

THE RELATION OF UNDERSTORY GRASSES IN LONGLEAF PINE ECOSYSTEMS
TO FIRE AND GEOGRAPHY

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ABSTRACT

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(Under the direction of Dr. Peter S. White)

Longleaf pine forests are a fire dependent community that once dominated the southeast. In order to manage the remaining fragments, it is important to consider the history of the area and the role of fire throughout history. One of the main fuels for ground fires in longleaf pine forests are the grass species of the understory community, and the function and ecology of these grasses influence the trajectory of the forest ecosystem. There are, however, areas within the longleaf range that lack the dominant grass species, wiregrass (*Aristida stricta*), from either natural gaps in wiregrass distribution or from the disappearance of wiregrass through disturbance. With the arrival of Europeans, the longleaf forest was described as “park-like”, with open midstories, grassy understories, and large sparse trees. However, the condition of these forests was greatly modified by Native Americans for thousands of years with the use of intentional fires for hunting and farming. The influence of fire, disturbance, and agriculture of Native Americans, as well as the later European settlers affected the understory diversity in general, the dominance of grass species in particular, and the fire dynamics in the longleaf areas. The affect of different dominant grasses in the understory of longleaf pine ecosystems on the fire behavior and community structure is largely unknown.

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TABLE OF CONTENTS

	Page
INTRODUCTION.....	1
LONGLEAF PINE DOMINANCE AND DECLINE.....	2
LONGLEAF PINE COMPOSITION.....	3
LONGLEAF PINE-WIREGRASS SANDHILLS.....	5
FIRE ADAPTATION.....	7
ANTHROPOGENIC DISRUPTIONS.....	9
WIREGRASS.....	11
HISTORY	14
Native American history.....	15
European history.....	16
History of fire in Southeast longleaf pine forests.....	16
FIRE REGIMES: SEASON AND INTENSITY.....	21
MANAGEMENT STRATEGIES.....	24
Fire management.....	25
Invasive species.....	28
Restoration of wiregrass.....	30
SUMMARY.....	31
LITERATURE CITED.....	32

INTRODUCTION

Longleaf pine forests are a pyrogenic community that once dominated the coastal plain and sandhills of the southeast. Only a small percentage remains and not all of this is well maintained by fire. In order to manage the remaining fragments of this once dominant forest, it is important to consider the history of the area. Since longleaf pine ecosystems are fire-adapted communities, the role of fire throughout history is also an important component in understanding this system. The main fuels for these fires are composed of the understory community, mostly the dominant grass species, and the function and ecology of these grasses are important components of these ecosystems. Wiregrass (*Aristida stricta*) is the dominant grass species found in longleaf pine forests at the xeric end of the soil moisture spectrum and is thought to be very influential to fire regimes and understory. The longleaf pine sandhills are mostly those areas within the longleaf range that occupy dry, sandy, well-drained soils and are characterized by a wiregrass understory. However, there are areas within the longleaf range and the sandhill areas that lack wiregrass and are instead inhabited by more colonizing species, such as those in the genera *Andropogon*, from either natural gaps in wiregrass distribution or from the disappearance of wiregrass through disturbance. The historical range of wiregrass will be considered, its disappearance from its original sites, and the role in fire management. It is necessary to understand what controls understory grass species and the effects of understory grasses on the fire regime if we are to restore these forests. The purpose of this paper is to review the history, fire relations, and distributions of the understory grasses in longleaf pine forests and sandhills.

LONGLEAF PINE DOMINANCE AND DECLINE

The originally recorded longleaf forest had a savannah structure with scattered large overstory trees and relatively open understories. The open understories were maintained by frequent fires. Both a cause and effect of these frequent fires was the herbaceous understory. Key components of the herbaceous understory are grasses. Across the range of longleaf, wiregrass (*Aristida stricta*) dominates areas from Virginia to northern South Carolina, and a similar wiregrass (*Aristida beyrichiana*) occupies the southern end of the longleaf gradient, from southern South Carolina into Northern Florida. The gap in the wiregrass range is filled in with *Andropogon* species and the western areas of the longleaf range also have bluestem species. The pine area was well documented in early maps of the southeast United States, mostly dominated by longleaf pine (*Pinus palustris*). Areas were also classified by pine density and soil type (Moll 1715, Barnwell 1721). The original range of longleaf pine was approximately 92 million acres, from Virginia to Florida and west into Texas, of which 74 million was longleaf dominated (the rest was a mixture of longleaf pine, loblolly pine (*P. taeda*) and slash pine (*P. elliottii*), and it is now reduced to only 2-3% of its original area. However, of that, only 674,000 acres are naturally regenerated and fire maintained in good condition (Frost 2000). This extensive fragmentation is not only due to agriculture, logging, and development, but also to post-settlement management techniques that favored faster growing pine species such as loblolly pine and slash pine and the interruption in the natural fire regime, which is the main disturbance of this system (Brockway and Lewis 1997).

In 1946 the distribution of longleaf pine was documented as 1/2 - 1/3 of the original area (Wahlenberg 1946). Wahlenberg (1946) refers to longleaf forests as a "subclimax" ecosystem because it endured long-time residence due to fire disturbances in large areas. A

survey conducted in 1905 in Coosa and Bibb counties in Alabama of all trees greater than one inch diameter at breast height (DBH) found 80-86% of the species were longleaf pine. In other areas with infrequent fires, only 6-28% of the trees were longleaf pine greater than one inch DBH (Wahlenberg 1946).

LONGLEAF PINE COMPOSITION

Although the first records of the longleaf forests portray the area as a monotonous stand of pines with a grass understory, there is much large and small scale diversity in the southeastern longleaf areas. Variations in topography, geology, soil type and moisture dictate the vegetation. Species composition is correlated primarily with soil moisture and hydrology; and fire frequency is the second most important factor (Glitzenstein et. al. 2003). The Coastal Plain varies with soil type from richly diverse savannas on poorly drained soils to the xeric sandhills that occur on the Fall Line. Bartram describes the soil types as sandy with cinereous colored clay that is fertile in savanna and coastal plain areas in South Carolina (Bartram 1791). According to Peet and Allard (1993), the vegetation types can be classified into four basic categories and 23 subcategories that depend on location, and soil moisture content. These community types are Xeric Longleaf Pine Woodland, Subxeric Longleaf Pine Woodland, Mesic Longleaf Pine Woodland, and Seasonally-wet Longleaf Pine Woodland. All of these forest types are dependent on frequent fires for maintenance. The absence of fire and the conversion of forests into agriculture has left a sparse area of the once dominant communities (Peet and Allard 1993). Similar forest associations were documented by Pessin (1933) that were dependent mainly on soil moisture and drainage.

Species composition in longleaf areas is dependent on soil texture, elevation, disturbance history, and fire frequency (Gilliam et. al. 1993, Rodgers and Provencher 1999).

There are gradients in composition that correlate to moist to dry soils and nutrient rich to poor soils. The canopy cover, understory, and midstory composition dramatically change with soil moisture. In dry sandy soils, mostly located at the Fall line in North and South Carolina, there are the sandhills, which contain a certain set of drought tolerant herbaceous species, a turkey oak midstory, and a medium dense canopy of longleaf pine. Flatwoods are also a longleaf area with relatively dry soils, but the slope and elevation distinguish them from the sandhills. Flatwoods have a similar canopy, and share some herbaceous species, but contain other species such as saw palmetto. Savannas are at the extreme moist end of the gradient, with a sparse overstory of longleaf, little to no midstory, and a highly diverse herbaceous understory. Large scale patterns are distinct and documented in Sorrie and Weakley (2001).

At small scales, small changes in elevation and soil type can affect the species composition and community type. Some species that cannot tolerate extremely dry conditions may grow in sandhills at slightly lower elevations, where more moisture would be available. James (thesis 1999) found small decreases in elevation in sandhill communities to change species composition with an increase in legumes and diversity in general. Although some species span the gradients, such as wiregrass and longleaf pine, species turnover can be seen at small scales when moisture availability changes. Gilliam et. al. (1993) recorded distinct compositions of species for elevation and soil texture gradients in longleaf areas, noting that at higher elevation where soils textures were more likely to contain more clay and moisture, more hardwood species will occur, such as dogwoods, hickories, and oaks. Schwarz (1907) also noted the small scale variations in longleaf, which correlated to slope,

elevation, and soil. In loamier soils, there is an increase in deciduous species and loblolly pine, and in the sandier soils, longleaf dominates the overstory.

Lawson (1952) wrote his account of North Carolina in 1714, and recorded the different vegetation across the landscape:

The Land being of several sort of Compost, some stiff, others light, some marl, others rich, black Mould, have barren of Pine, but affording Pitch, Tar and Masts; there vastly rich, especially on the Freshes of the Rivers, one part bearing great Timbers others being Savannas or Natural Meads, where no trees grow for several miles, adorned by Nature with a pleasant Verdure, and beautiful Flowers, frequent in no other Places, yielding abundance of Herbage for Cattle, Sheep, and Horses.

This description captures the diversity of the landscape in the southeast soils and vegetation, noting the gradient from rich pine areas to sparse, herbaceous savannas.

LONGLEAF PINE-WIREGRASS SANDHILLS

The Sandhills developed from the Fall Line created during the Pleistocene era by the successive lowering of the sea level, and is characterized by the increase in slope between the plateau of the Piedmont and the Coastal Plain (Turner 1949). Sandhills are ecosystems of the longleaf pine forests at the more xeric end of the moisture gradient. The difference in soil moisture is highly correlated to slight differences in elevation and soil texture (Gilliam et. al. 1993). Soils of the sandhills are coarse, dry, well drained, and have high potential for erosion and fire (Lesica and Cooper 1999).

Longleaf pine sandhills qualify as Southern Xeric Longleaf pine Woodlands (Peet and Allard 1993) and are characterized by the following species; *Aristida stricta* or *A. beyrichiana* (wiregrass), *Pityopsis graminifolia* (grass-leaf golden aster), *P. palustris*, *Quercus laevis* (turkey oak), *Q. incana* (bluejack oak), *Sporobolus juncea* (pineywoods

dropseed), *Licania michauxii* (gopher apple), *Diospyros virginiana* (persimmin), *Serenoa repens* (saw palmetto), *Cnidoscolus stimulosus* (tread softly), *Eriogonum tomentosum* (wild buckwheat), and *Croton argyranthemus* (silver croton) (Provencher et. al. 2000). The dominant overstory is longleaf pine that is relatively sparse, with an open canopy. The midstory consists of woody species, mainly turkey oak, bluejack oak, and sand post oak (*Q. margarretta*), while the understory is composed of wiregrass, legumes, and some woody shrubs, such as blueberry (*Vaccinium spp.*) and gallberry (*Ilex glabra*). The type of understory plant community is associated with the fire regime. Areas with high fire frequencies have small amounts of woody shrubs and the understory is dominated by wiregrass and fire-resistant herbs (Wells 1942).

The sandhills were first mapped by Thomas Baaet London as "Deserta Arenosa" in 1676, but was sparsely settled until late nineteenth century (Turner 1949). The area was occupied, however, by Native Americans for thousands of years before the Europeans settled. Early maps of the southeast recognized various Native American sects in the sandhills, including the Waxaus, Sugaus, Saraus, and Keouwees (Bowen 1747). The earliest Native American pottery was found on Ft. Bragg, which dated back to the Early Woodland period, about 1700-600 B.C. (Anderson and Mainfort 2002).

The first European settlers to the region began in 1740 and were of Scotch descent. The roads used followed old American Indian trails, and settlements began along streams. This pioneer occupancy remained at a low density for over a hundred years and minimally used the resources of the longleaf forest until the time of the Civil War. In 1875, the Raleigh and August railways entered into the sandhills, changing the population density, forest use,

and land value. After the forest resources were depleted, agriculture dominated the area with peaches, tobacco, and cotton (Turner 1949).

FIRE ADAPTATION

Some communities have evolved to depend on disturbances, such as fire, in order to reproduce and thrive. Fire is an essential aspect of the community and its alteration and removal can have deleterious effects on the diversity, structure and function of the community. Evolution processes, such as reproductive events following fires, are a part of pyrogenic communities, and without fire as a trigger to reproduce, loss of species is projected.

Many species in the longleaf pine-wiregrass sandhills are adapted to fire and regeneration following a burn is mainly by vegetative means, rather than through the seedbank (Plocher 1999). Longleaf pine forests are a pyrogenic ecosystem. Frequent fires maintain the characteristic community structure. Fire was a natural disturbance of the longleaf ecosystem, historically ignited by lightning, occurring approximately every 1 – 10 years (Christensen 1981). Without fire, the diverse grasslands are colonized by woody species and species diversity declines because of litter accumulation and shade (Vogl 1972).

Periodic fires benefit sandhill ecosystems by excluding invasive plants that are not adapted to fires, reducing the density of the midstory vegetation, thereby reducing competition, releasing nutrients stored in the biomass into the soil, controlling harmful insects and pathogens, and decreasing fuel accumulation, which prevent disastrous wildfires (Brockway and Lewis 1997). Longleaf pines become fire resistant after one year of growth when the secondary needles that protect the apical bud replace the flammable primary needles (Grace and Platt 1995). Longleaf pines have physiological trade-offs; in return for

fire resistance, they are slow growing and poor resource competitors. They are shade intolerant and require at least 20 years of growth before being able to reproduce, while sand pine (*P. clausa*), an invasive southern pine, can reproduce successfully after only 5 years of growth (Grace and Platt 1995, McCay 2000). Herbs, however, need at least three years from the fire to reach maximum abundance and richness in pine-wiregrass flatwoods (Maliakal et. al. 2000).

Frequent fires (annually or biannually) increase diversity in the understory and maintain dominance of longleaf pines by increasing the growth and survivorship of the species. This increase occurs with the reduced competition of woody species and decrease in litter, which reduces shading, and releases nutrients in the soil (Brockway and Lewis 1997, Glitzenstein et. al. 1995). Without fire, longleaf pine forests will develop into a mixed hardwood forest dominated by oaks (Kush and Meldahl 2000). Heyward (1939) noticed the relationship between fire suppression and the invasion of hardwood species. In a ten year study in areas of the Coastal Plains from South Carolina to Louisiana it was noted that without fire, hardwoods regenerate under the longleaf pine and once established they are very difficult to eliminate.

While longleaf pine is in its seedling stage, it is fire resistant, and without fire, it may be outcompeted by faster growing tree species, or infected with brown spot needle blight, which is caused by *Scirrhia acicola* (Kush and Meldahl 2000). Longleaf pines and wiregrass are not only fire resistant, but assist in spreading local lightning ignited fires into low intensity burns that reach the whole region (Brockway and Lewis 1997), and are therefore considered ecosystem engineers for this community.

The suppression of the natural fire regime is a significant alteration to this ecosystem. Without fire, the regeneration of longleaf pine declines and is replaced by less fire-resistant woody species. The canopy fills in and becomes dense with oaks and fire intolerant southern pines, while the understory herbs and legumes are outcompeted by woody shrubs, such as gallberry and saw palmetto (Brockway and Lewis 1997, Glitzenstein et. al. 1995, Maliakal et. al. 2000). This denser canopy and greater litter abundance prevents light from reaching the forest floor and further reduces longleaf pine and wiregrass regeneration and the herbaceous understory cover (Sparks et. al. 1998).

ANTHROPOGENIC DISRUPTIONS

Disturbance is a critical aspect of community structure. Reice (1994) states that the common state of ecosystems is in a recovery stage from the last disturbance event. Therefore natural disturbance regimes are essential in determining the species composition, diversity, and structure of a community. Anthropogenic disruptions to these disturbance patterns can have detrimental affects on the integrity of the community. Aside from disturbance disruptions, humans also have the ability to change ecosystems through their own actions, such as logging, agriculture, urbanization, and overgrazing. These alterations directly affect community structure and indirectly influence the natural disturbance patterns.

Longleaf pine-wiregrass sandhills are fire-adapted communities that have undergone human induced changes in the natural fire regime. The changes include active fire suppression, disruptions that allow nonlocal species to invade, and fragmentation. The effects of these changes in the historical fire patterns have deleterious consequences on the community structure. The alteration in the structure includes a denser canopy replacing longleaf pine with hardwoods, and reducing cover and diversity of the understory. These

changes also affect the behavior of fires that sweep through the area, which, in turn, affect the population dynamics of the endemic species. Human alteration of disturbance regime could have consequences on the community structure (Menges et. al. 1993) and on populations of species that have adapted their life strategies to the natural disturbance patterns, such as the rare species of American chaffseed (*Schwalbea americana*), found in longleaf pine savannas (Kirkman et. al. 1998).

Anthropogenic disturbances in the southeast forests include turpentine, siveicultural treatments, grazing by cattle, sheep, and hogs, fire suppression, and logging (McCay 2000). Turpentine included extraction and cutting after fifteen years, leaving some large trees as seed trees, but turpentine activities slowed in the 1920's and ceased in some areas, such as Florida, in 1948. Fire suppression was a method used to protect the trees used to extract turpentine (McCay 2000). Remaining longleaf pines were not sufficient to regenerate historical populations because dispersal distances are only 20 – 40 meters and turpented areas allowed for invasion of nonnative species, which easily outcompeted the longleaf pine. Hogs were introduced by the Spanish in 1539 and they fed on the underground storage of longleaf pine saplings in the grass stage and can eat up to 400 saplings per day. The extent and density of hogs in the southeast was vast until fence laws were past in the 1870's. Fire suppression tactics allowed other tree species, such as loblolly pine to regenerate under the stands of longleaf (Frost 2000).

The primary disruption to the landscape is the extensive fragmentation and habitat loss. The noncontiguous areas prevent the spread of necessary low intensity fires. However, the practice of fire suppression in the remaining natural areas is also detrimental to the landscape.

WIREFRASS

Wiregrass is considered by some to be a “keystone” species in the longleaf range because of its ability to carry fire and influence on ground level microclimate (Noss 1989, Clewell 1989, Duever 1989). Wells and Shunk (1931) considered wiregrass so important that they noted “to one who travels in the coastal plain of the southeastern United States, one of the most distinctive vegetation habitat complexes is that of the erect, tenuous-bladed wire grass in scattered tussocks on the dry loose sand hills and ridges.” Wiregrass, with the occurrence of fire, influences the species composition of the understory of longleaf areas. Wiregrass is also associated with high concentrations of rare species in the southeast (Hardin and White 1989). Because of the dominant presence of wiregrass in remnant communities, the term “keystone” is not semantically correct and the term “ecosystem engineer” would be more appropriate for such an abundant species (Jones et. al. 1994). In either case, historically, wiregrass is an essential component of longleaf areas.

Although wiregrass is an important species in sandhill ecosystem, there are areas where wiregrass is absent or minimally present, and other native grasses dominate the understory. The cause of this difference is thought to be historical land use patterns (Rodgers and Provencher 1999), although data for this hypothesis is nonexistent. Because wiregrass is a poor competitor, other grasses may be able to dominate an area through changes in disturbance patterns. The affect of different dominant grasses in the understory of sandhill ecosystems on the fire behavior and community structure is unknown.

Wiregrass dominated, frequently burned sites have greater species richness in the understory than frequently burned bluestem (*Andropogon and Schizachyrium spp.*) dominated sites (Rodgers and Provencher 1999). The difference in dominance is thought to

be due to anthropogenic disturbances and soil properties, which also affect the richness, however, there is no statistical evidence to support this hypothesis (Rodgers and Provencher 1999). Since invasive grasses, such as cogongrass (*Imperata cylindrical*) could interfere with the fire regime as to decrease understory diversity, it is possible that the different dominant native grasses affect the fire patterns and therefore the community richness. These grasses could also have different competitive abilities and reduce diversity through outcompeting herbaceous species.

Although it is assumed that wiregrass is key to the longleaf pine ecosystem because of its affect on fire behavior, the theory has not been tested. In the areas that lack wiregrass, analogous species, such as bluestems may have similar effects on fire behavior and substitute for wiregrass without diminishing the community diversity or structure (Noss 1989).

Wiregrass is also used as an indicator for high species richness (Kirkman et. al. 2004).

Wells and Shunk (1931) noted the distribution of wiregrass as a dominant understory species in longleaf pine that spanned over a wide range of soil types in North Carolina, from sandy to loamy soils. In Louisiana and Mississippi, *Andropogon* species were more commonly dominant, and broomsedge (*Andropogon virginicus*) was noted to prefer moister regions of the longleaf range. Chapman (1932) also distinguished between the two hemispheres of grasses. He notes that the north and west range of longleaf is dominated by *Andropogon* and *Carex* species, while in the east and south, wiregrass is more predominant. Schwarz (1907) described the understory of longleaf and the different characteristics of the two dominant grasses; wiregrass and broomsedge. In unburned areas, wiregrass is denser than in burned areas and nutrient availability is higher due to the presence of a mold that grows on the soil in the absence of fire. Wiregrass also served as an indicator of coarse,

sandy soil (Wells and Shunk 1931) and wiregrass persists even when longleaf is cut and scrub oaks dominate (Turner 1949).

The different ranges of wiregrass and *Andropogon* species are linked to soil characteristics. Wiregrass dominates sandier soils, while *Andropogon* species appear more on silt or loamy soils that are well drained (Wells 1942). However, in poorly drained hard panned subsoils (wiregrass dominated), calcium is leached readily, leaving the plants with high carbon contents. These plants are then highly combustible, and can burn yearly (Wells 1942). Grass species may also be related to fire frequency. Grasses such as *Andropogon*, *Panicum*, *Muhlenbergia*, *Schizachyrium*, *Sorghastrum*, and *Ctenium* increase in abundance under higher fire frequencies (Glitzenstein et. al. 2003).

Plants associated with longleaf in general, and wiregrass in particular, have high proportions of cellulose and lignin, which also allows these plants to burn readily. The anatomy of wiregrass, with blades made mostly of lignified fibers, makes it especially flammable, even hours after a rain (Wells and Shunk 1931, Wells 1942). Wiregrass also accumulates dead leaves at the base, which increase its flammability (Christensen 1981.)

In longleaf pine areas of Urania, Louisiana, annually burned plots produced an understory dominated by *Andropogon divergens* (Hack.) Anderss. and *A. scoparius* Michx (Bruce 1947). Lemon (1949) worked in longleaf-wiregrass areas and noted that *Andropogons* and *Panicums* increased after fire and he named them “fire-followers.” He assumed that in the absence of wiregrass, *Andropogons* would dominate the understory of burned pine forests. Wiregrass is very stable in relation to fire, but it does not invade or compete well. However it is able to survive fires, and resprouts readily because the meristems are below ground, protecting them from burning (Lemon 1949).

The presence of bluestem grasses is common after disturbance such as abandoned agriculture. In areas where Native Americans abandoned fields, European travelers noted in 1671 “broom grass” was found to be growing in the cleared land (Bushnell 1907). It is also noted that after disturbances, wiregrass fails to reclaim the understory (Wells and Shunk 1931). Peet and Allard (1993) concede that the dominance of bluestem on loamy soils is evidence that they are the original understory grass, rather than wiregrass, and not simply a product of soil disturbance.

HISTORY

Upon the arrival of Europeans to the southeast, the vegetation was frequently recorded as open pine areas with long grasses underneath, which can be assumed to be wiregrass due to the length of its blades. For example, Bartram (1791) describes southeast pine forest with open understory, stretching for miles as, “[he] rode [s]everal miles through a high fore[s]t of pines, thinly growing on a level plain, which admitted an ample view, and a free circulation of air...”. Descriptions like these are used as templates for longleaf pine restoration today and are often taken to represent pristine, untouched conditions. However, the condition of these forests was greatly modified by Native Americans for thousands of years with the use of intentional fires. The influence of fire, disturbance, and agriculture of Native Americans, as well as the later European settlers affected the understory diversity in general and the dominance of grass species in particular in the longleaf areas.

The vegetation and soil patterns were noted by Bartram during his tour of the southeast in the 1700’s. He describes the xeric sandhills of western Florida as an “endle[s] wa[s]tes...producing [s]carcely any vegetable [s]ub[s]tances, except a few [s]hrubby, crooked pine trees, growing out of heaps of white rocks, which repre[s]ented ruins of

villages, planted over plains, with clumps of mean [s]hrubs, which [s]erved only to perpetuate the per[s]ecuty power and rage of fire, and to te[s]tify the aridity of the [s]oil.” (Bartram 1791). However, areas in Georgian coastal plain are described as “mostly a fore[s]t of the great long-leaved pine (*P. palustris* Linn.) the earth covered with gra[s]s, inter[s]per[s]ed with an infinite variety of herbaceous plants, and embellied with extensive [s]avannas, always green, [s]parkling with pond water, and ornamented with clumps of evergreen, and other trees and [s]hrubs...” And the soil of this type of vegetation “may be de[s]cribed after the following manner; the upper [s]urface, or vegetative mould, is a light [s]andy loam, generally nine inches or one foot deep, on a [s]tratum of cinereous coloured clay, except the [s]and-hills, where the loo[s]e [s]andy [s]urface is much deeper upon the clay...” (Bartram 1791). The vegetative diversity, soil gradient, and distinct community types were characterized then and those descriptions persist in preserved areas.

Native American history

The Native Americans altered the landscape of the southeast, which affected the natural ecosystems described by early travelers in the 16th and 17th century. Native American villages are present throughout North Carolina in the 1700’s and some areas were noted to have already been abandoned by the early 1700’s (Barnwell 1721, Bowen 1747). Along with the use of fires, some crops were planted, such as corn, squash, tobacco, and sunflowers in succession and intermittent. The different land use types, from hunting grounds to gardens and orchards kept by the Native Americans resulted in a heterogeneous landscape leading to patchy controlled fires, with some areas neglecting to burn and others burning very hot (Hammett 1992).

European history

Historically the south can be divided into the two sections which Europeans settled. The Spanish settled in the lower Gulf Coast areas of Florida to Texas, while the English settled along the Atlantic Coast from Jamestown, Virginia south into Florida. The Spanish controlled the areas from 1565 until 1821, when Florida ceded to the United States. They sparsely settled the along the Gulf Coast and left the longleaf pine regions practically untouched (Frost 2000). However, the goals for the English were mainly economic, with intentions for agriculture and exportable products (Smith 1624), and hence, destroyed more longleaf forests along the eastern side of its range.

The areas were described frequently as open enough to ride a carriage through between the trees because of the lack of a midstory. Longleaf was seen as an abundant resource that spanned tens of thousands of square miles used for resinous products (Mohr 1888). In the 1700's, longleaf products were exported to England for tar and pitch (Michaux 1819). Longleaf products include "paints, varnish, linoleum, paper, soap, ink, grease, synthetic camphor, etc.". Products from the longleaf pine trees in the south were exported as early as 1608 (Wahlenberg 1946). Wiregrass was used for cattle grazing, which was a profitable business in the Sandhill region until the time of the Civil War (Ivy 1923).

History of fire in Southeast longleaf pine forests

Fire is an integral part of the earth's history, occurring naturally since the formation of fuel, or vegetative material, as early as the Paleozoic era during the Carboniferous Period, when large deposits of coal formed approximately 400 million years ago. The formation of coal deposits are proof to the existence of ancient fires and the study of these coal specimens gives clues to the types of fires that have occurred through time (Komarek 1972). During the

Mesozoic era, 250-150 million years ago, fires are estimated to have been fast moving ground fires, evidenced by the type of flora, which includes a dominance of ferns. During the Tertiary Epoch, 33-5 million years ago, fires were widespread throughout the United States, formed brown coal, and are thought to be similar to the fires that currently burn in the southeast United States and Australia (Komarek 1972). These fires were caused naturally by lightning or spontaneous combustion (Komarek 1968, 1972). Although small fires ignited by lightning occur frequently, they are extinguished quickly by the ensuing rain. Fires can, however, persist during “critical fire weather”, defined by the United States Forest Service as high temperatures accompanied by low relative humidity and rainfall and strong winds (Komarek 1968). The ability of lightning to ignite an area depends on the characteristics of the vegetation, such as the bark structure, wetability, and moisture content (Taylor 1974). The topography and natural fire breaks of the area will also play a role in the amount of land burned with each ignition. Plateaus that contain flat areas with no natural firebreaks may burn completely with one ignition event, while inland areas that are more fragmented may need more lightning strikes to burn the same area of land (Frost 2000). Taylor (1974) estimated approximately 50,000 wildfires are caused by lightning per year world wide, which accounts for only 1% of all lightning strikes.

Fire has been used by Man for millions of years worldwide. The first prehistoric ancestor of *Homo sapiens sapiens* to use fire was the *Australopithecus promethicus*, which has been dated to the upper Pliocene and middle Pleistocene, 2-5 million years ago. However, the *Sinanthropus pekinensis*, or *Homo erectus*, was the earliest to have been known to have control over fire, which can be dated back to 250,000 to 1.6 million years ago (Stewart 1956). Early hominids used fire for heating and cooking, and purposely left

campfires smoldering for days in order to return to them and facilitate restarting a fire (Stewart 1956).

Homo sapiens sapiens have been present in the Western Hemisphere for 12,000 to 14,000 years, which is sufficient time for man-made fires to induce evolutionary genetic changes in vegetation (Guffy 1977). Pollen records indicate the presence of fire in the southeastern forest by the existence of charcoal in the pollen in sediment. From about 7000 BP, there was a significant increase in the amount of charcoal found in pollen records, indicating a more frequent fire regime, and a shift in the type of vegetation (Buell 1945). Although the southeast has a high frequency of lightning and thunderstorms, the increase in fires is attributed to the colonization of American Indians to the area (Buell 1946). The continual use of fire may have caused the vegetation shift to more fire-dependent species, such as wiregrass and longleaf pine, and the appearance of aromatic shrubs in the Coastal Plains (Mutch 1970). Platt et. al. (1991) found these types of pyrogenic characteristics in longleaf sandhills and flatwoods.

The fire dependent characteristics of the vegetation were known to the Native Americans living in the southeast. They set fire regularly to the area in order to improve hunting and increase the production of legumes. The first reference to intentional burning of the forest is by Morton in 1632 (Morton 1967). The survey of the border between Virginia and North Carolina was continually interrupted by fires set by Native Americans in 1727 (Byrd 1967). Bartram in his travels through the southeast also is witness to the use of fire by Native Americans. He noted fire promoted the growth of grasses and legumes and protected the forest from harmful fires that kill trees (Bartram 1773). He also witnessed pines directly

ignited by lightning in severe thunderstorms, but such fire are quickly extinguished (Bartram 1791).

Fire was also used in Native American culture as part of communal hunting in drives (Smith 1624, Waselkov 1978). In 1728, Byrd observed the Native American's creating a ring of fire to drive the animals into a small circle and slaughter them (Byrd 1967). In areas of New England, Van der Donck noted in 1655 that the Native Americans set fires on a yearly basis to improve hunting grounds by thinning woods and making tracks more visible (Van der Donck 1846). In the southeast, Bartram (1791) also recorded annual burning of the coastal plains and longleaf forests by the Native Americans for the purpose of controlling shrubs, evidenced by burnt vegetation, charcoal in waterways, and fire-scarred roots of the shrubs. This frequency is corroborated with Wood (1639), who observes;

it being the cu[s]tome of the Indians to burne the wood in November, when the gra[ss] is withered, and leaves dried, it con[s]umes all the under wood, and rubbi[s]h, which otherwi[s]e would overgrow the country, making it unpa[ss]able, and [s]poyle their much affected hunting for that by this means in tho[s]e places where the Indians inhabite, there is [s]carce a bu[s]h or bramble, or any comber[s]ome underwood to be [s]eene in the more champion ground.

Wood (1639) not only observes the time of year of these annual burnings, but also reemphasizes the purpose these fires served to the population of Native Americans.

However, in 1632 Thomas Morton (1967) witnessed the burning twice a year, in spring and fall. Day (1953) sites cases throughout the northeast of fires cataloged by European settlers from 1583, set by Native Americans for a variety of purposes. In areas where the Native Americans died years prior, and therefore left the land unburned, the midstory grew and travel was difficult. Wood (1639) calls these areas "ragged plaine" because clothes would be torn by thorns of the under brush.

The common view in the 19th century was that the fires set by Native Americans were for the purpose of converting forest ecosystems into prairies, and the lack of midstory in areas was evidence that the last generation of the forest had no replacement trees. It was acknowledged that burning increased food supply directly and indirectly by increasing the availability of fruits and nuts, and attracting wild game. However, the European settlers valued timber and wood products more than food production for economic reasons. This difference in land value caused settlers to discredit the significance of fire to the landscape in favor of increasing the economic value of the land through timber products (Maxwell 1910).

Gifford Pinchot (1899) was the first to nationally recognize fire as a characteristic of forests, rather than a destructive factor. The forests of the United States have been burned for thousands of years before settlers came. Yet Pinchot (1899) calculated the yearly economic costs of forest fires to be \$50 million. He distinguished how fire shaped the vegetation in different areas of the United States. For example, according to Pinchot (1899), the prairies of the Midwest are treeless due to fires. The southeastern forests, or longleaf areas, are known to have a park-like atmosphere, characterized by a grassy understory and sparse midstory, which is “created and maintained” by the action of fire. Pinchot (1899) noted the resistance of longleaf pine to fire and that they are associated with grass, which is known to be flammable throughout their life cycle.

Schwarz (1907) noted the characteristics of longleaf pine as shade tolerant and fire resistant. At the turn of the century fires were known to be mainly surface fires, which rarely reached heights of 20-25 feet with excess debris. Surface fires occurred approximately yearly and the frequency and intensity depended on the density of the understory grass, the season of the fire, and the weather conditions. Although Schwarz (1907) stated the resistance

to fire of the longleaf pine, he noted the possibility of later damage to the trees and recommended protecting the trees from fire in order to preserve them for economic purposes.

Fire was used on turpentine plantations annually to clean the area by removing grasses and trash, thereby lessening the fire risk. Individual trees were protected by raking. The trees provided gum-yield after fires, but the yield was half that of the unscorched trees, with less foliage (Cary 1932). Summer fires were noted to reduced growth and increase mortality of the longleaf, while winter fires damaged trees less, but the intensity depended on the weather and fuel (Cary 1932).

The National Park Service began incorporating a policy of fire suppression nationally in 1916 (Agee 1974). The United States Forest Service studied the usefulness of prescribed burning in the longleaf areas from 1921, yet even in 1931 the condoning of these fires was preceded by warnings to the public from editors of journals not to start random fires (Greene 1931). Even though fire was being studied as an ecosystem component and management strategy in the 1930's, Pessin (1933) saw fire in a negative light, and suggested forest management strategies that included fire exclusion in order to recreate the longleaf forests of the past. Greene (1931) pointed out that longleaf pine had two enemies, exotic hogs brought by the Spanish, which the pines have no natural defense to, and brown spot needle disease, which is controlled by ground fires. Grasses, in general, are the main fuels for controlled burns, along with fallen pine needles, which accounts for the heavy grass understory (Greene 1931).

FIRE REGIMES: SEASON AND INTENSITY

Understory herbs are absent in pine forests that have been excluded from fire, while regularly burned pine forests develop diverse understories, dominated by grasses (Hodgkins

1958). Fire suppression also decreases the grass cover tremendously and decreases the amount of longleaf pine as recorded by Bruce (1947) in a 32 year experiment comparing unburned Louisiana pine lands to annually winter burned areas.

Historically fires are thought to occur during the summer growing season, mainly ignited by lightning, however management practices favor winter dormant season burns for ease in control and intensity. Species that are actively growing during the time of the burn are more susceptible to damage by the fire (Sparks et. al. 1998). Therefore, hardwoods growing within the longleaf pines exhibit increased mortality during growing season burns (Platt et. al. 1991) and oaks physically closer to longleaf pine trees also have higher mortality rates during fires because the intensity tends to be higher due to the pyrogenic nature of the longleaf pine (Rebertus et. al. 1989). However, intensity of the burn and the diameter of the oak trees also determine the probability of mortality and resprouting (Rebertus et. al. 1989).

Stoddard (1935) found that controlled burns in open pine areas increased the production of legumes and other wild animal food sources, but suggested late winter was the optimal season for prescribing fires. The increase in herb density may be temporary and decrease after a few years without subsequent burns (Hodgkins 1958). Hodgkins (1958) compared summer and winter burns in loblolly-shortleaf pine areas of Alabama and found that although summer fires initially top killed more hardwoods; they grew back after three years. The ability of fire to kill hardwoods depend on the DBH, season of burn, amount of carbohydrate stored in the hardwood, weather conditions, and the frequency of fire.

Hardwood mortality is increased when plant reserves are minimal, which is generally in the late spring and early summer (Hodgkins 1958). The response of any species to fire depends

on its ability to withstand the actual damage and compete with invading species for the newly cleared mineral soil (Lemon 1949).

Season of burn may also influence the flowering of the understory herb layer. Platt et. al. (1988) found greater flowering in herbs and shrubs during growing season burns than between them. He concluded that the growing season burns were hot enough to kill the underground apical meristems, which triggers dormant meristems to flower. However, Hiers et. al. (2000) found little correlation of flowering and subsequent pollination to season of burn, in longleaf pine savanna legumes. Sparks et. al. (1998) found that dormant season fires more effectively reduced woody species and litter layer, allowing more light penetration to the forest floor and therefore more regeneration. Dormant and growing season fires produced similar results for the phenological response of *S. americana* (Kirkman et. al. 1998). The seed production and flowering of wiregrass, a perennial bunchgrass, is greatest after a growing season burn (Outcalt 1994). Although there are slight differences in vegetation response to season of burn, it is suggested that the actual implementation of fire as a management tool is more important than the timing of the fire (Hiers et. el. 2000).

Glitzenstein et. al. (1995) did an extensive study looking at the population dynamics of longleaf pines in response to eight different seasons of burn. He found no statistic significance of season to diameter growth, damage, or recruitment of *P. palustris*. He suggested that season and frequency are of little consequence to the longleaf pine, however, the behavior of the fire, such as temperature, amount of crown scotch, and intensity, significantly affect the population dynamics of the fire-resistant longleaf pine.

Longleaf pine is therefore less affected by season of burns than intensity of burns. The intensity of the fire, however, is inversely proportional to the frequency, and also related

to the season, with higher intensity burns occurring during the growing season. Although, according to the Intermediate Disturbance Hypothesis, very frequent disturbances do not give species time to recover from the disturbance and decreases the overall diversity (Connell 1978, Huston 1979), plots burned on annual and biennial fire cycles produce the highest amount of grass cover compared to those burned less frequently (Vogl 1973). Glitzenstein et. al. (2003) also found an increase in species richness at high fire frequencies of 1-2 year intervals. Longleaf pine ecosystems can experience yearly fires and still maintain high diversity (i.e. Carolina Gamelands).

Fire temperature and intensity increase with greater pine needle density, which is directly related to the total basal area and density of the longleaf pines in the community (Grace and Platt 1995). Oak and other woody species also contain flammable biomass, which leads to even more intense fires. High intensity fires have a greater probability of damaging longleaf juvenile pines and increasing their mortality, instead of creating more favorable conditions for these fire-adapted species to persist with lower intensity ground fires (Grace and Platt 1995).

Invasive species, such as cogongrass, changes fire behavior by increasing fire intensity. The resulting fire increases the mortality of longleaf pines and other native species (Lippincott 2000).

MANAGEMENT STRATEGIES

Management practices have also favored planting fast growing pines, such as loblolly or slash pine, for commercial harvesting, which neglects a diverse understory and natural disturbance patterns. These commercial pines are planted at higher densities than natural

longleaf pine stands, and with site preparation and altered fire regimes; the community structure becomes degraded (Hedman et. al. 2000).

Fire management in Georgia, Florida, and Alabama after 1880 maintained the populations of bobwhite quail (*Colinus virginianus*) and Red cockaded woodpeckers (*Dendrocopos borealis*), an endangered species, which ate seeds from forbs and legumes that are fire-maintained (Komarek 1974). For optimal hunting of quail, fire is needed to decrease the competition of shrubs and hardwoods in order to maintain the quails' habitat (Stoddard 1931). Annual and biennial burning sustains the high diversity of understory grasses, which decline when fires are less frequent (Vogl 1972).

Fire management

Reinstating a managed fire regime is optimal for pyrogenic communities, but the response of rare species occurring in the community should be considered so the new disturbance regime does not disrupt the life cycle of the species, and therefore allow it to mature and reproduce successfully (Kirkman et. al. 1998). Annual and biannual prescribed fires are able to maintain longleaf pine dominance in the overstory (Brockway and Lewis 1997).

The applied frequency of fire is a controversial topic, considering that herbs need at least three years for full recovery (Maliakal et. al. 2000) and wiregrass takes six years to reach maturity (Outcalt et. al. 1999); however 5 years without fire is sufficient to allow for invasion of sand pine woody midstory species. Fire frequency may be more important than season of fire for management purposes (Kirkman et. al. 2004).

Although frequent winter burning results in the park-like structure first recorded by European pioneers, annual summer burning in loblolly pine grassland communities is more

effective in top killing hardwood species. Winter burning, if ceased, will result in the regeneration of a woody midstory because hardwoods are able to resprout after fires (Waldrop et. al. 1992).

In xeric barrens of Virginia, fire allowed longleaf pine to gain dominance, while turkey oak declined in density, and the understory species richness doubled (Plocher 1999). The absence of fire in longleaf pine forests of south Alabama permitted oak species to increase in density in the midstory and dominate saplings (Kush and Meldahl 2000). Oaks, such as turkey oak, sand post oak, and bluejack oak, are not as fire tolerant as longleaf pine, and are more vulnerable to early growing season fires (Glitzenstein et. al. 1995). Fire suppression causes increases in woody shrubs, oaks, and species that are not well adapted to fire (Maliakal et. al. 2000). The increase in basal area of oak and other woody species increases the competition with *P. palustris* and the understory herbs, and therefore greatly affects the overall diversity of the area. Periodic burning impedes the development of a woody midstory, which is known to inhibit understory growth and increase fire intensity (Brockway and Lewis 1997).

Fire frequency may not directly affect understory richness, but it plays a substantial role in maintaining an open canopy and available light and soil resources, which indirectly affects the herbaceous understory richness (Beckage and Stout 2000). Fire also acts to reduce the litter layer, which impedes establishment, survivorship and growth of young longleaf pine seedlings (Grace and Platt 1995).

The presence and abundance of longleaf pine is correlated to the understory diversity of the forest. It directly affects the understory by decreasing the available light that reaches the forest floor with litter accumulation and leaf interference. Pine basal area is specifically

related to abundance of legume species due to light availability (Hains et. al. 1999).

Longleaf pine has significantly more herbaceous understory diversity and cover than loblolly or slash pine (Hedman et. al. 2000). It also has an indirect effect by providing flammable fuel to help spread natural fires. Fire suppression leads to a thick layer of litter covering the forest floor, which prevents longleaf pine from establishing because it impedes contact with mineral soil (Kush and Meldahl 2000).

Species of these pyrogenic communities have adapted to frequent fires by responding to fires with flowering or setting seed in order to reduce competition in early life stages (Walker and Peet 1983, Hiers et. al. 2000, Kirkman et. al. 1998). *S. americana* is a rare plant found in the coastal plain of the southeast within a longleaf pine overstory. It is fire adapted to flower after a fire so its life cycle is not interrupted by subsequent fires. A possible mechanism for fire-induced flowering of rare species could be the increase in soil nutrients, such as nitrogen, after the fire (Kirkman et. al. 1998). For fragmented populations of rare species, an alteration of the fire regime, or any natural disturbance pattern, that the species have adapted to, could detrimentally affect survivorship of the population and the species as a whole (Kirkman et. al. 1998).

Fire causes high mortality of small, young trees, and reduces the competition for light, water, and nutrients for large and intermediate size longleaf pines (Glitzenstein et. al. 1995). Fire also reduces woody shrubs, such as gallberry, which acts as an inhibitor of understory growth (Brockway and Lewis 1997). Although fire itself is a positive, stabilizing disturbance for this community, fire followed by high levels of grazing or other disturbances could destabilize native vegetation (Lesica and Cooper 1999).

Wiregrass plays an important role in flammable litter accumulation to help spread naturally occurring fires that favor pyrogenic species, such as longleaf pine (Outcalt et. al. 1999). Loss of wiregrass from these communities, due to fire suppression or any anthropogenic disturbance, could accelerate the loss of overall species diversity (Walters et. al. 1994). Lack of fire in sandhill ecosystems can reduce wiregrass cover from 40% to less than 2% (Brockway and Lewis 1997). Wiregrass accumulates fire fuels for frequent surface fires, which influences the natural fire regime, and therefore the composition of the community (Outcalt et. al. 1999). Bunchgrasses in general affect fire behavior and benefit from frequent burning by maintaining nutrient stores and apical meristems in belowground biomass and sustaining high resilience from fire (Brockway and Lewis 1997). The clumping nature of wiregrass distribution leads to patchy fire events (Lippincott 2000) and replacement of uniformly distributed grass species can change the pattern of fire, creating less diversity through uniform disturbance events. This alteration can be caused by invasive species or even possibly other native species of bunchgrass that outcompete wiregrass with changes in the disturbance regime.

Longleaf pine forests are reduced to fragmented remnants encroached by development, but Heuberger and Foster (2003) demonstrated that small suburban fires can serve the purpose of increasing species diversity, flowering, and reducing woody shrubs.

Invasive species

Anthropogenic disturbance of the community, including logging and fire suppression, is thought to have triggered the invasion of sand pine (*P. clausa*) into longleaf areas (McCay 2000, Provencher et. al. 2000). Sand pine suppresses ground cover vegetation by producing a denser, closed overstory than *P. palustris* (Provencher et. al. 2000).

Sand pine can outcompete longleaf pine through faster growth, earlier maturity, and greater dispersal ability. Longleaf pine needs a minimum of twenty years to reach a reproductive age, while sand pine can produce viable seeds in five years. Sand pine also disperses twice as far as longleaf pine with smaller seed size. Once sand pine has fully invaded an area, the canopy becomes more dense and patchy, as opposed to the relatively open canopy created by the dominance of longleaf pine (McCay 2000). This dense cover impedes light from reaching the forest floor, inhibits the growth of shade intolerant, fire tolerant species, and favors the growth of shrubs (McCay 2000).

Removal of sand pine requires mechanical extraction with fuel chipping or harvesting (Provencher et. al. 2000). This removal followed by prescribed burning and planting of longleaf pine are suggested to return invaded sandhill areas to their natural community, however continual periodic burning is necessary to ward off sand pine, and approximately 65 years of natural recovery is necessary to fully restore the sandhills to reference conditions (Provencher et. al. 2000). However, mechanical removal of sand pine disturbs the area enough to allow for other invasive species to enter, such as *Sapium sebiferum* (Chinese tallow tree) and *Melia azedarach* (China berry). Removal of these species would also be appropriate to restore the natural longleaf pine – wiregrass sandhill (Provencher et. al. 2000).

Nonindigenous grasses have also begun to invade longleaf pine sandhills in Florida, including the rhizomatous grass from southeast Asia, cogongrass. This invasive is significantly taller than native grasses, such as wiregrass, and contribute a greater fuel load to prescribed and natural fires, creating more intense fires. This continuous fuel load also creates uniform burns, as opposed to patchy fire patterns found with wiregrass-dominated sites (Lippincott 2000). These homogeneous fires could produce less diverse understories by

reducing gaps and microhabitats created by patchy disturbances. The increased intensity of cogongrass fueled fires can create higher longleaf pine mortality and damage. Cogongrass not only has the ability to compete directly for light, space, water, and nutrients, with wiregrass, and juvenile longleaf pines, increasing the mortality of those species (Lippincott 2000).

Restoration of wiregrass

Reestablishment of wiregrass to areas that have lost its understory due to fire suppression is critical to restoring the plant community (Outcalt et. al. 1999). It is very difficult to replant wiregrass due to its low seed viability of about 15% and high transplant mortality (40%) (Outcalt et. al. 1999). Use of nonlocal populations of wiregrass in restoration efforts could genetically contaminate native populations; therefore it is suggested to use local, neighboring populations of wiregrass in the restoration process (Walters et. al. 1994, Gordon and Rice 1998). Wiregrass does not flower or produce seed without a defoliation trigger, which is usually fire, but can be cutting or grazing (Parrott 1967). Burning regimes were found to be important to the survival of wiregrass seedlings in connection to season and frequency. Seedling mortality is higher post growing season burns than post dormant season burns after the first and second year after establishment (Mulligan and Kirkman 2002).

Because longleaf pine does not regenerate well, mainly due to specific establishment needs, such as weather and seasonal conditions (McCay 2000), planting of longleaf pine seedlings is also suggested to reestablish the longleaf pine dominant overstory.

SUMMARY

The diminishing stands of the longleaf were noticed as early as the mid 1800's, which was partly due to the process of harvesting turpentine. It was noted that "if not protected, this noble species will almost disappear from the great region" (Ruffin 1858). However, even by 1946 it was thought that "there is no immediate danger that the longleaf will vanish as a species" (Wahlenberg 1946).

The condensed longleaf area and presence of rare and indigenous species in these areas heightens the concern for conserving the remaining areas and restoring original longleaf areas from their current state. Fire is an integral part of the maintenance and restoration of longleaf pine forests. Humans have used fire in longleaf areas for thousands of years, possibly affecting the evolutionary trajectory of the species, and in order to continue this use, understanding the history of fire in the southeast and the physical effects on the species that reside in the area is necessary. The influence of understory species on community structure and fire behavior is largely overshadowed by the study of overstory species. Since longleaf pine forests rely on periodic ground fires to persist, understory plants that fuel these fires have a fundamental role in this ecosystem.

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