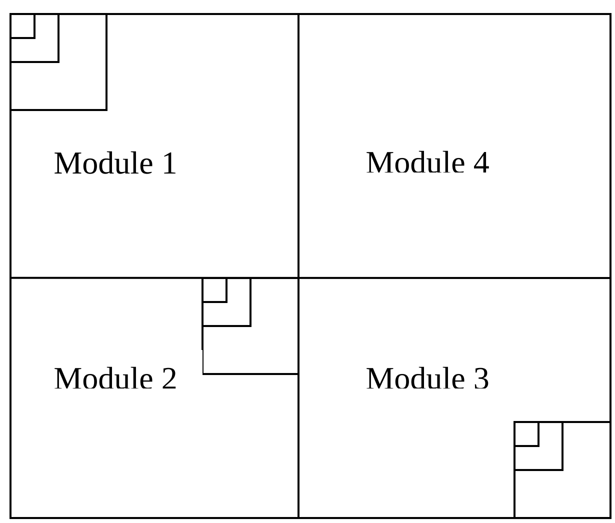
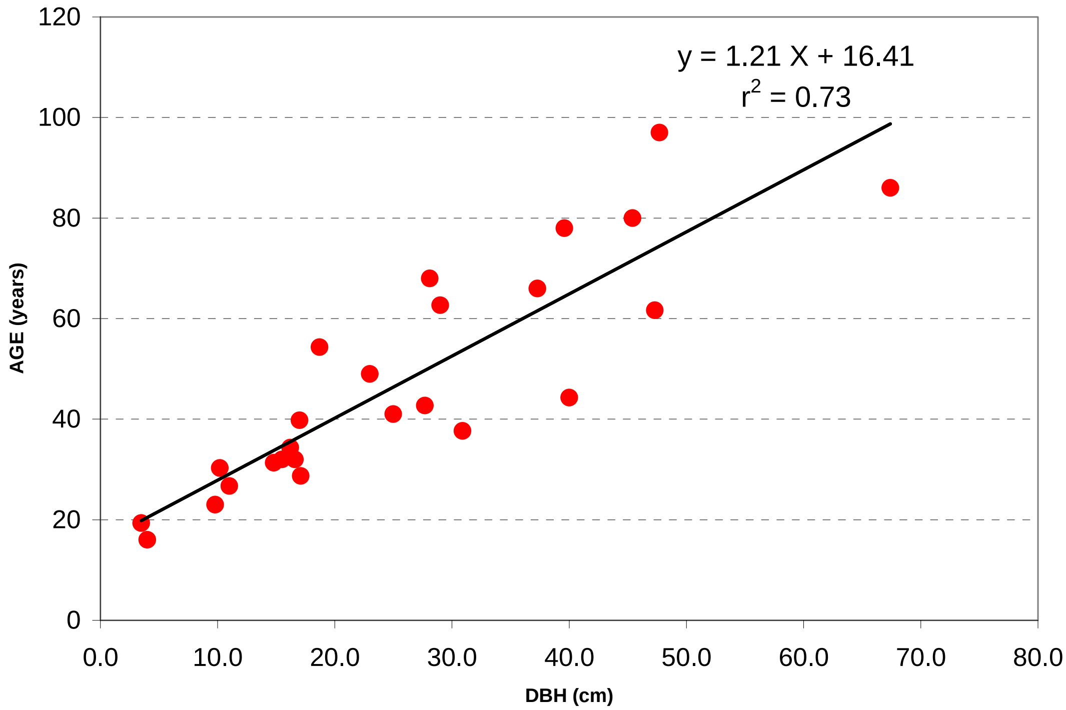


b.

Figure 2.1 Nested vegetation sampling design a. 20 x 20 m^2 plots in transect, spanning depressions from ecotone anchor plots b. Nested sampling within one 20 x 20 m^2 plot Adopted from Peet et al. (1998)



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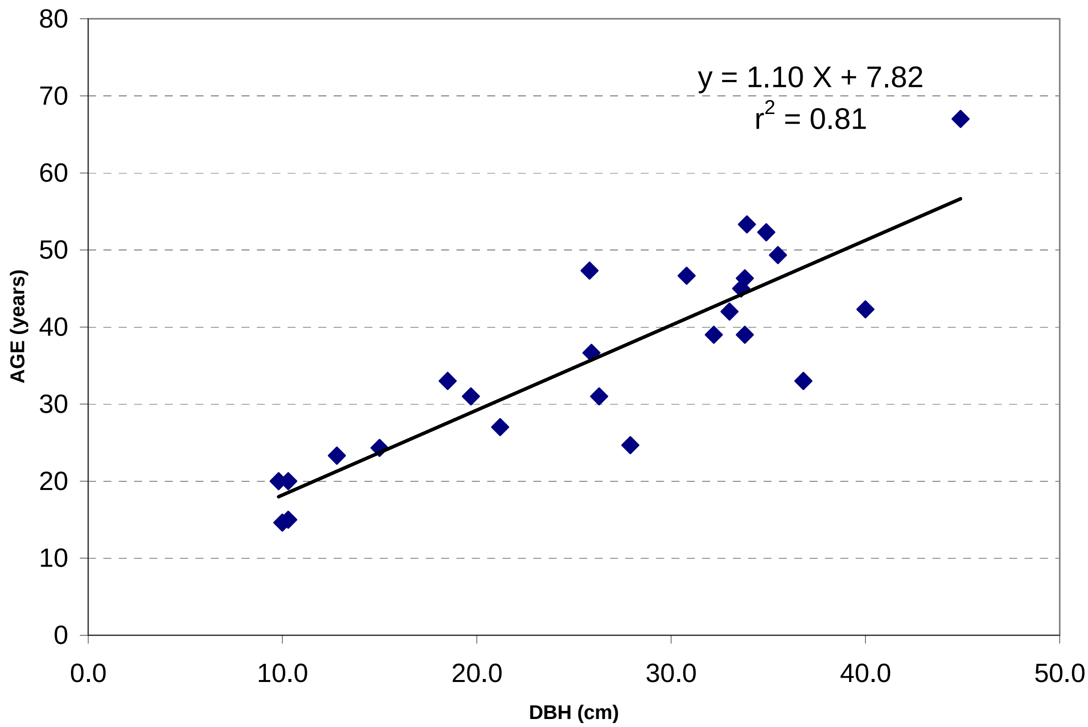

b.

Fig 2.2- Relationship of age (years) and dbh (cm) for dominant species of oak

a. Laurel oak (*Quercus laurifolia)*
b. Live oak *(Quercus virginiana)*

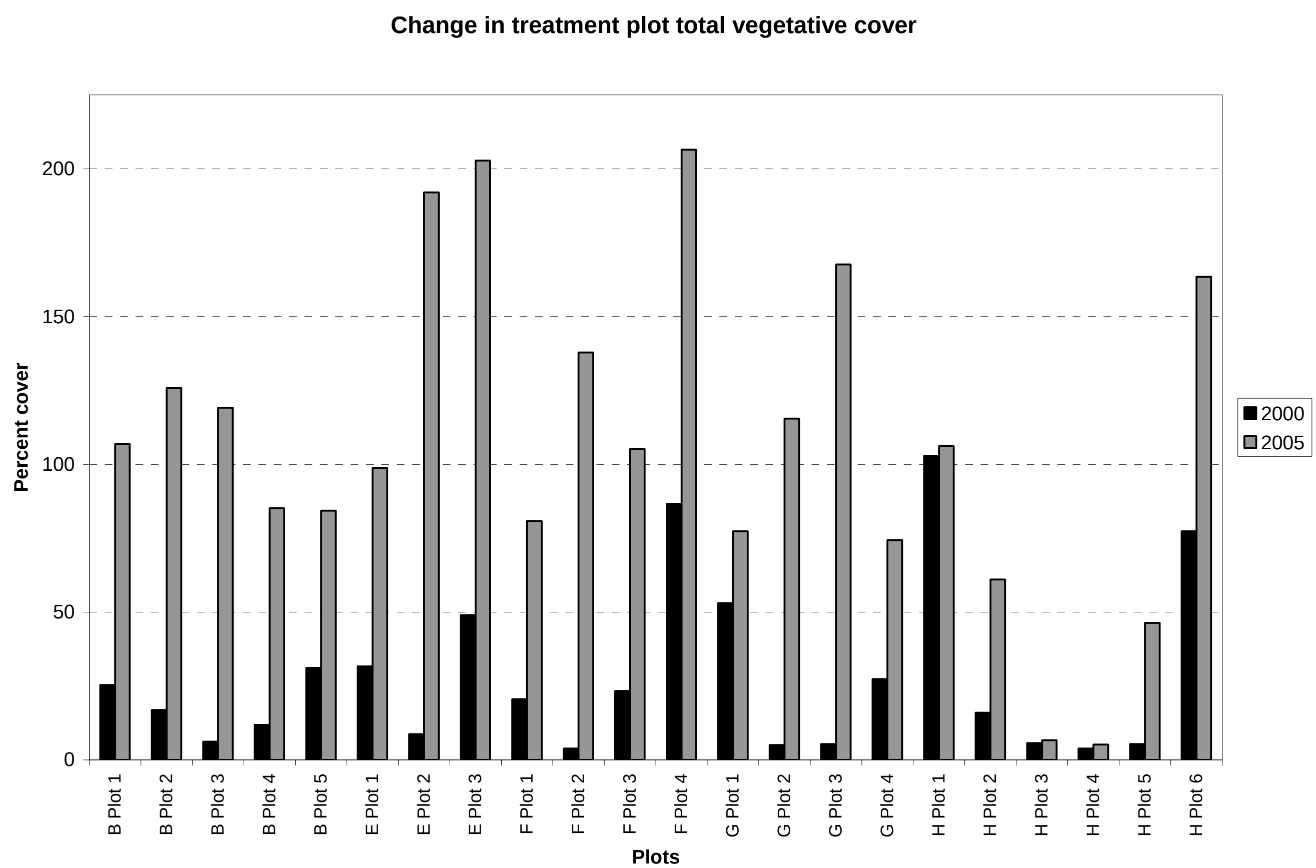

Figure 2.3 a. Pre- and post-treatment vegetation of depression wetland b. Total percent vegetative cover in treatment plots before and after treatment

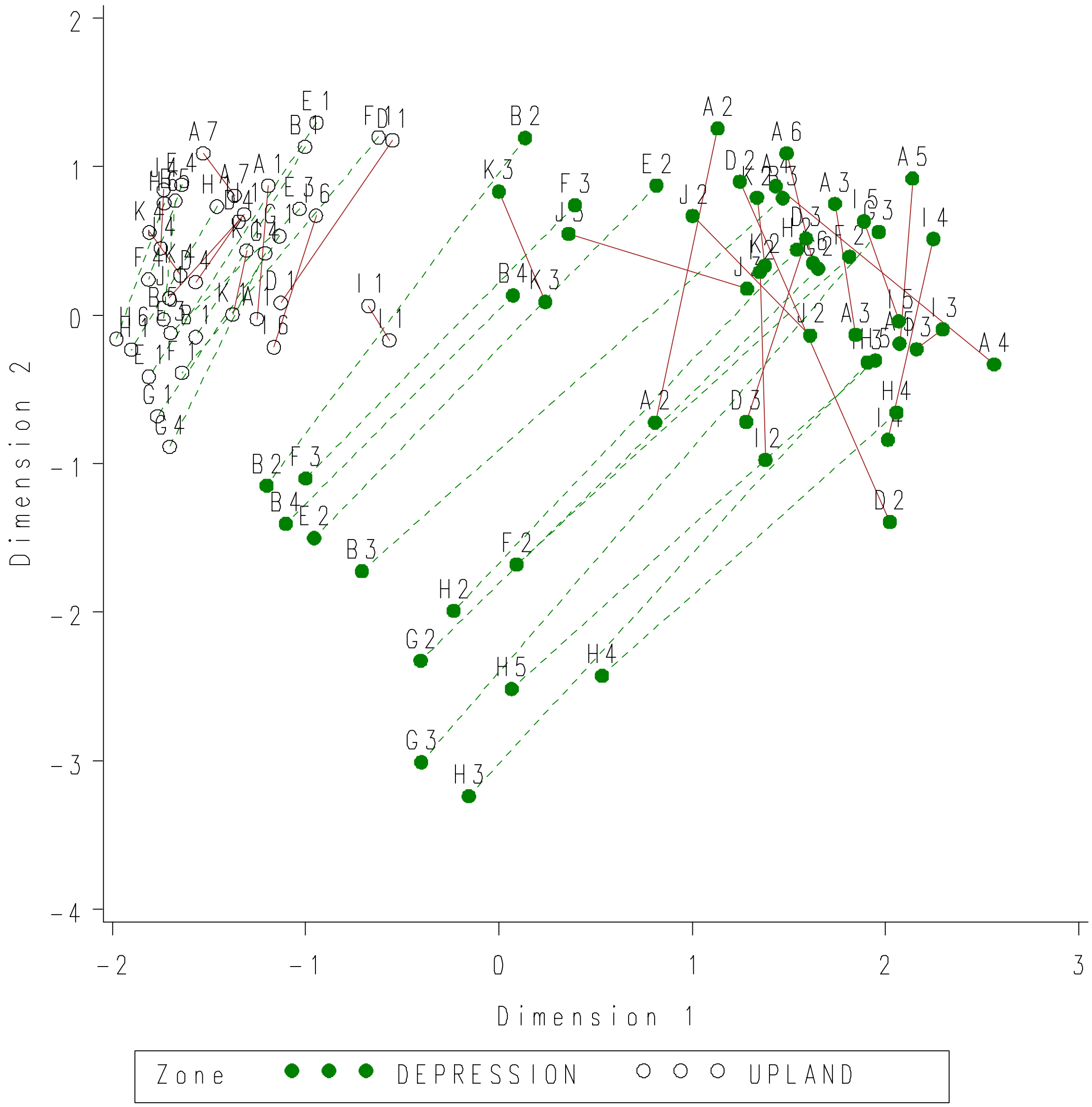

Figure 2.4 The four-dimensional non-metric multidimensional scaling four-dimensional solution for species presence-absence at the 100-m^2 level

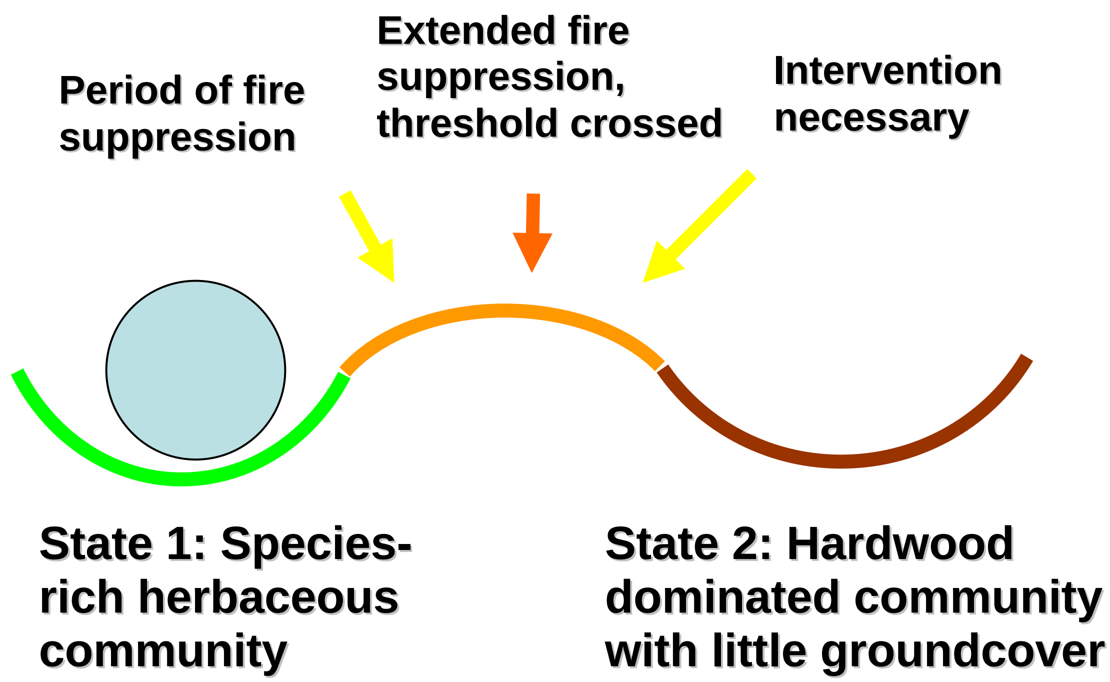

Figure 2.5 Conceptual model of alternative stable community states of dry-end depression wetlands within the longleaf pine ecosystem

Effect	Area (m^2)	Numerator df	Denominator df	F Value	Pr > F
Treatment x Area	1	1	39.8	25.87	< 0.0001
Treatment x Area	10	1	47.6	19.58	< 0.0001
Treatment x Area	100	1	51.1	19.79	< 0.0001
Treatment x Area	200	1	51.4	19.43	< 0.0001
Treatment x Area	300	1	51.5	18.66	< 0.0001
Treatment x Area	400	1	51.6	19.84	< 0.0001

Table 2.1 Mixed-models analysis of variance for mean species-richness for nested sampling scales. Treatment includes two levels: removal or control.

Contrast	Numerator df	Denominator df	F Value	Pr>F
Treatment x Zone for Control	4	24.7	88.72	<0.0001
Treatment x Zone for Removal	4	26.3	32.14	<0.0001
Treatment x Zone for Interior	4	14.9	45.42	<0.0001
Treatment x Zone for Upland	4	18.1	2.07	0.1269

Table 2.2 Four degree of freedom multivariate contrasts from the mixed-models analysis. The response variables are the 4 dimension coefficients from the NMDS analysis.

Table 2.3 Pearson correlation of species presence-absence changes on all plots 2000-2005

Species	Pearson Correlation	Species	Pearson Correlation
Panicum anceps	0.69027	*Oldenlandia boscii*	0.31944
Eupatorium compositifolium	0.56309	*Pluchea camphorata*	0.31944
Mecardonia acuminate	0.53452	*Scleria ciliata*	0.31944
Panicum verrucosum	0.53452	*Callicarpa americana*	0.28284
Polypremum procumbens	0.50709	*Eragrostis virginica*	0.28284
Erechtites hieracifolius	0.47673	*Pseudognaphalium obtusifolium*	0.28284
Cyperus haspan	0.44721	*Rhynchospora pusilla*	0.28284
Dichanthelium wrightianum	0.44721	*Solanum carolinense*	0.28284
Acalypha graciliens	0.44544	*Passiflora incarnate*	0.27566
Carex festucacea	0.41703	*Rhynchospora globularis*	0.26591
Phytolacca americana	0.41703	*Boltonia diffusa*	0.24254
Diodia virginiana	0.38983	*Dichanthelium strigosum*	0.24254
Iva microcephala	0.38592	*Jacquemontia tamnifolia*	0.24254
Ludwigia linearis	0.38592	*Ludwigia repens*	0.24254
Polygonum hydropiperoides	0.38592	*Lygodium japonicum*	0.24254
Dichanthelium acuminatum	0.38139	*Piriqueta cistoides*	0.24254
Carex verrucosa	0.35355	*Rhynchospora nitens*	0.24254
Eleocharis spp.	0.35355	*Saccharum baldwinii*	0.24254
Eupatorium capillifolium	0.35355	*Scirpus cyperinus*	0.24254
Saccharum giganteum	0.35355	*Solidago canadensis*	0.24254
Dichanthelium erectifolium	0.34783	*Trichostema dichotomum*	0.24254
Rubus cuneifolius	0.33806	*Cephalanetus occidentalis*	0.20851
Ludwigia glandulosa	0.31944		

Species	Pearson Correlation	Species	Pearson Correlation
Panicum virgatum	-0.22990	*Prunus caroliniana*	-0.31277
Quercus falcate	-0.23570	*Nyssa sylvatica*	-0.34901
Crataegus flava	-0.24254	*Quercus laurifolia*	-0.38592
Smilax lasioneuron	-0.24254	*Sassafras albidum*	-0.38983
Vaccinium myrsinites	-0.24254	*Crataegus aestivalis*	-0.48685
Parthenocissus quinquefolia	-0.27566	*Prunus serotina*	-0.73679

CHAPTER 3

CONCLUSIONS

Selection of reference sites and appropriate restoration endpoints is a continual challenge within restoration ecology. Historical information can be difficult to obtain and contemporary benchmark locations are rare, particularly in disturbance-maintained ecosystems. There is growing emphasis on experimental approaches (Choi 2004, Asbjornsen et al. 2005) to define goals and on realistic recovery time frames (Zedler and Callaway 1999). This study demonstrates how ecosystem management driven by objectives to promote biological diversity and preservation of rare communities can help define endpoint goals for restoration. Guided by knowledge of community development and land use legacies, we prioritized a strategy to reintroduce fire management in a fire-suppressed wetland habitat through reconnection of fire corridors with the surrounding upland.

Our investigation of the hardwood encroachment process indicates that depressions provide a fire shadow, which allows a central nucleus of oaks to establish and expand, thus homogenizing vegetation across environmental gradients. We have developed a conceptual model to guide understanding of important thresholds in the hardwood succession process (Figure 3.1) Within depression wetlands, community structure begins to shift from a species-rich understory of graminoids and forbs toward woody dominance after a period of fire suppression sufficient to allow oaks to reach a fire-tolerant stage (Guerin 1993). Once established, fire-resistant litter accumulates and creates a surrounding fire shadow. Clusters of hardwoods then transition into expanding patches of a self-sustaining alternative community and are unaffected by reinstatement of fire, necessitating active intervention to restore herbaceous dominance.

Our strategy for restoring such depressions was to achieve an open habitat structure through canopy removal and to promote fine fuel development for reintroduction of the frequent fire regime necessary to maintain species-rich herbaceous domination. Following hardwood canopy removal and reintroduction of fire, five years of passive revegetation has allowed succession to direct wetland self-design (Mitsch and Wilson 1996, Asbjornsen et al. 2005).

Future Considerations

Some dominant or abundant species of southeastern grass-sedge marshes do not survive well in seedbanks (Kirkman and Sharitz 1994, Kirkman et al. 2001). In particular, species such as *Leersia hexandra* and *Panicum hemitomon* were largely absent from the restored communities. Therefore, a next step could be experimental reintroductions of these species, and plantings could determine whether or not dry-end depressions provide appropriate habitat. Future research could also address questions such as: 1. Are there priority effects in marsh species assemblies? a. Will these perennial, rhizomatous grasses regain dominance when planted in an established community? b. If these species are planted initially, what are the effects on the resulting community composition? 2. What role do these dominant grasses have in the community structure and regulation of species-richness within marshes? Beyond dominant species, rare and threatened species could be identified and prioritized for reintroduction. These dry-end depressions could be potential restoration sites for two federally threatened ecotone plants: pondberry (*Lindera melissifolia*) and American chaffseed (*Schwalbea americana*).

Another factor that is likely to influence the rate and direction of vegetation recovery is the timing of climatic conditions. Periods of extreme drought or extended inundation following hardwood removal may play a deterministic role in restoration trajectories, resulting in different community compositions. An alternative vegetation development pathway could impact the resulting fuel structure, which is crucial to the reinstatement of frequent fire. Even within restoration sites, hardwood succession may be particularly aggressive during prolonged dry periods, creating additional management needs.

Future restoration efforts will be increasingly challenged by the presence of invasive species, and the longleaf pine ecosystem is probably no exception. In this study, numerous (244) seedlings of Japanese climbing fern (*Lygodium japonicum)* emerged from the soil samples, although this species was largely absent from the soil collection sites. Japanese climbing fern is an invasive exotic that has spread throughout north Florida and southern Georgia (Lott et al. 2003) and is becoming a significant concern in the longleaf pine system. In addition to the formation of thick vegetation mats that can eliminate native groundcover species, Japanese climbing fern is a somewhat fire-tolerant species that can climb into the tree canopy. In abundance, this species creates a ladder of fuels which significantly alters fire behavior (Global Invasive Species Database 2005).

Applicability to other ecosystems

Our goal of increased habitat heterogeneity and biodiversity may provide a new approach to restoration, particularly in rare ecosystems where reference information is limited. This methodology will probably be best realized in systems that harbor legacies of an alternative state such a persistent seedbank, and in situations that permit flexibility in post-treatment actions. Our focus on restoring fuel structures, frequent fires and the feedback processes between the two might be particularly applicable to the management of other long-needled pine ecosystems, including western ponderosa pine forests.

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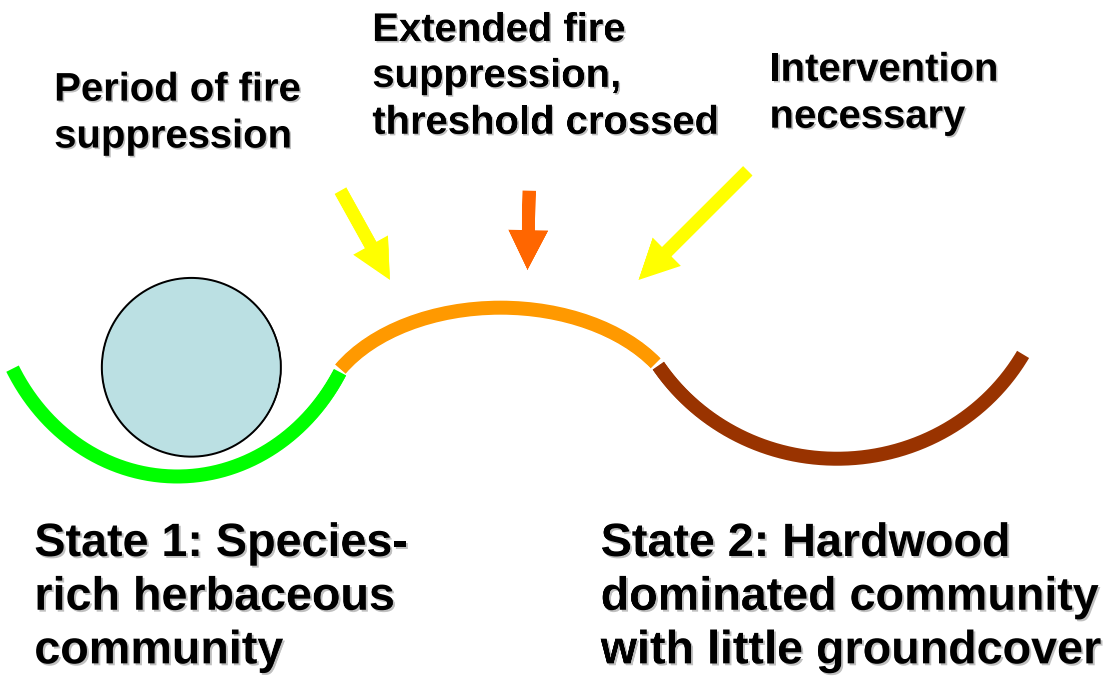

Figure 3.1 Conceptual model of alternative stable community states of dry-end depression wetlands within the longleaf pine ecosystem

APPENDIX A- ADAPTIVE MANAGEMENT

All treatment plots were mowed in 2002, and all hardwoods still alive in 2003 were girdled again using machetes and sprayed with Arsenal 11 (imazapyr). In 2004, all hardwood removal sites were treated with a mixture of 4 quarts Garlon IV (triclopyr) to 28.3 g Escort in 113.6 liters of water per 0.4 ha. Red River 90 (surfactant) was added at the rate of 1.9 liters per tank of the above mixture. In May 2006, two sites (E, F) were mowed and burned using a drip torch mounted on an ATV to control woody vines, particularly *Smilax* species, and hardwood sprouts. Hardwood saplings and vines were spot-treated with Garlon IV at two additional sites (G, H) in September of 2006.

APPENDIX B- Species list

Species	Authority	Standing Vegetation	Seedbank
Acalypha gracilens	Gray	X	X
Acer rubrum	L.	X	
Agalinis fasciculata	(Ell.) Raf.	X	X
Agalinis obtusifolia	Raf.	X	
Agalinis setacea	(Gmel.) Raf.	X	
Ageratina aromatica	(L.) Spach.	X	
Aletris farinosa	L.	X	
Ambrosia artemisiifolia	L.	X	
Ampelopsis arborea	(L.) Koehne	X	
Amsonia ciliata	Walt.	X	
Amsonia tabernaemontana	Walt.	X	
Anagallis minima	(L.) Krause		X
Andropogon virginicus	L.	X	
Anthaenantia villosa	(Michx.) Beauv.	X	
Arachis hypogaea	L.	X	
Aristida palustris	(Chapm.) Vasey	X	
Aristida purpurascens	Poir	X	
Aristida stricta	Michx.	X	
Aristolochia serpentaria	L.	X	
Asclepias cinerea	Walt.	X	
Asclepias michauxii	Decne.	X	
Asclepias obovata	Ell.	X	
Asclepias tuberosa	L.	X	
Asclepias verticillata	L.	X	
Asclepias viridiflora	Raf.	X	
Asimina angustifolia	Kral	X	
Aslepias longifolia	Michx.	X	
Axonopus furcatus	(Fluegge) Hitchc.	X	
Baccharis halimifolia	L.	X	
Balduina uniflora	Nutt.	X	
Berchemia scandens	(Hill) K. Koch	X	
Boltonia diffusa	Ell.	X	
Botrychium biternatum	(Sav.) Underw.	X	
Brickellia eupatoridides	L.	X	
Buchnera americana	Gand.	X	
Bulbostylis ciliatifolia	(Ell.) Fern.	X	
Callicarpa americana	L.	X	
Calycocarpum lyonii	(Pursh) Gray	X	
Campsis radicans	(L.) Seem. ex Bureau	X	
Carex festucacea	Schk. ex Willd.	X	X
Carex gigantea	Rudge	X	
Carex glaucescens	Ell.	X	
Carex godfreyi	Naczi	X	
Carex stritula	Michx.	X	
Carex verrucosa	Muhl.	X	

Ceanothus americanus	L.	X	
Celtis laevigata	Willd.	X	
Celtis occidentalis	L.	X	
Cenchrus echinatus	L.	X	
Centella asiatica	(L.) Urban	X	
Centrosema virginianum	(L.) Benth.	X	
Cephalanthus occidentalis	L.	X	
Chamaecrista nictitans	L.	X	
Chamaesyce cordifolia	(Ell.) Small	X	
Chamaesyce maculata	(L.) Small	X	
Chrysopsis mariana	(L.) Ell.	X	
Cirsium horridulum	Michx.	X	
Clematis crispa	L.	X	
Clitoria mariana	L.	X	
Cnidoscolus stimulosus	(Michx.) Engelm. & Gray	X	
Commelina erecta	L.	X	
Conyza canadensis	(L.) Cronq.	X	X
Crataegus aestivalis	(Walt.) T & G	X	
Crataegus flava	Ait.	X	
Crataegus spathulata	Michx.	X	
Crataegus uniflora	Muenchh.	X	
Croptilon divaricatum	(Nutt.) Gray	X	
Crotalaria purshii	DC.	X	
Crotalaria rotundifolia	(Walt.) Gmel.	X	
Croton argyranthemus	Michx.	X	
Croton elliottii	Chapm.	X	
Croton glandulosus	L.	X	
Croton michauxii	Michx.	X	
Ctenium aromaticum	(Walt.) Wood	X	
Cucumis anguria	L.	X	
Cuphea carthagenensis	(Jacq.) MacBr.	X	
Cyperus filliculmis	Vahl	X	
Cyperus haspan	L.	X	X
Cyperus pseudovegetus	Steud.	X	X
Cyperus retrorsus	Chapm.	X	X
Dalea carnea	(Michx.) Poir.	X	
Dalea pinnata	(J.F. Gmel.) Barneby	X	
Desmodium ciliare	(Muhl. ex Willd) DC.	X	
Desmodium floridanum	Chapm.	X	
Desmodium glabellum	(Michx.) DC.	X	
Desmodium laevigatum	(Nutt.) DC.	X	
Desmodium lineatum	DC.	X	
Desmodium obtusum	(Muhl. ex Willd) DC.	X	
Desmodium paniculatum	(L.) DC.	X	
Desmodium perplexum	Schubert	X	
Desmodium strictum	(Pursh) DC.	X	
Desmodium viridiflorum	(L.) DC.	X	
Dichanthelium aciculare	(Desv. ex Poir.) Gould & Clark	X	

Dichanthelium acuminatum	(Sw.) Gould & Clark	X	X
Dichanthelium erectifolium	Nash	X	X
Dichanthelium ovale	Ell.	X	
Dichanthelium sphaerocarpon	Ell.	X	
Dichanthelium strigosum	(Muhl. ex Elliott) Freck.	X	X
Dichanthelium tenue	Muhl.	X	X
Dichanthelium wrightianum	(Scribner)	X	X
Dichondra carolinensis	Michx.	X	
Digitaria cilaris	(Retz.) Koel.	X	
Digitaria filiformis	(L.) Koel.	X	
Diodia teres	Walt.	X	
Diodia virginiana	L.	X	
Diospyros virginiana	L.	X	
Drosera brevifolia	Pursh	X	X
Dyschoriste oblongifolia	(Michx.) Kuntze	X	
Eleocharis atropurpurea	(Retz.) J. & K. Presl		X
Eleocharis microcarpa	Torr.	X	
Eleocharis nigrescens	(Nees) Steud.		X
Elephantopus elatus	Bertol.	X	
Eragrostis hirsuta	(Michx.) Nees	X	
Eragrostis spectabilis	(Pursh) Steud.	X	
Eragrostis virginica	(Zuccagni) Steud.	X	X
Erechtites hieracifolius	(L.) Raf.ex DC.	X	
Eryngium prostratum	Nutt.		X
Eryngium yuccifolium	Michx.	X	
Eupatorium album	L.	X	
Eupatorium capillifolium	(Lam.) Small	X	X
Eupatorium compositifolium	Walt.	X	X
Eupatorium hyssopifolium	L.	X	
Eupatorium leptophyllum	DC.	X	
Eupatorium leucolepis	(DC) T&G	X	
Eupatorium linearifolum	Walt.	X	
Eupatorium semiserratum	DC.	X	
Eupatorium serotinum	Michx.	X	
Euphorbia pubentissima	Michx.	X	
Eustachys floridana	(Champ.) Wood		X
Eustachys glauca	(Champ.) Wood		X
Euthamia caroliniana	(L.) Greene ex Porter & Britton	X	
Evolvulus sericeus	Sw.	X	
Fimbristylis autumnalis	(L.) R & S	X	
Fimbristylis puberula	(Michx.) Vahl.	X	
Fuirena breviseta	(Coville) Coville in Harper	X	X
Galactia erecta	(Walt.) Vail	X	
Galactia mollis	Michx.	X	
Galactia regularis	(L.) Britton et al.	X	
Galactia volubilis	(L.) Britt.	X	
Galium pilosum	Ait.	X	
Gamochaeta falcata	(Lam.) Cabrera		X

Gamochaeta pensilvanica	(Willd.) Cabrera		X
Gaura filipes	(L.) Benth. & Hook. f. ex Gray	X	
Gaylussacia dumosa	(Andrz.) T. & G.	X	
Gaylussacia frondosa	(L.) T. & G.	X	
Gratiola pilosa	Michx.	X	
Gratiola ramosa	Walt.	X	X
Gymnopogon ambiguus	(Michx.) BSP	X	
Habenaria quinqueseta	(Michx.) A. Eaton	X	
Helianthemum carolinianum	(Walt.) Michx.	X	
Helianthemum rosmarinifolium	Pursh	X	
Helianthus angustifolius	L.	X	X
Helianthus radula	(Pursh) T & G	X	
Heterotheca subaxillaris	(Lam.) Britt & Rusby	X	
Hieracium gronovii	L.	X	
Houstonia procumbens	(J.F. Gmel.) Standl	X	X
Hypericum crux-andreae	(L.) Crantz	X	X
Hypericum curtisii	(Englem. & Gray)	X	
Hypericum gentianoides	(L.) BSP	X	X
Hypericum gymnanthum	Engler & Gray	X	X
Hypericum harperi	R. Keller	X	
Hypericum hypericoides	(L.) Crantz	X	X
Hypericum mutilum	L.	X	
Hypericum setosum	L.	X	
Hypericum suffruticosum	Adams & Robson	X	
Hypoxis spp.		X	
Ilex opaca	Ait.	X	
Ionactis linariifolia	(L.) Greene	X	
Ipomoea cordatotriloba	Dennst.	X	
Ipomoea pandurata	(L.) G.F.W. Meyer	X	
Ipomoea quamoclit	L.	X	
Iva microcephala	Nutt.	X	X
Jacquemontia tamnifolia	(L.) Griseb.	X	
Juncus dichotomus	Ell.	X	X
Juncus effusus	L.	X	
Juncus elliottii	Coville		X
Juncus marginatus	Rostk.	X	X
Juncus ovata	(Walt.)Lindau	X	
Juncus repens	Michx.	X	X
Lactuca canadensis	L.	X	
Lechea minor	L.	X	
Leersia hexandra	Sw.	X	
Leersia virginica	Willd.	X	
Lespedeza angustifolia	(Pursh.) Ell.	X	
Lespedeza bicolor	Turcz.	X	
Lespedeza procumbens	Michx.	X	
Lespedeza repens	(L.) Bart.	X	
Lespedeza stuevei	Nutt.	X	
Lespedeza virginica	(L.) Britt.	X	

Liatris gracilis	Pursh	X	
Liatris graminifolia	(Walt.) Willd.	X	
Licania michauxii	Prance	X	
Lindernia dubia	(L.) Pennell	X	
Linum medium	(Planch.) Britt.	X	
Liquidambar styraciflua	L.	X	
Lobelia puberula	Michx.	X	
Lonicera japonica	Thunb.	X	
Ludwigia alternifolia	Spach	X	
Ludwigia glandulosa	Walt.	X	X
Ludwigia linearis	Raf.	X	X
Ludwigia repens	Walt.	X	X
Ludwigia spathulata	Forst.	X	X
Ludwigia virgata	Walt.	X	
Lygodium japonicum	(Thunb.) Sw.	X	X
Mecardonia acuminata	(Walt.) Small	X	X
Melochia corchorifolia	L.	X	
Mikania scandens	(L.) Willd.	X	
Mimosa quadrivalvis	(Dry.) MacBride	X	
Mitchella repens	L.	X	
Mitreloa sessilifolia	(Walt.) G. Don	X	
Mollugo verticillata	L.	X	
Muhlenbergia capillaris	(Lam.) Trin.	X	
Myrica cerifera	L.	X	
Nyssa sylvatica	marsh.	X	
Oenothera fruticosa	(Rose) Small	X	
Oldenlandia boscii	(DC.) Chapm.	X	X
Oldenlandia corymbosa	L.	X	
Oldenlandia uniflora	L.	X	X
Orbexilum lupinellus	Michx.	X	
Oxalis spp.		X	
Panicum anceps	Michx.	X	X
Panicum floridanum	Michx.	X	
Panicum hians	Ell.	X	
Panicum notatum	Fluegge	X	
Panicum verrucosum	Muhl.	X	X
Panicum virgatum	L.	X	
Parthenocissus quinquefolia	(L.) Plauch.	X	
Paspalum plicatulum	Michx.	X	
Paspalum setaceum	Michx.	X	
Passiflora incarnata	L.	X	
Pediomelum canescens	Michx.	X	
Penstemon australis	Small	X	
Pentodon pentandrus	(Schum. & Thonn.) Vatke	X	
Phlox flordana	L.	X	
Phlox pilosa	Benth.	X	
Phyllanthus urinaria	L.	X	
Physalis angulata	L.	X	

Physalis pubescens	L.	X	
Phytolacca americana	L.	X	X
Pinus elliottii	Engelm.	X	
Pinus palustris	Mill.	X	
Pinus taeda	L.	X	
Pirequeta cistoides	(L.) Griseb.	X	
Pityopsis graminifolia	(Michx.) Nutt.	X	
Pleopeltis polypodioides	(L.) Watt	X	
Pluchea camphorata	(L.) DC.	X	X
Polygala grandiflora	Walt.	X	
Polygala mariana	L.	X	
Polygala nana	Mill.	X	
Polygonum hydropiperoides	Blume	X	X
Polypremum procumbens	L.	X	X
Prunus caroliniana	(Mill.) Ait.	X	
Prunus serotina	Ehrh.	X	
Prunus umbellata	Ell.	X	
Pseudognaphalium obtusifolium	(L.) Hilliard & B. L. Burtt	X	
Pteridium aquilinum	(L.) Kuhn	X	
Pterocaulon pycnostachyum	(Michx.) Ell.	X	
Quercus falcata	Michx.	X	
Quercus incana	Bartr.	X	
Quercus laurifolia	Michx.	X	
Quercus margaretta	Ashe	X	
Quercus nigra	L.	X	
Quercus virginiana	Mill.	X	
Rhexia mariana	L.	X	X
Rhexis alifanus	Walt.	X	
Rhus copallinum	L.	X	X
Rhynchosia difformis	(Ell.) DC.	X	
Rhynchosia tomentosa	(L.) H. & A.	X	
Rhynchospora corniculata	(Lam.) Gray	X	
Rhynchospora debilis	Gale	X	
Rhynchospora globularis	(Chapm.) Small	X	X
Rhynchospora grayi	Kunth	X	
Rhynchospora harveyi	Boott	X	
Rhynchospora inundata	(Oakes) Fern.	X	
Rhynchospora nitens	(Vahl) Wood	X	X
Rhynchospora perplexa	Britt. ex Small	X	
Rhynchospora pusilla	Chapm.	X	X
Rhynchospora rariflora	(Michx.) Ell.	X	
Rhynchospora reniformis	(Pursh) DC.	X	
Rhynchospora tracyi	Britt. ex Small	X	
Richardia scabra	L.	X	
Rubus cuneifolius	Michx.	X	X
Rubus trivialis	Michx.	X	
Rudbekia hirta	L.	X	
Ruellia caroliniensis	(Walt. ex Gmel) Steud.	X	

Rumex crispus	L.	X	
Saccharum baldwinii	Baldw.	X	
Saccharum giganteum	(Walt.) Muhl.	X	
Sagittaria graminea	Michx.	X	
Salix nigra	Marsh	X	
Salvia lyrata	L.	X	
Sassafras albidum	(Nutt.) Nees	X	
Schizachyrium tenerum	Nees	X	
Scirpus cyperinus	(L.) Kunth	X	
Scleria ciliata	Michx.	X	X
Scleria reticularis	Michx.	X	
Scutellaria integrifolia	L.	X	
Sericocarpus tortifolius	(Michx.) Nees	X	
Setaria corrugata	(Ell.) Schult.	X	
Setaria pumila	(Poir.) Roem. & Schult.	X	
Seymeria cassioides	(J.F. Gmel.) S.F. Blake	X	
Sida rhombifolia	L.	X	
Sisyrinchium spp.		X	X
Smilax auriculata	Walt.	X	
Smilax bona-nox	L.	X	
Smilax glauca	Walt.	X	
Smilax lasioneuron	Hook.	X	
Smilax rotundifolia	L.	X	
Smilax smallii	Morong	X	
Solanum americanum	Mill.	X	
Solanum carolinense	L.	X	
Solidago canadensis	L.	X	X
Solidago odora	Ait.	X	
Solidago stricta	Ait.	X	
Solidago tortifolia	Ell.	X	X
Sorghastrum nutans	(L.) Nash	X	
Sorghastrum secundum	(Ell.) Nash	X	
Sporobolus compositus	(Poir.) Merr.	X	
Sporobolus floridanus	Chapm.	X	
Sporobolus junceus	(Michx.) Kunth	X	
Stellaria media	(L.) Vill.	X	
Stillingia sylvatica	Garden ex L.	X	
Strophostyles helvula	(L.) Ell.	X	
Strophostyles umbellata	(Muh. ex Willd.) Britt.	X	
Stylisma aquatica	(Walt.) Raf.	X	
Stylisma humistrata	(Walt.) Chapm.	X	
Stylodon carneus	(Medic.) Moldenke	X	
Stylosanthes biflora	(L.) BSP	X	
Symphotrichum adnatum	(Nutt.) G. L. Nesom	X	
Symphotrichum concolor	(L.) G. L. Nesom	X	
Symphotrichum dumosum	(L.) G. L. Nesom	X	
Symphyotrichum pilosum	(L.) A. Love & D. Love	X	
Taxodium distichum	(L.) L. Rich	X	

Tephrosia florida	(Dietr.) Wood	X	
Tephrosia spicata	(Walt.) T. & G.	X	
Tephrosia virginiana	(L.) Pers.	X	
Toxicodendron pubescens	(Salisb.) Gillis	X	
Toxicodendron radicans	(L.) Kuntze	X	
Tragia smallii	Shinners	X	
Tragia urens	L.	X	
Tragia urticifolia	Michx.	X	
Trichostema dichotomum	L.	X	
Tridens ambiguus	(Ell.) Shcult.	X	
Triplasis americana	Beauv.	X	
Ulmus alata	Michx.	X	
Utricularia subulata	L.	X	
Vaccinium arboreum	Marsh.	X	
Vaccinium corymbosum	L.	X	
Vaccinium myrsinites	Lam.	X	
Vaccinium stamineum	L.	X	
Vernonia angustifolia	(L.) Britt.	X	
Viola lanceolata	L.	X	X
Viola obovatum	Walt.	X	
Viola palmata	LeConte	X	
Vitis aestivalis	Michx.	X	
Vitis rotundifolia	Michx.	X	
Wahlenbergia marginata	(Thunb.) A. DC.	X	
Xyris caroliniana	Walt.	X	
Xyris jupicai	L. Rich.	X	
Yucca filamentosa	L.	X	