STRUCTURE AND COMPOSITION OF VEGETATION ON LONGLEAF PINE (*Pinus palustris*) PLANTATION SITES COMPARED TO NATURAL STANDS OCCURRING ALONG AN ENVIRONMENTAL GRADIENT AT THE SAVANNAH RIVER SITE

A Thesis

Presented to

the Graduate School of

Clemson University

In Partial Fulfillment

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Master of Science

Forest Resources

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by

Gregory Paul Smith

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Advisor: Dr. Victor B. Shelburne

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To the Graduate School:

This thesis entitled "Structure and Composition of Vegetation on Longleaf Pine (*Pinus palustris*) Plantation Sites Compared to Natural Stands Occurring Along an Environmental Gradient at the Savannah River Site" and written by Gregory Paul Smith is presented to the Graduate School of Clemson University. I recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science with a major in Forest Resources.

Victor B. Shelburne

Dr. Victor B. Shelburne
Thesis Advisor

We have reviewed this thesis
and recommend its acceptance:

David H. Van Lear

Dr. David H. Van Lear

Joan L. Walker

Dr. Joan L. Walker

Accepted for the Graduate School:

Lee Boggs

ABSTRACT

The decline of natural longleaf pine stands in the southeastern United States has been well documented. This decline is due in large part to several factors, mainly, European settlement, the turpentining industry, timber removal, expanding agriculture, development, and fire exclusion. Vast expanses of longleaf and slash pine plantation have replaced millions of acres of natural longleaf pine. Comparing the current vegetation patterns and relationships on disturbed plantation sites to natural, or relatively undisturbed, longleaf pine stands is a necessary component for the restoration of the longleaf pine ecosystem.

This study compared the structure and composition of vegetation, primarily the herb layer, of longleaf plantations sites to that of natural longleaf pine stands at the Savannah River Site, South Carolina. Fifty-four longleaf plantation plots were compared to thirty remnant plots occurring along a soil moisture gradient. Three distinct site units (xeric, sub-xeric, and sub-mesic) were identified for both groups of plots using ordination, cluster analysis, and discriminant function analysis. Plantations plots had an overall classification rate of 78% while the natural plot classification rate was 87%. The xeric site unit demonstrated the most similarity between both groups of plots in regard to vegetation composition and structure. The presence or absence of the B horizon was the most significant environmental variable discriminating among groups of plots for both plantations and natural stands.

Although overall species richness was significantly greater on natural plots (74.00 species per 0.1 hectare) compared to plantations (57.11 species per 0.1 hectare), roughly 90% of species found on plantation sites were judged to be representative of natural longleaf communities. This lack of a major compositional difference between xeric plantation and natural stands suggests that on xeric sites restorating the herbaceous layer of longleaf plantations may not be as complex as often thought.

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TABLE OF CONTENTS

Table of Contents (Continued)

Table of Contents (Continued)

List of Tables (Continued)

List of Tables (Continued)

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

THE LONGLEAF PINE ECOSYSTEM

Introduction

As the world population continues to increase and cause the loss of many natural landscapes, people have begun to realize the importance of our natural resources. In response to growing public demands in the 1970's and 1980's, management policy changed to put a stronger emphasis on environmental quality objectives. This evolution of forest management practices suggested an incremental approach toward holistic, ecological concepts (Fedkiw 1997). As a result, concepts such as "ecosystem management" and "ecosystem restoration" have become more important to professionals dealing in natural resources.

This is especially true with respect to the longleaf pine ecosystem of the South (Noss 1989). Longleaf pine forests can harbor more species of vascular plants than almost any other forest type in the United States (Peet and Allard 1993), and it is well known that fire played an important role in maintaining these diverse ecosystems (for examples, Christensen 1988, Haywood et al. 1997). Since European settlement, the turpentining industry, timber removal, expanding agriculture, development, and fire suppression have drastically reduced the acres of natural longleaf stands. Longleaf and other pine plantations now occupy much of the land that supported natural longleaf vegetation types.

There is a growing interest in the structure and composition of pine plantations and how they compare to natural longleaf stands. This information is needed to assess the potential for restoration and to develop protocols for restoration. Information about the distribution of longleaf pine communities along environmental gradients (e.g. Christensen 1988, Harcombe et al. 1993, Peet and Allard 1993, Jones et al. 1984) is available, but little has been published regarding the composition and structure of plantations relative to the same environmental gradients.

This study describes current vegetation patterns and relationships on disturbed plantation sites and compares them to natural, or relatively undisturbed, longleaf pine stands at the Savannah River Site. The sites sampled were mostly pine-dominant, upland sites. Keeping in mind that the ultimate management goal of these plantation sites is restoration to their "natural" state, an understanding of the historical/natural ecosystem conditions, current conditions, and processes that effected the changes is required (Walker and Boyer 1993).

Ecological Restoration of the Longleaf Pine Ecosystem

The decline of the longleaf pine ecosystem has been well documented. Longleaf pine once dominated as much as 92 million acres throughout the Southeastern United States (Frost 1993). This natural range covered most of the Atlantic and Gulf Coastal Plain regions, from southeastern Virginia to eastern Texas and south into the northern two-thirds of Florida, with extensions into the Piedmont and mountains of northern Alabama and northwest Georgia (Landers et al. 1995). Most recent estimates show that there may be as little as 3.2 million acres of natural longleaf pine left (USDA Forest Service, Forest Inventory and Analysis, unpubl. data). For this reason, there has been an increase in the efforts to sustain the natural longleaf stands that remain and to restore these ecosystems on a portion of the sites from which they have been extirpated (Mitchell et al. 1997).

Restoration ecology aims to reestablish or rehabilitate damaged or lost plant populations or species assemblages native to the area of interest (Bowles and Whelan 1994). Even with other studies of vegetation and soils of longleaf pine ecosystems (for example, Marks and Harcombe 1981, Pessin 1933, Gilliam et al. 1993), few studies have been on a large enough scale to accurately describe the variation in the structure of these ecosystems (Carter et al. 1997). The result of these deficiencies has been the slow progress of restoration and management of longleaf pine ecosystems. One of the major objectives of this project is to accurately describe the structure and composition of vegetation in both plantation and natural stands that are currently, or were once dominated by longleaf pine. The intent of this objective is to create a database that can be used to aid in the restoration of longleaf pine ecosystems across the southeastern United States.

The objectives of the study are as follows:

1. Describe the structure and composition of vegetation, primarily the herb layer, on disturbed longleaf plantation sites and natural longleaf stands occurring along a soil moisture gradient.

2. Using multivariate statistical analyses, classify communities from both plantations and natural stands that exist along the gradient.

3. Compare the species composition of plantation sites with that of undisturbed vegetation remnants of the Savannah River Site.

4. Suggest management options that will aid in the restoration of plantation sites.

CHAPTER II

LITERATURE REVIEW

Presettlement Conditions and Vegetation

There has been a considerable effort to describe presettlement vegetation in the Southeast. In this project, "historical/natural" and "presettlement" are terms that refer to ecosystem conditions and function prior to European exploitation (Walker and Boyer 1993). Walker and Boyer (1993) also mention that understanding natural/historical ecosystem conditions is one element needed to develop an effective restoration program.

Descriptions of presettlement forests can be deduced from (1) historical accounts by travelers, botanists, explorers, settlers, etc., and (2) assessments of current vegetation information with an eye for the presence of remnant indicator species, assessments of natural fire frequencies, etc. (Frost 1997). White (1997, manuscript in preparation) reviewed the historical accounts. The following are some of the early accounts of travelers who journeyed through the Savannah River Site and surrounding areas.

Many early accounts make reference to the abundance of burning grass in the pine understory. As Tobler traveled through this area, he noted in his 1737 diary (Cordle 1939; White 1997, unpubl.) that they:

> "found much burnt off grass...good for horses. In the afternoon the land became first mountainlike, which was gradually sloping upward, then again level. The land became more mountainlike and now and then very poor and sandy."

In 1805 Michaux (Clark 1973, Michaux 1805) described an area of the fall line sandhills that he encountered during his travels. In his journal he notes the extensive expanse of pine barrens that covered the land (White 1997, unpubl.).

> "Fifteen miles on this side of Winesborough the pine barrens begin, and thence to the sea side the country is one of continued forest composed of pines." He then went on to describe the "lowlands" as having "even and regular soil, formed by a blackish sand, rather deep in parts...Seven tenths of the country are covered with pines of longleaf pine, frequently spaced 20 feet apart - not damaged by annual spring fires, and are preferred to form fences for plantations."

Logan (1859) described the extensive cane breaks of the middle country in a description of the Upper Carolina country (White 1997, unpubl.). He referred to the pines as "unbroken lines of evergreen for hundreds of miles, from the alluvial country to the south." Another account from Tuomey (1848) observed that, "From Aiken to South Edisto the country sinks gently, but the ridge between the two rivers is elevated, and is an uninterrupted pine barren." Confirmation of this pine as longleaf was done by Mills (1925) (Frost 1997). These are just a few examples of the descriptions of what is now the Savannah River Site and surrounding areas.

Current vegetation information also provides valuable information about possible historic vegetative conditions at the SRS. However, the reliability of these assessments is directly related to the sampling of the most undisturbed, natural sites that can be found. Most communities have experienced some type of change in vegetation due to fire exclusion, reduction in fire frequency, or change in season of burn. Therefore, almost all of the natural stands are not identical to the originals (Frost 1997). Frost (1997) describes 12 different presettlement vegetation types and exemplary sites (Table 2.1) that were once found at the SRS. Of the 12 cover types, this project was conducted in the pine-dominated, upland sites. These cover types are described by Frost (1997) as (1) xeric longleaf pine and longleaf-turkey oak, (2) dry-mesic and mesic longleaf pine savanna, (3) longleaf pine-pyrophytic woodland complex, and (4) pyrophytic hardwood woodland.

Table 2.1. Presettlement vegetation types at the Savannah River Site.

Vegetation/Cover Type	Acres	Percent
1) Xeric longleaf pine and longleaf-turkey oak	7,551	3.8
2) Dry-mesic and mesic longleaf pine savanna	102,610	51.7
3) Longleaf pine-pyrophytic woodland complex	7,384	3.7
4) Pyrophytic hardwood woodland	19,865	10.0
5) Mixed mesic hardwood forest	6,883	3.5
6) Wetland pyromosaic--sandy or mucky soils[a]	18,485	9.3
7) Wetland pyromosaic--silty or clayey soils[b]	5,719	2.9
8) Bottomland hardwoods, levee forests, oak flats	5,278	2.7
9) Swamp forests and ponded sites other than Carolina bays	12,089	6.1
10) Carolina bays, upland depressions	1,938	1.0
11) Udorthents	7,241	3.6
12) Surface water	3,407	1.7

[a]Pocosin, canebrake, pond pine and loblolly pine forest, bottomland hardwood and baldcypress
[b]Bottomland hardwood, hardwood/canebrake, baldcypress , and *Nyssa biflora*

Land Use History

Land use history in the southeastern United States has significantly altered the landscape of South Carolina. In the longleaf pine ecosystem, land uses included 100 to 400 years of agriculture, open range grazing by hogs and other livestock, logging, naval stores industry, and the elimination of naturally occurring wildfires that have left less than three percent of the landscape as natural vegetation (Frost 1993). Even though most regard the "presettlement" era as being the time before European settlers arrived, a large portion of the longleaf pine region had already been domesticated by Native American Indians. The extent of Indian agriculture, however, has never been determined (Frost 1993). Even without knowing the full impact of Indian cultivation and burning, it is generally regarded as having caused minimal soil disturbance (Herndon 1967, Trimble 1974).

The earliest European settlers arrived in the 1730's and 1740's, first taking the best land along the river and gradually moving into the upland, longleaf pine dominated communities (Frost 1997). The use of agriculture spread rapidly and from the period of 1750-1850 almost all longleaf pine communities of more fertile soil were converted to farmland and pasture (Frost 1993). After the Civil War, the demand for cotton increased and a significant shift in settlement from the waterways to the upland sandhills occurred (Brooks and Crass 1991). Intensive land use followed as production of cotton and other crops, naval stores, fuelwood, timber, and the number of hogs increased. There was also an increase in "shifting agriculture" in the 19th and 20th centuries where "worn-out" land was abandoned for "new" land, with the abandoned land left to regenerate back to forest (White and Gaines 1997).

Silvicultural Practices at the Savannah River Site

The most natural form of site preparation at the SRS has been fire. Although fire has always been used as a site preparation technique, the frequency of fire has changed over the years. Fire will be discussed in more detail later in this report.

Prior to World War I, site preparation involved the use of mules and horses to plow fields for planting. After World War II, there was an increase in the use of tractors and surplus pasture lands were converted to cropland or succeeded to loblolly pine (Frost 1993). In 1951, according to the Savannah River Operations Office (1974), approximately 34 percent of the land at the SRS was in old fields, 15 percent in swamp and stream bottom, and 51 percent in mixed pine and scrub oak, with most pine as cutover second growth. This prompted the initial focus of the SRS to reforest abandoned farmland (White and Gaines 1997). Well into the 1970's, extensive replanting of slash, loblolly, and longleaf pine occurred on these sites using mechanical and chemical site preparation. Since the 1950's, the SRS has used V-blades on planters to make furrows for improvement of pine growth (White and Gaines 1997). Through the 1980's, shearing and raking were common site preparation techniques that were used but gave way to other less intensive methods such as drum chopping, chainsaw felling, and prescribed burning (White and Gaines 1997). During the 1990's, site preparation for pine stands has largely been burning and in the hardwood stands more mechanical site preparation has been used.

In a panel discussion at the Tall Timbers Fire Ecology Conference (Glitzenstein et al. 1993), Joan Walker, a plant ecologist for the U.S. Forest Service, stated in reference to silvicultural treatments on pine communities that, "The actual impact that these methods can have on plants varies not only with the site preparation method itself, but also with the characteristics of each plant species." The effects on the habitat in which these plant species survive must also be considered when dealing with site preparation techniques (Glitzenstein et al. 1993). Some habitats are more sensitive to site preparation than others.

Vegetation of the Savannah River Site

Factors that affect the variation in vegetation include soil properties, moisture availability, topography, and disturbance history (Rome 1988). Several multi-variate models have been developed for southeastern vegetation communities and have been used to better understand the complex associations of mostly natural ecosystems. What makes this study unique is that few models have been developed to describe current vegetation on disturbed plantation sites.

Christensen (1979) describes the ecosystems of the xeric sandhills and ridges as the longleaf pine-turkey oak forest. This forest type dominates sandy soils along the Atlantic Coastal Plain. Where there is increased moisture availability, due to changes in soil or topography, the xeric, sandhill vegetation grades into pine-dominated savannas and flatwoods (Christensen 1979). There is a difficult distinction, however, between these two locations due to the migration of sandhill dominants that can survive in more mesic conditions. It is also important to recognize that many of these upper coastal plain flatwoods are frequently successional from cropland abandonment. These flatwoods are higher quality sites and were the first sites chosen for agriculture. Dominant pine species on these sites are *Pinus palustris, P. elliottii,* or *P. taeda.*

Table 2.2 describes several community site types of the Savannah River Site (Jones et al. 1984). There have been several other current vegetation classifications made at the

Table 2.2. Hardwood site types and successional site types associated with the Aiken Plateau on the Savannah River Site (Jones et al. 1984).

Site	Management/Successional Type	Hardwood Site Type
Xeric, thick upland sands	*P. palustris-Q. laevis-A. stricta* *P. palustris-Q. laevis-P. aquilinium*	*Q. laevis-G. dumosa*
Subxeric sands	*P. palustris-R. reneformis* *P. palustris-S. albidum* *P. palustris-N. sylvatica-C. pallida*	*Q. incana-C. pallida*
Upland flats	*P. taeda-P. serotina-L. japonica* *or* *P. elliottii-N. sylvatica* *P. elliottii-S. albidum-D. rotundifolium* *P. elliottii-P. serotina-Q. nigra*	*Q. marilandica-V.stamineum-A. virginicus*
Upland slopes	*P. echinata-P. taeda*-hardwood	*Q. alba-C. florida-C. maculata*
Well-drained alluvial terraces	*P. taeda-L. styraciflua-P. barbonia*	*L. styraciflua-A. rubrum-P. barbonia*

SRS by Jones et al. (1981), Workman and McLeod (1990), and Imm (1997). The SRS is included in the Southeastern Evergreen Forest Association as defined by Braun (1950). Within the six forest types of the association, this study deals with the pine and oak-pine forest communities supporting longleaf pine vegetation, particularly the herbaceous layer. These communities include *Pinus palustris* forests, *P. taeda* and pine-hardwood forests, and *P. elliottii* forests.

Soils of the Savannah River Site

Using Frost's treatment (1997) as a guide, it was determined that **xeric** sites are located on Lakeland, Blanton, and Troup soil series, **sub-xeric** sites on Troup, Lucy, Fuquay, Dothan, Neeces, and Wagram series, and **sub-mesic** sites on Ailey and Vaucluse series. Longleaf pine vegetation of the coastal plain varies tremendously with soil drainage from very xeric sandhill sites to the more floristically rich savannas and flatwoods of poorly drained soils (Mohr 1901, Harper 1914b, Wells 1932, Braun 1950, Wharton 1978, Christensen 1988). Because of this pattern, soil moisture is expected to be a critical factor controlling the composition of longleaf vegetation (Peet and Allard 1993).

The Use of Fire on the Savannah River Site

Another factor involved in this study is the frequency and effect of fire on the areas to be sampled. Presettlement forests were frequently burned by lightning, Native Americans and European settlers (Frost 1993). Fires occurred across the landscape of the coastal plain as often as every one to three years, and only about five percent of the landscape was completely protected from fire (Frost 1995). The majority of these fires during this period occurred most likely during the growing season, when the chance of ignition by lightning strikes is greatest (Streng et al. 1993). When investigating presettlement vegetation conditions, however, fire frequency will be of great importance because only the longleaf ecosystem that has been fire-maintained and has had continued chronic fire exposure will resemble the natural longleaf system of the southeast (Peet and Allard 1993). Waldrop et al. (1992) also found in their study of fire regimes for pine-grassland communities that frequent burning over a long period is needed to re-create and maintain the pine-grassland community that was once observed by the first European settlers.

In the absence of frequent burning, the diverse, herbaceous-dominated, ground cover vegetation is rapidly displaced by hardwood trees and shrubs (Streng et al. 1993). Conversely, ground cover vegetation containing large numbers of flowering plants typically is present in habitats in which fires occur frequently (Platt et al. 1988). The understory in these forests is made up of prairie vegetation along with many deciduous shrubs and trees that are kept in a very low suckering stage by reoccurring fires (Kozlowski and Ahlgren 1974).

CHAPTER III

METHODS AND DATA ANALYSIS

Study Area

The Savannah River Site is a 192,323-acre circular tract of federal land that occupies parts of Aiken, Barnwell, and Allendale Counties, South Carolina (Cooke 1936). It is located northeast of the Savannah River on the upper Atlantic Coastal Plain of South Carolina (Figure 3.1). The Savannah River Site (SRS) has three major geologic/ physiographic regions. These regions are the sandier, excessively drained and droughty areas called the **Sandhills Region**, the more productive sandy loams and loamy soils of the **Upper Loam Hills Region**, and the more fertile, well-drained soils of the **Red Hills Region** (Myers et al. 1986). The SRS is drained by five major stream drainages which include Upper Three Runs, Four Mile Creek, Penn Branch, Steel Creek, and Lower Three Runs (Jones et al. 1981).

Vegetation at the SRS is distributed across a moisture gradient extending from xeric, droughty, deep sandy ridges to hydric, flooded marshes and swamps (Van Lear and Jones 1987). Present vegetation at the SRS largely reflects past disturbance or manipulation by man (Jones et al. 1981). These disturbed sites are old fields that were the result of intensive agriculture and subsequently replanted with pine, less intensive agricultural sites that were left to regenerate naturally, cutover forests that have had a continuous forest cover of scrub oak/pine, and areas where the natural fire regime has been altered or suppressed.

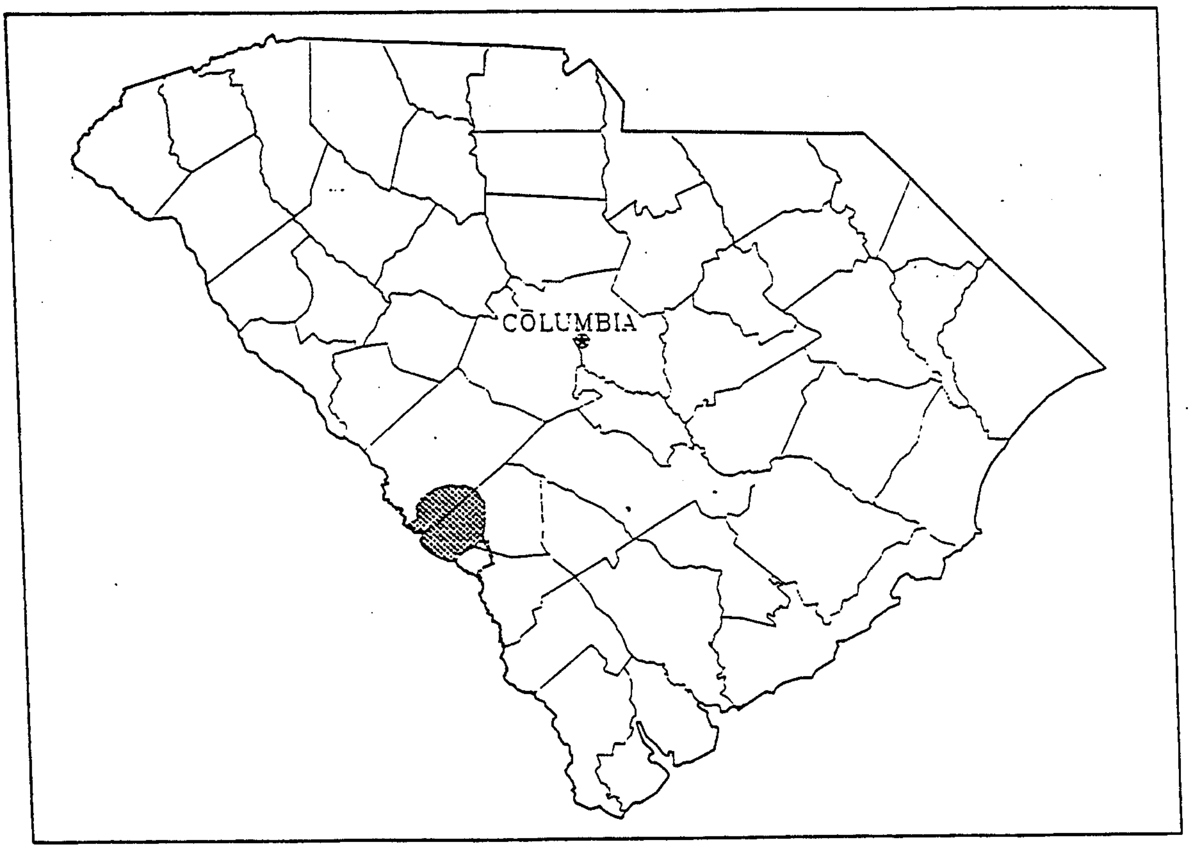

Figure 3.1. Location map of the Savannah River Site, New Ellenton, South Carolina.

Mean annual precipitation in the study area averages about 45 inches. Mean annual temperature is about 63°F and ranges from a mean annual maximum of 75°F to a mean annual minimum of 51°F. The growing season is roughly 261 days a year (USDA Soil Conservation Service 1990).

Methods

Site Selection

Plantation sites were located at the SRS by using a predetermined set of criteria that each site was required to meet. The following criteria were used to identify 54 plantation sites located at the SRS. Sites must have been (1) dominated by longleaf or slash pine only, (2) planted between 1955 and 1965, (3) located on one of three different soil moisture classes, and (4) burned at least once within the past five years. This method of site selection was accomplished through the use of Geographical Information System (GIS) ARC/INFO software from the Savannah River Forest Service-GIS laboratory. Due to the stringent criteria set for selection of plantation sites, slash pine plantations originally dominated by longleaf pine were incorporated into this study to increase the sampling area. I expect ground vegetation to be consistent between slash pine and longleaf plantations because prior history and site preparation methods were similar.

I sampled disturbed pine plantation sites at the SRS that are in the 33-43 year-old age class. I chose this age class based on current data from White and Gaines (1997) that shows the greatest proportion of longleaf pine was planted or seeded at the SRS between 1955 and 1965. Sampling 33-43 year-old stands that have been exposed to similar fire regimes, site preparation techniques, and disturbance history provides consistent sampling across the environmental gradient. When we unable to find a sufficient number of 33-43 year-old stands, some variation in stand age was necessary.

Site preparation techniques used on the study sites are one of the variables that were considered investigated during this project. It was important to choose plantation sites that have been exposed to similar site preparation in order to retain some homogeneity.

Natural longleaf pine stands were located at the SRS using a variety of methods. First, candidate stands were identified in an ongoing inventory by Cecil Frost, Plant Ecologist, North Carolina Department of Agriculture, under an ongoing contract. Additional plots were located using information from local botanists, ecologists, United States Forest Service personnel, GIS software, satellite imagery, digitized maps linked to databases, and reconnaissance work in the field to locate other suitable natural stands. Thirty (30) stands supporting natural longleaf pine vegetation were located and sampled. Natural longleaf vegetation was determined largely from observations from the investigator. Criteria used to help determine natural vegetation included, but was not limited to (1) observations of vegetation structure, by layer, under known fire regimes, (2) presence of remnant fire frequency indicator species, (3) presence of remnant fire frequency indicator communities, and (4) known historical records of remnant or natural areas (Frost 1997).

The oldest, most undisturbed natural stands at the SRS were sampled. Natural stands at the SRS can be described as stands that are typically 85 years old or greater and have little or no sign of disturbance. Many of these natural stands at the SRS are second-growth longleaf pine that have had little disturbance due to harvesting. There was some age variation accepted due to the scarcity of natural stands at the SRS. These stands generally ranged from 65 to 85 years and usually had remnant longleaf scattered throughout the stand.

Field Sampling

The sampling methods of the North Carolina Vegetation Survey (NCVS) were used (Peet et al. 1998). The methods used are described in the following sections.

Site Characteristics

While sampling, sites were characterized as accurately and in as much detail as possible. This included referencing plot configuration (and methods used), providing map location data, providing data necessary to direct researchers to the site, and characterizing the physical environment of the site, vegetation, and disturbance history (Peet et al. 1998). Site characteristics were grouped into the several categories including general information, plot configuration, plot documentation, map location, relocation instructions, vegetative characteristics, site physical characteristics, and soils. These categories are discussed in more detail in the sampling methodology.

Plot Configuration

Plot size for most NCVS plots was 20 x 50 meters (1000m^2 or 0.1 ha) (Figure 3.2). An alternative configuration of 20 x 20 meter (400m^2) plots was used for sampling several of the natural longleaf stands. This alternative plot size was necessary due to the relatively small patches of natural longleaf pine scattered throughout the Savannah River Site. Using a smaller plot size (400m^2) was the only method available to ensure

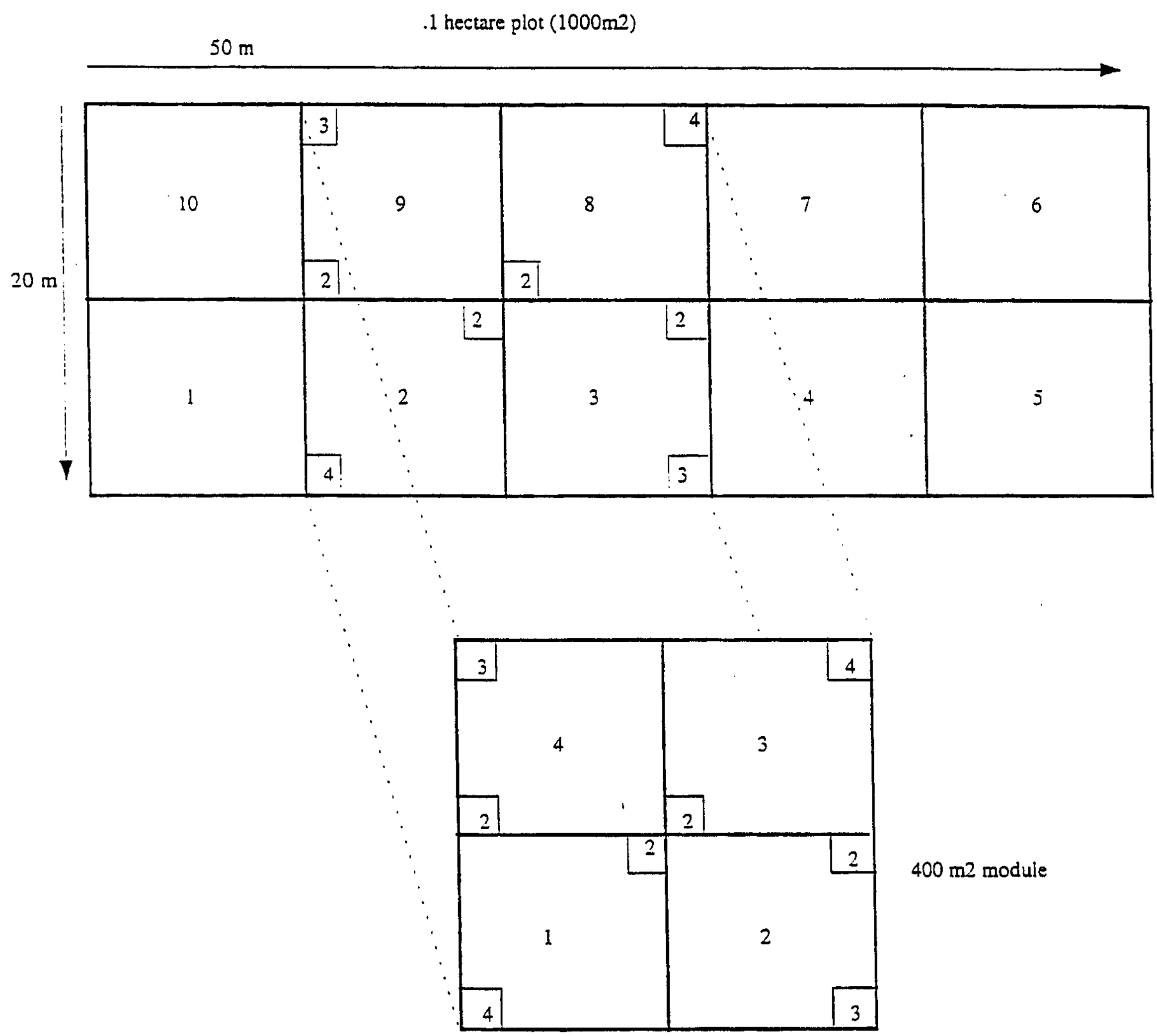

Figure 3.2. Plot design for North Carolina Vegetation Survey plots.

homogenous sampling of natural vegetation. This alternative plot size (400m^2) is within the size range recommended by Mueller-Dombois and Ellenberg (1974) for sampling forest vegetation. The widespread use of these NCVS plots in a variety of forested vegetation types and the consequent availability of substantial comparative vegetation data at this scale led to the adoption of these plot sizes.

The NCVS uses the module concept within these plots. Within each 0.1 ha (1000 m^2) plot, there was a 2 x 5 array of 10 x 10m modules (100 m^2 or 0.01 ha). Within this 2 x 5 array of modules, there was a prescribed block of four focal modules (in a 2 x 2 array). The four focal modules were intensively sampled. An aggregate count of woody stems was made in the remaining six modules, and this area (600 m^2) was searched for species not encountered in the four focal modules measured previously. In the alternative configuration of 400m^2 plots, all four modules was treated as focal modules and intensively sampled according to NCVS methodology. For complete instruction on plot configuration, refer to the North Carolina Vegetation Survey (Peet et al 1998).

Marking Sites

Once a suitable site was found, sampling proceeded as follows. The long axis (50 m) of the plot was positioned to encounter the least amount of variation in vegetation. This minimizes the heterogeneity of the vegetation and environment. A 50 m tape was used to establish the plot midline. Rebar was placed at each end of the midline and at 10 m intervals along the tape. The plot was completed by placing two 20 m tapes at 90 degree angles to the midline tape. The midpoint of one 20 m tape is located 10 m from the starting point of the 50 m (midline) tape, the midpoint of the other is at 30 m (Peet et al. 1998).

Presence and Cover Data

Presence is the occurrence of a species (based on emergence of a stem or stems) within an area of a given size and location. The species must be rooted in the module. Presence is a vegetation parameter compatible across all plant growth forms that can be used for many analytical procedures (ordination and classification). Presence/absence data taken from the nested plots in the NCVS provide fundamental data for characterization of community composition and structure, species richness, diversity and species/area relationships (Peet et al. 1998).

Cover is defined as the percentage of ground surface obscured by the vertical projection of all aboveground parts of a given species onto that surface. Percentage cover provides an index of a species' potential contribution to community production. In the NCVS protocol, cover is the only quantitative vegetative parameter compatible across all plant growth forms. Percent cover was estimated visually by the researcher during this study. The cover classes and percentage cover ranges that will be used in this study are: 1=trace, 2=0-1%, 3=1-2%, 4=2-5%, 5=5-10%, 6=10-25%, 7=25-50%, 8=50-75%, 9=75-95%, 10>95% (Peet et al. 1998).

Tree Stem Data

By using tree stem data collected by the NCVS method, I calculated stem basal area and density. These measures were used in various quantitative analyses, and I was able to compare them to already existing information. Tree stem tallies are simply the numbers of stems in the following diameter classes in centimeters: 0-1, 1-2.5, 2.5-5, 5-10, 10-15, 15-20, 20-25, 25-30, 30-35, and 35-40 cm. Trees in excess of 40 cm were tallied separately to the nearest cm. The area surveyed for stem count may be a specified percentage of the modules, such as 20% subsample for a dense area or a 300% subsample (sampling outside the boundary of the fixed plot) for a sparse area to get a more accurate estimate.

Collecting Site Characterization Data

General plot information was recorded first, followed by location data, completed plot map, completed plot documentation, site characterization data and notes on frequency/severity of disturbance, community structure, and any other special features of the plot.

Soil samples for chemical analysis were collected in the center of each of the four focal modules and numbered accordingly. NCVS procedure is to collect a core of mineral soil to a depth of 10 cm for chemical analysis. 250-500 g of soil per sample were collected. Soil samples for textural analysis were collected in the middle of the plot along the midline. A sample of the A and B or C horizon was collected and depth to maximum clay and depth of litter layer recorded. The soil series and a description of the soil profile were also recorded on the cover sheet. Soil samples were analyzed by Brookside Labs (308 S. Main St., Knoxville, OH 45781).

Environmental variables describing the topography of the plot were also measured and recorded. Landform index (LFI), terrain shape index (TSI), and aspect were measured and used to determine the exposure, micro-relief, and general "lay of the land."

Analytical Procedures

SAS

Vegetation data were prepared and summarized by a series of SAS-based computer programs (Peet et al. 1997). These programs were used to check for errors in raw herb and tree files and to compare plot data codes to the master species file for errors. A series of SAS data manipulation programs were then employed to calculate the mean species richness of each plot at the five depth levels (nested subplots) and to calculate sapling, tree and total density (# per hectare) and basal area (m^2 per hectare).

Ordination and Classification

A series of multivariate techniques was used for analysis of data. Detrended Correspondence Analysis (DCA) (DECORANA, Hill 1979a), which ordinates species and samples simultaneously, was the method of ordination used to analyze vegetation data (McCune and Mefford 1999). DCA or DECORANA© was used to analyze species abundance by organizing and displaying data in multidimensional space (Hill 1979a). The distance between groups relate the relative degree of similarity or difference (Hutto et al. 1997).

Due to the relative homogeneity of plots within each respective group (plantation or natural), I used percent cover as the importance value of species in ordination. A species with a high importance value may be considered of a higher ecological importance and/or dominant vegetative component.

I also compared the structure and composition of vegetation on plantation sites to that of natural sites using ordination and classification to determine the degree of similarity or difference between the two types. Species presence/absence was used in the ordination. I chose to use presence/absence over cover values due to variation in species abundance levels between plantations and natural sites. The variation in species abundance levels between the two types can be attributed to a number of factors such as age, burn history, land use history, and differences in physical and environmental variables. By using presence/absence, all species present on a plot are recorded a value of one (1) and species absent are recorded a value of zero (0). This method of ordination and classification makes all species equal and does not weigh more heavily for species higher abundance levels.

Cluster analysis of vegetation was performed by Two Way Indicator Species Analysis (TWINSPAN, Hill 1979b). TWINSPAN© is a polythetic diverse classification that simultaneously classifies both species and plots using the main matrix for vegetation data (McCune and Mefford 1999). This is a subjective classification, and allows the investigator to draw a separation between the groups in the initial ordination of plots (Hutto et al. 1997). TWINSPAN was used in conjunction with DCA to reduce this subjectivity while delineating groups of similar plots. TWINSPAN was also used to identify indicator or diagnostic species that were strongly correlated to a certain community association.

Discriminant Analysis

Stepwise discriminant analysis and discriminant analysis (SAS 1985) techniques were used to classify stands into groups (or populations) on the basis of a set of environmental variables (Afifi and Clark 1990). Soil and landform variables were used in the analysis. The soil variables used in the analysis were presence/absence of B horizon (BHOR), percent clay in A horizon (CLAA), percent sand in A horizon (SNDA), percent clay in respective horizon (CLA), percent sand in respective horizon (SND), soil pH (PH), percent organic matter (OM), nitrogen release (N), calcium (Ca), magnesium (Mg), potassium (K), and sodium (Na). Landform variables used in the analysis were transformed aspect (TASP), landform index (LFI), and terrain shape index (TSI). Stepwise discriminant analysis was used to determine which of these variables were significant at the 0.15 level of significance for plantations and at the 0.20 level of significance for natural sites. Significant variables can best describe the groups identified using ordination/classification.

Discriminant analysis was then used to accurately predict site unit membership using the discriminating environmental variables that were identified for both plantation and natural stands. The best classification is accomplished by developing a discriminant function for each group, and the highest resulting score is indicative of site unit membership. The resubstitution model is not the best classification model to use, mainly because resubstitution underestimates the true probabilities of misclassification by using the same sample to derive the discriminant function, thereby producing biased estimates (Afifi and Clark 1990). The cross-validation model for classification derives the discriminant function from one sample and applies it to another to estimate the proportion misclassified. This method provides the most accurate model of classification by producing unbiased estimates.

Analyses of Variance

To describe the structure and composition of vegetation on longleaf plantations and natural stands at the Savannah River Site plot data I used ANOVA (SAS 1985). Groups of similar plots were established through ordination and cluster analysis. The groups within each treatment (plantation or natural) were then subjected to analysis of variance (ANOVA). ANOVA (SAS 1995) was used to test the significance of environmental and physical variables at the $\alpha = 0.05$ level of significance using Tukey's Studentized Range (HSD) Test. Variables tested were species richness (# per plot), landform and terrain shape indices (%), basal area pine and hardwood (m^2 per hectare), density of pine and hardwood (# per hectare), percent clay and percent sand in their respective horizons, soil pH, percent organic matter (humus), nitrogen release, calcium, magnesium, potassium, and sodium (kg per hectare). Transformed soil physical variables were tested to ensure no violations of ANOVA assumptions were committed.

Tests of Significance

Standardized t-tests (SAS 1995) at the $\alpha = 0.05$ level of significance were used to test for significant differences between plantations and natural stands. Mean environmental and physical variables as well as species abundances were tested for significant differences between plantation and natural sites occurring on similar soil moistures. Mean species richness (# per plot), basal area of pine and hardwood (m^2 per hectare), density of pine and hardwood (# stems per hectare), percent sand and clay in the respective horizons (%), soil pH, organic matter (%), and level of nitrogen, calcium, magnesium, potassium, and sodium (kg per hectare) in the soil were tested.

To describe differences in the composition and structure of vegetation between plantation and natural sites at the Savannah River Site, comparisons were made of mean abundance values of similar plant species occurring on both plantation and natural sites. These differences between were determined by separating plots into one of three soil moisture classes (MC1-3: Table 3.1), taking the overall mean abundance value of each similar species in that moisture class, and testing for significant differences at $\alpha = 0.10$ level of significance. Species abundance (based on cover class) was determined by calculating the mean species abundance (or cover) in each plot, summing the means of each species for each plot in the appropriate moisture class, and dividing by the total number of plots in that moisture class. This provides the overall mean species abundance in each moisture class for both plantation and natural sites.

Table 3.1. Soil moisture classes used to determine plot membership for species abundance comparison.

Moisture Class	**Percent Sand (%)**	**Percent Clay (%)**
MC 1	≥85	≤10
MC 2	0	0
MC 3	≤64	≥24

CHAPTER IV

RESULTS

Interpretation of DECORANA and TWINSPAN Results

Several ordinations were made to determine the best grouping of ecological site units based on vegetation and environmental data. There is always some subjectivity in the interpretation of the ordination results (particularly plantations); few vegetation data sets ever exhibit a multivariate normal distribution (Causton 1988). I interpreted discrepancies among DCA and TWINSPAN outputs based on my knowledge of plot data. Also, original physiographic groupings from DCA and TWINSPAN were redefined following discriminant analysis of the data.

Analysis of Plantation Sites

Ordination and Cluster Analysis

The primary data matrix for plantation sites consisted of 54 plots and 265 species. Ordination arranged these plots along an axis that represented soil moisture gradient (axis 1) that showed a beta diversity of 3.5 standard deviations (Figure 4.1). Based on ordination and cluster analysis, I separated these plots into three groups. Plots near the origin of the graph exist on the extreme xeric end of the soil moisture gradient, while plots near the end of the graph exist on the more mesic end of the gradient. Groups were labeled I, II, and III, with I on the mesic and III on the xeric end of the gradient. There was also some variation among plots on the xeric end of Axis 2. The source of this variation has not been determined, and is most likely the result of some disturbance due to previous land use. Axis 2 showed a beta diversity of 2.5 standard deviations.

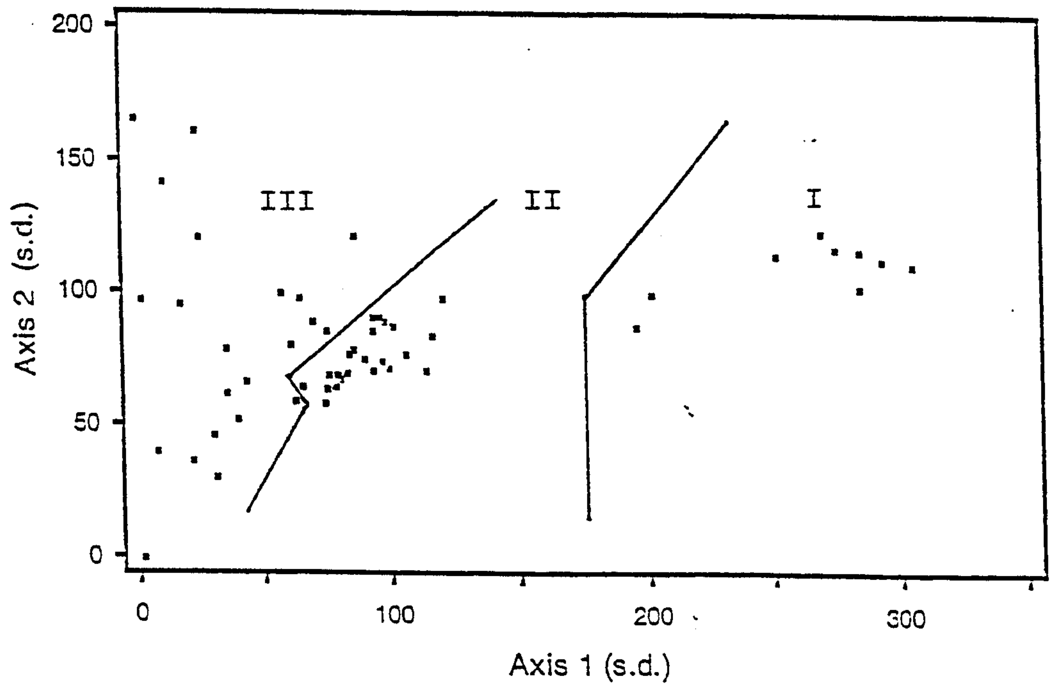

Figure 4.1. Ordination of 54 plantation plots using full importance values.

Elimination of Outliers

Several outliers were detected in the initial ordination of plantations. Outliers can be defined as deviant stands that are of unusual species composition or other observation that appears to be inconsistent with the remainder of the data set (Afifi and Clark 1990, Barnett and Lewis 1984, Causton 1988). An outlier can have a profound effect on data and cause severe distortions in the ordination. Hill and Gauch (1980) noted that the most persistent difficulties with DCA are in coping with outliers and discontinuities in the data. They also state that the only way to deal with extreme outliers is to remove them. After careful examination of DCA and TWINSPAN results and plot data, I determined that three plots were outliers. These plots were removed and ordination was performed on the resulting data set.

Discriminant Analysis

Of the fifteen environmental variables used in stepwise discriminant analysis, three significant variables were found at the 0.15 level of significance for plantations (Table 4.1). These variables were (1) presence/absence of B horizon, (2) soil pH, and (3) percent sand in B or C horizon.

Discriminant function analysis determined the classification success rate for each ecological site unit or group. The coefficients for the discriminant linear function can be found in Table 4.2. The resubstitution success rate was 81% (Table 4.3) and misclassified a total of eight plots. The cross-validation success rate was 78% (Table 4.4) and misclassified nine plots. The cross-validation function represents the best classification model that could be created by producing unbiased estimates (Causton 1988).

Table 4.1. Significant environmental variables identified by stepwise discriminant analysis (SAS 1995).

Variable	Partial R^2	F value	Prob. > F	Wilks' Lambda	Prob. < Lambda
BHOR[a]	1.0000	______[d]	0.0001	0.0000	0.0001
PH[b]	0.1459	8.713	0.0048	0.0000	0.0001
SND[c]	0.0743	4.015	0.0505	0.0000	0.0001

[a]presence or absence of B horizon
[b]soil pH
[c]percent sand in A or B horizon
[d]variance could not be calculated

Table 4.2. Coefficients of the linear discriminant function for plantation groups I, II, and III.

Coefficient	I Sub-mesic	II Sub-xeric	III Xeric
Constant	-322588064	-322588101	-380.82618
BHOR[a]	645175516	645175516	0
SND[c]	1.55810	1.65698	1.95136
PH[b]	115.37838	122.04025	125.01124

[a]presence or absence of B horizon
[b]soil pH
[c]percent sand in A or B horizon

Table 4.3. Classification success rate of discriminant analysis using resubstitution for plantation groups I, II, and III.

Group	I Sub-mesic	II Sub-xeric	III Xeric	Total
I	6 **66.67**	3 33.33	0 0.00	9 100.00
II	5 22.73	17 **77.27**	0 0.00	22 100.00
III	0 0.00	0 0.00	23 **100.00**	23 100.00
Total	11 20.37	20 37.04	23 42.59	54 100.00

Overall classification rate = **81%**

Table 4.4. Classification success rate of discriminant analysis using cross-validation for plantation groups I, II, and III.

Group	I Sub-mesic	II Sub-xeric	III Xeric	Total
I	5 **55.56**	4 44.44	0 0.00	9 100.00
II	5 22.73	17 **77.27**	0 0.00	22 100.00
III	0 0.00	0 0.00	23 **100.00**	23 100.00
Total	10 18.52	21 38.89	23 42.59	54 100.00

Overall classification rate = **78%**

Vegetative Structure

Structurally, the only variable significantly different among all three groups was basal area of pine (Table 4.5). Group I had the highest pine basal area and averaged 29.65 m^2 per hectare while group III had the lowest and averaged 18.98 m^2 per hectare. Mean basal area and density of hardwood stems were significantly higher for group III (2.79 m^2/ha and 1983 stems/ha) than for groups I (0.82 m^2/ha and 536 stems/ha) and II (0.38 m^2/ha and 240 stems/ha). Pine density for group I averaged 1288 stems per hectare and was found to be significantly higher than group II with 512 stems and group III with 850 stems per hectare. There were no significant differences in species richness among the three groups. Mean species richness ranged from a low 53.44 species per plot for group I to a high of 60.73 species per plot for group III.

Landform

Landform and terrain shape had very little effect on community association on plantation sites. The upland plantation sites had very little change in topography and were relatively flat. There were no significant differences found among any of the plantation groups using these variables (Table 4.6).

Soil Physical and Chemical Properties

With respect to soil physical variables, there were no differences in mean percent sand or clay in the A horizon among the three groups (Table 4.7). There were, however, significant differences in percent sand and clay in the C horizon of group III and the B horizons of groups I and II. Group III soils averaged 92.48 percent sand and 5.11 percent clay in the C horizon. Comparatively, groups I and II average percent sand were 65.00

Table 4.5. Mean values of structural variables of plantation groups for the Savannah River Site. Means in each row with different letter indicate significant difference at $\alpha = 0.05$. Mean values presented as ±SE (standard error).

Variable	I Sub-mesic (n=9)	II Sub-xeric (n=22)	III Xeric (n=23)
Species Richness (# per plot)	53.44a±4.18	60.73a±2.79	55.09a±2.83
Basal area pine (m^2 per ha)	29.65a±2.25	24.50b±0.66	18.98c±1.48
Basal area hardwood (m^2 per ha)	0.82b±0.14	0.38b±0.11	2.79a±0.47
Density pine (# stems per ha)	1287.80a±190.00	511.30b±54.81	849.60b±87.77
Density hardwood (# stems per ha)	535.60b±122.36	240.00b±44.63	1982.80a±405.04

Table 4.6. Mean values of environmental variables of plantation groups for the Savannah River Site. Means in each row with same letter indicate insignificant difference at $\alpha = 0.05$. Mean values represented as ± SE (standard error).

Environmental variable	I Sub-mesic (n=9)	II Sub-xeric (n=22)	III Xeric (n=23)
Landform index	0.16a±0.029	0.15a±0.008	0.16a±0.008
Terrain shape index	0.010a±0.002	0.023a±0.007	0.016a±0.003

Table 4.7. Mean A, B, and C horizon soil physical property values of plantation groups for the Savannah River Site. Means in each row with different letter indicate significant difference at $\alpha = 0.05$. Mean values are presented as ± SE (standard error).

Soil physical variable	**I Sub-mesic (n=9)**	**II Sub-xeric (n=22)**	**III Xeric (n=23)**
A horizon sand (%)	90.11a±0.77	88.95a±0.68	92.04a±1.39
A horizon clay (%)	5.04a±1.05	3.84a±0.33	3.40a±0.33
B horizon sand (%)	65.00b±4.45	69.50b±2.46	______[1]
B horizon clay (%)	27.86a±4.77	23.24a±2.16	______[1]
C horizon sand (%)	______[2]	______[2]	92.48a±0.33
C horizon clay (%)	______[2]	______[2]	5.11b±0.36

[1] B horizon absent from soil
[2] C horizon absent from soil

and 69.50, and percent clay were 27.86 and 23.24, respectively. This difference can be attributed to the typic quartzipsamment soils of group III. These soils generally have a very thin A horizon and a sandy C horizon greater than 200 cm thick, thus forming a very thick sandy epipedon. By definition, these soils have no B horizon. This is supported by similar work from Jones (1991) which indicates that the most discriminating physical soil variable within the uplands landform association of this region is the thickness of the sandy epipedon, or uppermost soil horizons.

Soil chemical variables varied little among the three groups (Table 4.8). Group I had a significantly lower mean pH (4.42) than group II (4.68) and III (4.65). The acidic nature of Group I soils is typical of more mesic sites. The only other significant difference found was potassium, in which group III averaged 21.29 kg per hectare in the soil, significantly lower than group I (30.18) and group II (29.52). Coarse grained soils have been found to lose potassium quickly by leaching.

Ecological Groupings of Plantation Sites

TWINSPAN was used to find indicator species for each group of plantation sites identified (Table 4.9). Generally, an indicator species is a species of narrow ecological amplitude with respect to one or more environmental factors (Allaby 1994). For this study, indicator species are defined more loosely as the most characteristic community members and include species typical of and vigorous in a particular environment. Good indicator species for group I sites included *Pinus elliottii*, *Pinus taeda*, and *Chimaphila maculata*. Indicators of group II sites included *Dichanthelium commutatum*, *Desmodium vridiflorum*, and *Centrosema virginianum*. *Quercus laevis*, *Quercus incana*, and *Bonamia patens* proved to be good indicators of group III sites.

Table 4.8. Mean soil chemical values of plantation groups for the Savannah River Site. Means in each row with different letter indicate significant difference at α=0.05. Mean values are expressed as ± SE (standard error).

Soil chemical variable	**I Sub-mesic (n=9)**	**II Sub-xeric (n=22)**	**III Xeric (n=23)**
PH	4.42b±0.11	4.68a±0.05	4.65a±0.03
Organic matter (%)	1.18a±0.15	1.14a±0.07	1.11a±0.06
Nitrogen (kg/ha)	46.44a±3.79	46.76a±1.73	44.99a±1.60
Calcium (kg/ha	316.49a±28.20	289.74a±26.67	240.72a±13.55
Magnesium (kg/ha)	54.50a±2.63	54.64a±2.92	45.93a±0.88
Potassium (kg/ha)	30.18a±2.76	30.19a±2.05	21.30a±0.99
Sodium (kg/ha)	18.81a±0.89	21.45a±1.44	17.61a±0.43

Table 4.9. Constancy and average importance values (constancy:importance value) of diagnostic species of the three ecological groupings for plantation sites at the Savannah River Site.

Species	**Group I (Sub-mesic)**	**Group II (Sub-xeric)**	**Group III (Xeric)**
Pinus elliottii	100:40.83		
Desmodium laevigatum	77:0.33		
Quercus falcata	67:0.47		
Pinus taeda	100:2.3	77:1.71	
Chimaphila maculata	100:0.36	64:0.33	
Gelsemium sempervirens	100:1.34	45:0.38	
Dichanthelium commutatum		64:0.39	
Dichanthelium acuminatum		59:0.28	
Centrosema virginianum		77:0.20	
Desmodium vridiflorum		68:0.17	
Desmodium ciliata		64:0.26	
Dichanthelium aciculare		68:0.42	91:0.40
Silphium compositum			57:0.29
Cnidoscolus stimulosus			70:0.30
Eriogonum tomentosum			74:0.41
Gaylussacia dumosa			74:2.71
Euphorbia ipecacuanhae			78:0.30
Bonamia patens			96:0.45
Quercus incana			96:1.82
Quercus laevis			96:8.30

Community Characteristics of Plantation Groups

Group I-- Nine plots were identified as group I. This was the smallest of the three groups identified. Group I sites averaged 27.86 percent clay in the B horizon. Mean percent sand in the B horizon was 65.00. Soils were well-drained and ranged from arenic plinthic paleudults to arenic paleudults. Based on soil moisture and vegetation, I classified group I as sub-mesic. These sites are generally considered to be the most mesic of all the plantation sites sampled.

Pine basal area averaged 29.65 m^2 per hectare. Pine stem density averaged 1287 stems per hectare. Being the most mesic sites sampled, it was a little surprising to find the mean species richness only 53.44 species per hectare, relatively low compared to the other two groups. The high basal area and density of pine stems may be a strong contributor to the low species richness by shading out some of the shade intolerant species, particularly sun-loving herbaceous species. Mean landform index was 0.16. Mean terrain shape index was 0.010.

Group I sites had a canopy dominated by *Pinus elliottii* with *P. taeda* and *P. palustris* common associates. Common sub-canopy and mid-story species included *Diospyros virginiana*, *Prunus serotina*, *Sassafras albidum*, *Quercus nigra*, *Q. margaretta*, and *Q. marilandica*. The shrubby layer was dominated by *Rhus copallina*, *R. toxicodendron*, *Vaccinium stamineum*, and *V. arboreum*. There was a heavy vine layer composed mostly of *Gelsemium sempervirens*, *Vitis rotundifolia*, *Smilax glauca*, and *S. bona-nox*. The most common herbaceous species found were *Desmodium lineatum*, *D. laevigatum*, *Chimaphila maculata*, *Solidago odora*, *Tragia urens*, and *Eupatorium compositifolium*. Common grasses found were *Andropogon virginicus*, *Gymnopogon brevifolius*, and *Panicum anceps*.

Group II-- Twenty-two plots were identified as group II. These sites occupied a wide range of soil moistures from somewhat excessively drained, grossarenic paleudults, to well-drained, typic hapludults. Due to soil moisture and vegetation, these sites were classified as sub-xeric. Soil physical variables were fairly consistent among group II sites. B horizon clay averaged 23.24 percent. B horizon sand averaged 69.50 percent.

Mean pine basal area was 24.50 m^2 per hectare. Mean basal area of hardwoods (0.38 m^2/ha), density of pine (511 stems/ha), and density of hardwoods (240 stems/ha) were lowest of all three ecological groupings. Group II had the highest mean species richness with 60.73 species per plot. The high mean species richness level may be attributable to the low density pine and hardwood stems, opening the canopy more and allowing more radiant heat and sunlight to reach the forest floor, thus providing favorable conditions for herbaceous growth. Mean landform index was 0.15. Mean terrain shape index was 0.023.

The dominant canopy tree was *Pinus palustris* with *P. taeda* a common associate. Common sub-canopy and mid-story species consisted of *Carya pallida*, *Quercus nigra*, *Q. marilandica*, *Prunus serotina*, *Sassafras albidum*, and *Diospyros virginiana*. *Rhus copallina*, *R. toxicodendron*, *Vaccinium stamineum* and *V. arboreum* were common in the shrub layer. Vine species also had a high constancy on group II sites. Common species of vines found were *Smilax bona-nox*, *S. Glauca*, *Centrosema virginianum*, and *Vitis rotundifolia*. A fairly species rich herbaceous layer consisted mainly of *Eupatorium glaucascens*, *Solidago odora*, *Tragia urens*, *Eupatorium compositifolium*, *Desmodium strictum*, *D. ciliare*, *D. vridiflorum* and *Rubus spp.* Common grasses found were *Dichanthelium commutatum*, *D. angustifolium*, *D. aciculare*, *Gymnopogon brevifolius*, and *Andropogon virginicus.*

Group III--Twenty-three plots were identified as Group III. These were the most xeric sites found at the Savannah River Site. All but two of the twenty-three sites occurred on Lakeland soils, which are excessively drained, rapidly permeable typic quartzipsamments on slopes ranging from 0 to 6 percent. Blanton and Troup sands comprised the remainder of group III soils. These sandy soils are very similar in texture to Lakeland sands and are generally found on the same landscape. By definition there was no B horizon present in group III soils. Discriminant analysis found that the presence or absence of the B horizon was the most discriminating variable separating group III sites from groups I and II (Table 4.1). The mean percent sand in the C horizon was 92.00 percent.

Group III pine basal area averaged 18.98 m^2 per hectare. The low volume of basal area is what we might expect given that group III sites were classified as most xeric in terms of soil moisture and exposure. Group III had a mean pine density of 849 stems per hectare. Hardwood density averaged 1982 stems per hectare, with the large majority of these in the sapling class (0-2.5cm diameter). Hardwood basal area averaged 2.79 m^2 per hectare. Group III averaged of 55.08 species per plot. The plantation sites we sampled in group III were mostly upland pine sites that had very little topography or micro-relief.

Group III sites had a canopy dominated almost entirely by *Pinus palustris*. Common sub-canopy trees were *Quercus laevis*, *Q. incana*, *Q. nigra*, *Q. margaretta*, and *Carya pallida*. Those species were also very abundant in the mid-story along with *Prunus serotina*, *Sassafras albidum*, *Diospyros virginiana*, *Crateagus spp.*, and *Vaccinium arboreum*. Group III had a shrub layer composed mostly of *Vaccinium stamineum*, *Gaylussacia dumosa*, *Rhus toxicodendron*, and *R. copallina*. Common herbaceous associates were *Solidago odora*, *Tragia urens*, *Hieracium gronovii*, *Hypericum* *hypericoidies*, *Pityopsis aspera*, *Stipulicida setacea*, *Dyschoriste oblongifolia*, *Bonamia patens*, *Cirsium repandum*, *Coreopsis major*, *Helenium amarum*, *Cnidoscolus stimulosus*, *Eriogonum tomentosum*, *Silphium compositum*, *Galactia regularis*, *Aster linariifolius*, and *Euphorbia ipecacuanhae*. There were also many species of grass, but their abundances were extremely low. Some of the more common species of grasses found were *Andropogon virginicus, Gymnopogon brevifolius, Dichanthelium aciculare,* and *Sporobolus junceus.*

Analysis of Natural Stands

Ordination and Cluster Analysis

The primary data matrix for natural stands consisted of 30 plots and 297 species. Ordination arranged these plots along a soil moisture gradient (axis 1) that showed a beta diversity of 3.5 standard deviations (Figure 4.2). Based on ordination and cluster analysis, I separated these plots into three groups, with plots (group III) near the origin of the graph on the extreme xeric end of the gradient, and plots (group I) near the end of the graph on the more mesic end of the gradient. Axis 2 showed a beta diversity of 2.5 standard deviations.

Discriminant Analysis

Of the fifteen environmental variables used in discriminant analysis, eleven were found to be significant at the 0.20 level of significance (Table 4.10). These variables were (1) presence/absence of B horizon, (2) landform index, (3) soil magnesium, (4) sodium, (5) calcium, (6) nitrogen, and (7) potassium, (8) organic matter, (9) percent sand in respective horizon, (10) percent clay in the respective horizon, and (11) percent sand in the A horizon.

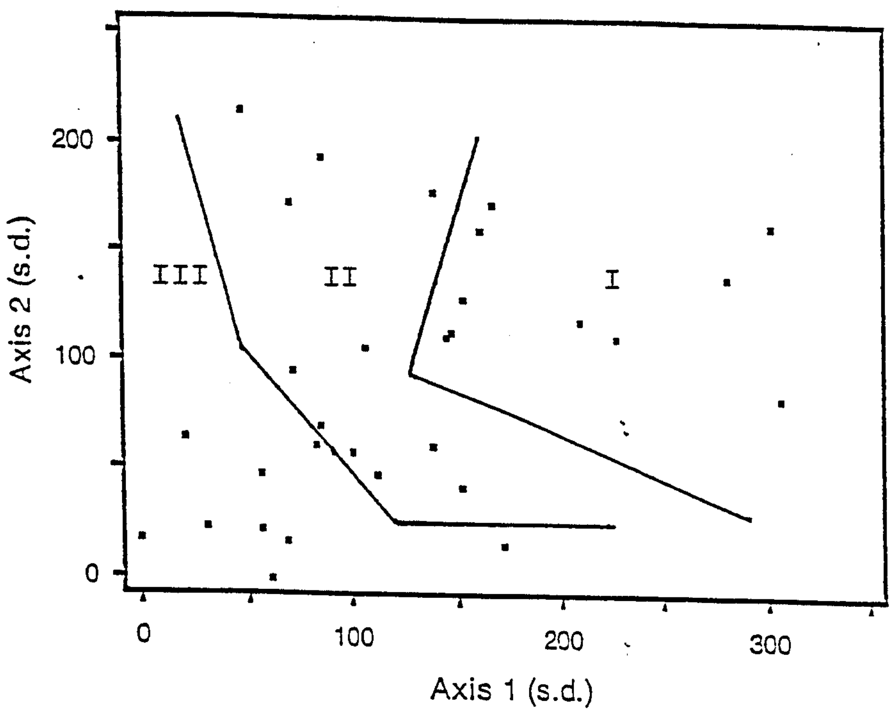

Figure 4.2. Ordination of 30 natural plots using full importance values.

Table 4.10. Significant environmental variables identified by stepwise discriminant analysis (SAS 1995) for natural longleaf sites.

Variable	Partial R^2	F value	Prob. > F	Wilks' Lambda	Prob. < Lambda
BHOR	0.6477	24.823	0.0001	0.35227273	0.0001
LFI	0.4693	11.495	0.0003	0.18696044	0.0001
MG	0.3358	6.321	0.0060	0.12417101	0.0001
NA	0.2688	4.368	0.0241	0.09103651	0.0001
CA	0.2072	3.005	0.0693	0.07217574	0.0001
SND	0.1950	2.665	0.0920	0.05810088	0.0001
CLA	0.2923	4.337	0.0265	0.04111608	0.0001
N	0.2483	3.304	0.0576	0.03090612	0.0001
OM	0.1795	2.078	0.1527	0.02535910	0.0001
K	0.2268	2.640	0.0988	0.01960728	0.0001
SNDA	0.2059	2.204	0.1410	0.01557076	0.0001

Discriminant function analysis was then performed to find classification success rates for each ecological site unit or group. The coefficients for the discriminant linear function can be found in Table 4.11. The resubstitution success rate was 100% (Table 4.12). The cross-validation success rate was 87% with four plots missclassified (Table 4.13).

Vegetative Structure

The most obvious difference structurally among groups of natural stands was basal area of hardwoods (Table 4.14). Group I had the highest mean hardwood basal area with 12.27 m^2 per hectare, group II the lowest with 0.71 m^2 per hectare, and group III had an intermediate mean hardwood basal area of 5.53 m^2 per hectare. These three groups were found to be significantly different from one another. Group II had the highest mean pine basal area with 15.10 m^2 per hectare and was found to be significantly different from groups I (5.47 m^2 per hectare) and III (9.70 m^2 per hectare). There were no differences found in mean density of pine and hardwood stems among the three groups.

Landform

Mean landform index was significantly higher in group I (0.21) than groups II (0.12) and III (0.15) (Table 4.15). Terrain shape index averaged 0.024 for group I, 0.023 for group II and 0.024 for group III with no significant differences among them.

Soil Physical and Chemical Properties

Differences in soil physical variables among groups of natural stands were very similar to those of plantation sites. Mean percent clay in the A horizon revealed no

Table 4.11. Coefficients of the linear discriminant function for natural groups I, II, and III.

Coefficient	I Sub-mesic	II Sub-xeric	III Xeric
Constant	-1200	-1083	-1216
BHOR	11.4583	9.22169	-11.83694
LFI	-0.05171	-0.01350	-0.0673
MG	11.49447	9.87653	10.09476
NA	5.28247	5.44886	6.85332
CA	685.11152	622.52148	755.97242
SND	1.22582	1.87381	2.54448
CLA	0.74447	1.48799	1.90205
N	-1.95423	-2.08465	-2.64942
OM	5.81565	5.02301	6.64942
K	-159.30816	-136.95557	-145.98690
SNDA	17.25898	16.162000	16.39823

Table 4.12. Classification success rate of discriminant analysis using resubstitution for natural groups I, II, and III.

Group	I Sub-mesic	II Sub-xeric	III Xeric	Total
I	10 **100.00**	0 0.00	0 0.00	10 100.00
II	0 0.00	11 **100.00**	0 0.00	11 100.00
III	0 0.00	0 0.00	9 **100.00**	9 100.00
Total	10 33.33	11 36.67	9 30.00	30 100.00

Overall classification rate = **100%**

Table 4.13. Classification success rate of discriminant analysis using cross-validation for natural groups I, II, and III.

Group	**I Sub-mesic**	**II Sub-xeric**	**III Xeric**	**Total**
I	8 **80.00**	1 10.00	1 10.00	10 100.00
II	1 9.09	9 **81.82**	1 9.09	11 100.00
III	0 0.00	0 0.00	9 **100.00**	9 100.00
Total	9 30.00	10 33.33	11 36.67	30 100.00

Overall classification rate = **87%**

Table 4.14. Mean values of structural variables of natural groups for the Savannah River Site. Means in each row with different letter indicate significant difference at $\alpha = 0.05$. Mean values represented as ± SE (standard error).

Variable	**I Sub-mesic (n=10)**	**II Sub-xeric (n=11)**	**III Xeric (n=9)**
Species richness (# per plot)	75.10a±4.49	71.09a±4.63	76.33a±6.06
Basal area pine (m^2 per ha)	5.47b±1.31	15.10a±1.77	9.70b±1.31
Basal area hardwood (m^2 per ha)	12.27a±1.56	0.71b±0.30	5.53c±0.99
Density pine (# stems per ha)	296.00a±103.61	329.73a±48.61	166.67a±26.61
Density hardwood (# stems per ha)	1175.00a±179.23	1509.73a±523.28	2320.55a±371.27

Table 4.15. Mean values of environmental variables of natural groups for the Savannah River Site. Means in each row with different letter indicate significant difference at $\alpha = 0.05$. Mean values represented as ± SE (standard error).

Environmental variable	**I Sub-mesic (n=10)**	**II Sub-xeric (n=11)**	**III Xeric (n=9)**
Landform index	0.21a±0.138	0.12b±0.102	0.15b±0.155
Terrain shape index	0.025a±0.013	0.031a±0.009	0.024a±0.007

significant difference among the three groups (Table 4.16). There was a significantly higher mean percent sand in the A horizon of group III (93.22) compared to groups I (87.20) and II (88.40). There was no difference in percent clay in the B horizon between group I, which averaged 24.78 percent, and group II, which averaged 24.00 percent, but there was a large significant difference between those groups and the percent clay in the C horizon of group III, which averaged only 4.84 percent. Similar to plantations, group III soils were largely typic quartzipsamments and had an extremely high percent sand and low percent clay. The opposite is true when comparing mean percent sand between group III (92.00) and groups I (64.60) and II (71.36). Percent sand was significantly higher in group III soils than in soils of groups I and II.

Soil chemical variables among natural groups showed some variation (Table 4.17). The most striking difference was the percent organic matter (humus) among natural groups. All three groups were found to be significantly different from one another, all due to differences expected among xeric to mesic plots, ranging from an average high of 3.18 percent humus for group I, to an average low of 1.46 percent humus for group III. Other significant differences were noted in levels of soil nitrogen and potassium. Group I had higher levels of both nitrogen and potassium in the soil than groups II and III.

Ecological Groupings of Natural Sites

Each group of natural stands defined by ordination/classification revealed a distinguishable group of vegetation and set of associated physical and environmental variables. TWINSPAN was used to find indicator species for each group of natural stands identified (Table 4.18). Several good indicators of group I sites include *Quercus stellata*,

Table 4.16. Mean A, B, and C horizon soil physical property values of natural groups I, II, and III for the Savannah River Site. Means in each row with different letter indicate significant difference at $\alpha = 0.05$. Mean values presented as ± SE (standard error).

Soil physical variable	I Sub-mesic (n=10)	II Sub-xeric (n=11)	III Xeric (n=9
A horizon sand (%)	5.18a±0.74	5.55a±1.79	3.06a±0.22
A horizon clay (%)	87.20b±1.03	88.45b±1.83	93.22a±0.43
B horizon sand (%)	64.60b±5.14	71.36b±5.64	______[1]
B horizon clay (%)	24.78a±4.47	24.00a±4.86	______[1]
C horizon sand (%)	______[2]	______[2]	92.00a±1.35
C horizon clay (%)	______[2]	______[2]	4.84b±0.76

[1]B horizon absent from soil
[2]C horizon absent from soil

Table 4.17. Mean soil chemical values of natural groups I, II, and III for the Savannah River Site. Means in each row with different letter indicate significant difference at α = 0.05. Mean values expressed as ± SE (standard error).

Soil chemical value	**I Sub-mesic (n=10)**	**II Sub-xeric (n=11)**	**III Xeric (n=9)**
pH	4.88a±0.10	4.79a±0.06	4.84a±0.08
Organic matter (%)	3.18a±0.23	2.23ab±0.40	1.46b±0.10
Nitrogen (kg/ha)	87.92a±3.15	67.14b±6.14	54.43b±2.26
Calcium (kg/ha)	418.22a±87.71	370.34a±46.44	295.00a±28.65
Magnesium (kg/ha)	79.71a±0.23	55.59a±0.40	57.87a±0.10
Potassium (kg/ha)	49.33a±3.47	34.77b±2.34	30.50b±1.57
Sodium (kg/ha)	32.68a±3.09	30.99a±2.93	39.69a±1.07

Table 4.18. Constancy and average importance values (constancy:importance value) of diagnostic species of the three ecological groups for natural sites at the Savannah River Site.

Species	Group I (Sub-mesic)	Group II (Sub-xeric)	Group III (Xeric)
Clitoria mariana	90:0.43		
Chimaphila maculata	80:0.35		
Helianthus hirsutus	80:0.58		
Amorpha herbacea	40:1.50		
Quercus hemisphaerica	80:0.50		
Quercus stellata	100:8.36		
Aristolochia serpentaria	80:0.30		44:0.30
Scutellaria elliptica	70:0.33		44:0.40
Quercus falcata	70:5.35		
Pinus taeda	70:3.87	100:12.34	
Aristida behrichiana		82:6.22	33:0.36
Quercus incana		45:1.10	100:0.90
Quercus laevis		64:1.93	100:15.61
Paspalum floridanum			67:0.30
Galactia regularis			67:0.37
Cirsium repandum			78:0.44
Cnidoscolus stimulosus			89:0.40
Stillingia sylvatica			67:0.37
Opuntia compressa			100:0.23

Aristolochia serpentaria, and *Clitoria mariana*. Group II indicators included *Aristida beyrechiana* and *Pinus taeda*. *Opuntia compressa*, *Cnidoscolus stimulosus*, and *Cirsium repandum* were good indicators of group III sites.

General Community Characteristics of Natural Groups

Group I--Ten sites were identified as group I through ordination and classification. These sites are considered the most mesic of the natural stands found and sampled in this study. I classified group I sites as sub-mesic based on soil moisture and vegetation. Percent clay in the B horizon averaged 24.78 percent. Percent sand in the B horizon averaged 64.60 percent. Group I soils ranged from well-drained arenic plinthic paleudults to well-drained typic hapludults. Group I had had the highest mean levels of organic matter (3.18%), pH (4.88), nitrogen (87.92 kg/ha), calcium (418.22 kg/ha), magnesium (79.71 kg/ha), and potassium (49.33 kg/ha) in the soil.

Pine basal area averaged 5.46 m^2 per hectare. Hardwood basal area averaged 12.23 m^2 per hectare. Mean density of pine was 296 stems per hectare and density of hardwoods averaged 1175 stems per hectare. Group I had a mean species richness of 75.10 species per plot. Mean landform index was 0.21. Mean terrain shape index was 0.025.

Group I canopies were generally mixed pine and hardwood dominants. Common canopy associates were *Pinus palustris*, *P. taeda*, *Quercus falcata*, and *Q. stellata*. There was a common sub-canopy and mid-story comprised of *Carya pallida*, *Prunus serotina*, *Nyssa sylvatica*, *Diospyros virginiana*, *Quercus marilandica*, *Q. falcata*, *Q. stellata*, and *Q. hemisphaerica*. There was a thick vine layer dominated by *Gelsemium sempervirens*, *Clitoria mariana*, *Smilax bona-nox*, *S. glauca*, and *Vitis rotundifolia*. Common shrubs included *Vaccinium stamineum*, *R. toxicodendron*, and *Rhus copallina*. Group I had a lush herbaceous layer comprised mostly of *Bonamia patens*, *Dyschoriste oblongifolia*, *Liatris spp.*, *Solidago odora*, *Tephrosia virginiana*, *Aster tortifolius*, *A. linariifolius*, *Coreopsis major*, *Pteridium aquilinium*, *Aristilochia serpentaria*, and *Helianthus hirsutus*. Common grasses found were *Andropogon virginicus*, *Dichanthelium angustifolium*, and *Scleria triglomerata*.

Group II--Eleven sites were identified as group II through ordination and classification. Group II averaged 24.00 percent clay and 71.36 percent sand in the B horizon. Soils covered the entire soil moisture gradient and ranged from excessively drained typic quartzipsamments to well-drained typic hapludults. Group II sites were classified as sub-xeric based on soil moisture and vegetation. Group II had fairly low mean pH (4.79), magnesium (55.58 kg/ha), and sodium (30.98 kg/ha) levels in the soil.

Group II averaged 15.09 m^2 per hectare of pine basal area. Mean basal area of hardwoods was 0.706 m^2 per hectare. There was an average of 71.09 species per plot for group II sites. Pine density averaged 330 stems per hectare and mean hardwood density was 1510 stems per hectare. Sites were fairly well exposed and had a landform index of 0.12. Terrain shape index was 0.023.

Group II had a canopy dominated almost entirely by pine. *Pinus palustris* and *P. taeda* were the common canopy trees. Common sub-canopy and mid-story associates were *Quercus laevis*, *Q. margaretta*, *Q. nigra*, *Q. marilandica*, *Prunus serotina*, *Nyssa sylvatica*, *Vaccinium arboreum*, *Carya pallida*, *C. tomentosa*, and *Diospyros virginiana*. Common shrubs were *Vaccinium stamineum*, *V. arboreum*, *Rhus copallina*, *R. toxicodendron*, and *Gaylussacia dumosa*. Group II had a fairly thick structure of vines composed mainly *Smilax bona-nox*, *S. glauca*, *Vitis rotundifolia*, and *Gelsemium sempervirens*. Common herbaceous species were *Bonamia patens*, *Pityopsis aspera*, *Solidago odora*, *Tephrosia virginiana*, *Aster tortifolius*, and *Carphephorous bellidifolius*. The only species of grass common to group II sites was *Andropogon virginicus*.

Group III--Ordination and classification identified nine sites as group III. Mean percent sand for group III was 93.22 percent in the A and 92.00 percent in the B horizons. Group III soils ranged from typic quartzipsamments to grossarenic paleudults. There was no B horizon associated with group III soils. Soils in this group maintained a sandy epipedon greater than 200 cm thick. Soils from group III natural sites were remarkably similar to group III plantation sites in regard to soil texture. We classified group III sites as xeric based on soil moisture. Mean percent clay in the C horizon was 4.83 percent. Group III sites had the lowest percent organic matter with a mean of 1.46 percent. Group III also had the lowest mean levels of soil nitrogen (54.44 kg/ha), calcium (294.99 kg/ha), and potassium (30.50 kg/ha). This low level of soil minerals is most likely the direct result of excessive leaching due to soil texture.

Group III averaged 76.33 species per plot. Mean pine and hardwood basal area was 9.69 and 5.35 m^2 per hectare. Group III had an open canopy of pine with a mean density of 167 stems per hectare. Hardwood density averaged 2321 stems per hectare. As we mentioned earlier in plantation sites, a large proportion of hardwood stems fall into the sapling size class (0–2.5 cm diameter). Mean landform index was 0.15. Mean terrain shape index was 0.02.

The dominant canopy species was *Pinus palustris*. Common sub-canopy and mid-story species included *Quercus laevis*, *Q. incana*, *Q. margaretta*, *Q. nigra*, *Carya pallida*, *Diospyros virginiana*, and *Prunus serotina*. *Vaccinium stamineum*, *V. arboreum*, *Gaylussacia dumosa*, and *Rhus copallina* dominated the shrubby layer. Common herbaceous associates included *Eriogonum tomentosum*, *Opuntia compressa*, *Stipulicida setacea*, *Euphorbia ipecacuanhae*, *Bonamia patens*, *Pityopsis aspera*, *Tragia urens*, *Tephrosia virginiana*, *Cnidoscolus stimulosus*, and *Solidago odora*. There was a common grass layer composed mostly of *Andropogon virginicus*, *Dichanthelium oligiosanthes*, *D. acuminatum*, *Aristida purpurascens*, and *Sporobolus junceus*.

Comparison of Longleaf Pine Plantation Sites to Natural Stands

I have successfully identified and described groups of similar sites on both longleaf pine plantations and natural, or remnant stands which has answered the question of whether or not distinct plant communities exist along an environmental gradient on these sites. These data are of particular interest to natural resource professionals concerned with the current status of the longleaf pine ecosystem, its degree of disturbance and change, and its potential for restoration. Determining the degree of similarity in the structure and composition of vegetation on longleaf plantations versus natural stands will be valuable in determining the current status of plantations and its potential for restoration.

Ordination of Plantations and Natural Stands

The primary data matrix for both plantations and natural stands consisted of 84 plots and 361 species. Ordination separated all eighty-four plots into two groups (Figure 4.3). These groups were derived from the first order division of TWINSPAN. Plots were separated into two distinct associations based on origin (plantation or natural). Ordination arranged each of these groups along a distinct soil moisture gradient (axis 1) that showed

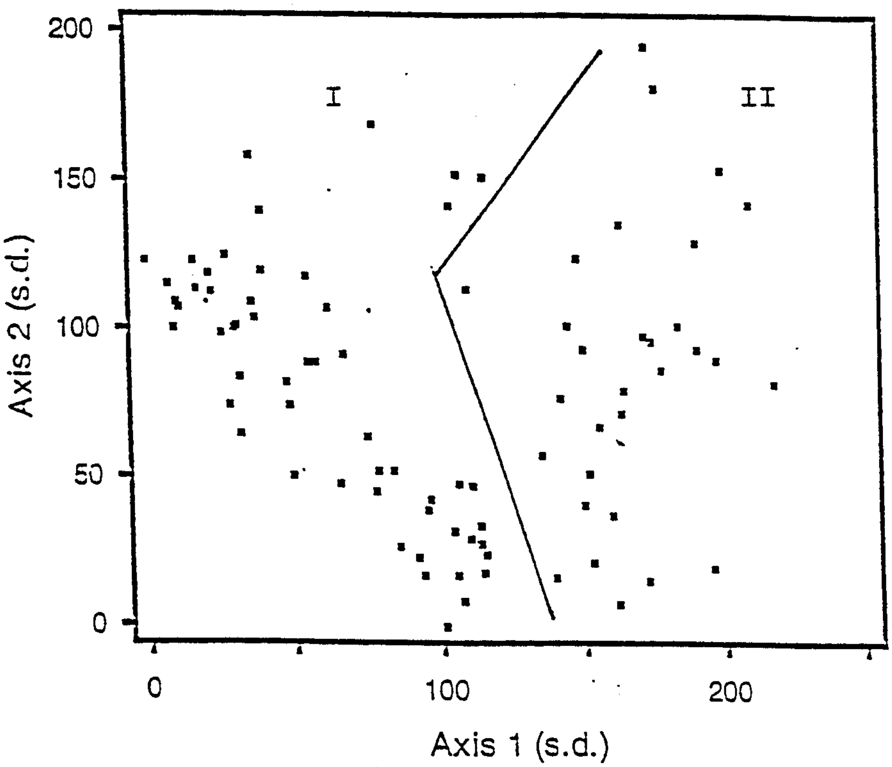

Figure 4.3. Initial ordination of both plantation and natural plots (n=84) using species presence/absence values and first order division.

an overall beta diversity of 2.5 standard deviations. Group I plots were identified as plantation sites and arranged along a soil moisture gradient that has a beta diversity of 1.5 standard deviations. Plots near the origin of the graph exist on the mesic end of the soil moisture gradient, while plots near the center of the graph exist on the xeric end of the gradient. Group II plots were identified as natural stands and arranged along a soil moisture gradient that showed a beta diversity of 1.0 standard deviations. Plots near the center of the graph exist on the xeric end of the soil moisture gradient, while plots near the end exist on the mesic end of the gradient.

The second order of division of TWINSPAN was used to further break down plot groupings. Plots were then separated into four groups (Figure 4.4). These groups exist along the same presumed soil moisture gradients noted above. Groups were labeled I, II, III, and IV. Of the four groups identified, groups I and II were of plantation origin and IV was of natural origin. Group III was the only group of plots that displayed combination of plantation and natural stands (Figure 4.5). Group III occurred on the xeric end of the soil moisture gradient. This would indicate that on the most xeric sites, similar vegetation may exist on both plantation and natural stands. Group III was further divided by the third order of division. Group III_A identifies plots of plantation origin while group III_B identifies plots of natural origin.

Variation Among Sites--Plantation vs. Natural

Overall mean species richness of plantation sites ranged from a low of 53.44 species per 0.1 hectare on sub-mesic sites to a high of 60.73 species per 0.1 hectare on sub-xeric sites (Table 4.19). Overall mean species richness of natural sites ranged from a low of 71.09 species per 0.1 hectare on sub-xeric sites to a high of 76.33 species per 0.1

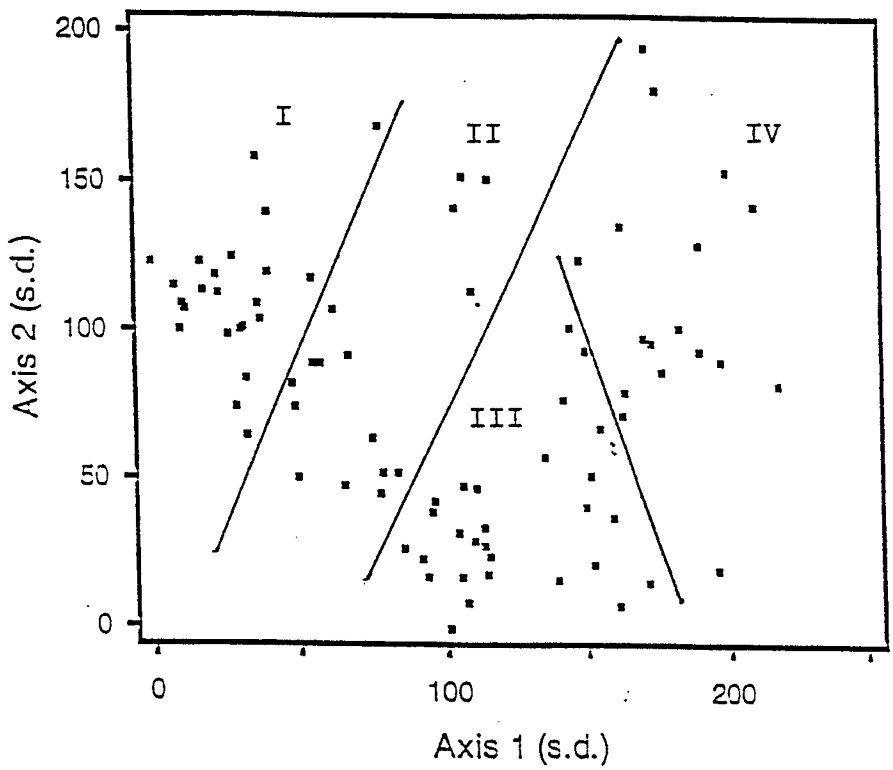

Figure 4.4. Ordination of both plantation and natural plots (n=84) using species presence/ absence values and second order division.

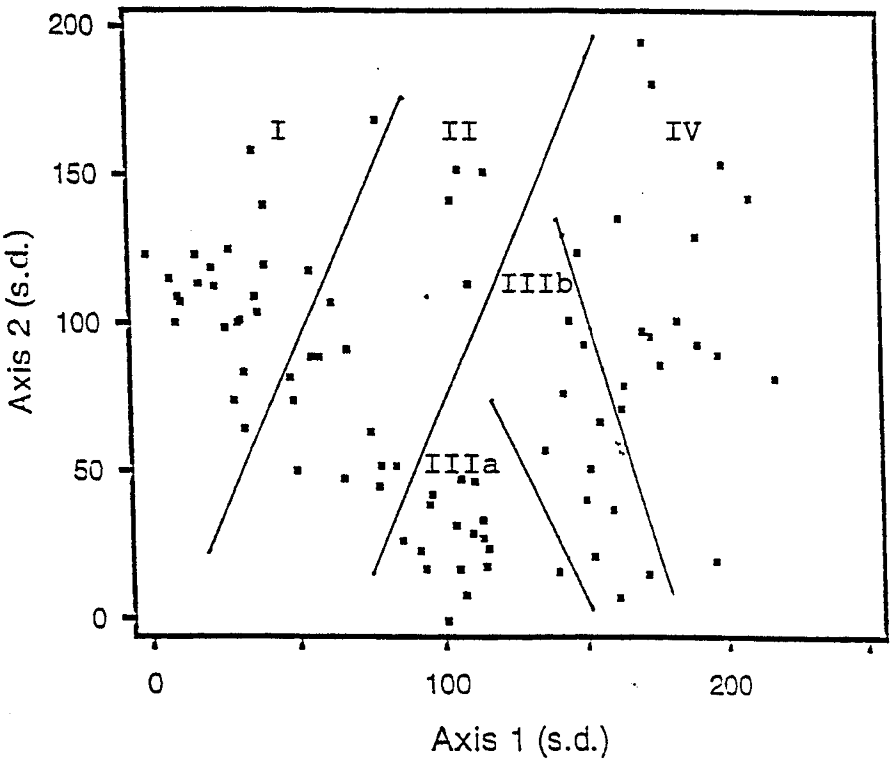

Figure 4.5. Final ordination of both plantation and natural plots (n=84) using species presence/absence values.

Table 4.19. Mean species richness at the 5 sample sizes and mean total species richness of longleaf plantations by group.

Sample Scale	**I Sub-mesic (n=9)**	**II Sub-xeric (n=22)**	**III Xeric (n=32)**
.001m^2	0.18	0.12	0.31
.10m^2	0.76	0.88	1.11
1.0m^2	3.19	3.41	4.65
10m^2	11.04	10.29	13.06
100m^2	27.33	29.30	28.16
Total-1000m^2	53.44	60.73	55.09

hectare on xeric sites (Table 4.20). The species richness across all natural stands was found to be significantly higher compared to plantations (74.00 versus 57.11 species per plot).

Based on ordination and cluster analysis, I determined that the most similar groups of plots between plantation and natural stands were those that occurred on the most extreme mesic and xeric ends of the soil moisture gradient. Physical variables from plantations and natural stands on the mesic end of the gradient were then tested for significant differences. Only plots occurring on the most mesic soil textures sampled were subjected to analyses. The two groups of mesic plots (plantation and natural) selected for analyses were derived mostly from the ordinated group I plantation sites and group IV natural stands (Figure 4.5). These groups, however, are not identical to the ordinated groups and should be viewed as separate entities. The two groups of plots selected were classified as sub-mesic based on soil moisture. Mean species richness was significantly higher on natural stands averaging 72.93 species per plot compared to 56.53 species per plot on plantations (Table 4.21). Such a large difference in species richness may be associated with basal area and density of pine and hardwood stems on these sites. Natural stands had a significantly lower mean basal area of pine and hardwood and density of pine stems than plantation sites. Natural stands had a mean pine basal area of 9.25 m^2 per hectare and 7.56 m^2 per hectare of hardwood. Natural stands also had a significantly lower mean density of pine with 355 stems per hectare. Comparing those means to pine basal area (26.65 m^2/ha) and density (720 stems/ha) on plantation sites indicates a more favorable environment for herbaceous growth on natural stands due to increased sunlight from reduced canopy coverage and less competition from woody species. These

Table 4.20. Mean species richness at the 5 sample sizes and mean total species richness for natural longleaf groups.

Sample Scale	**I Sub-mesic (n=10)**	**II Sub-xeric (n=11)**	**III Xeric (n=9)**
$0.01m^2$	0.30	0.40	0.48
$.10m^2$	1.88	2.19	1.89
$1.0m^2$	6.75	7.22	5.91
$10m^2$	19.40	18.50	18.24
$100m^2$	43.20	42.07	42.42
Total-$1000m^2$	75.10	71.09	76.33

Table 4.21. Mean values of structural variables of selected mesic plantation and natural sites at the Savannah River Site. Rows with same letter indicate insignificant difference at $\alpha = 0.05$. Mean values are presented as ± SE (standard error).

Variable	**Plantation Sites Group I (n=21)**	**Natural Sites Group IV (n=14)**
Species richness (# per plot)	56.52a±2.39	72.92b±4.11
Basal area pine (m^2 per ha)	26.64a±1.12	9.25b±1.70
Basal area hardwood (m^2 per ha)	0.44a±0.11	7.56b±1.69
Density pine (# stems per ha)	719.95a±107.36	354.78b±71.94
Density hardwood (# stems per ha)	325.19a±74.08	1120.87b±143.21

conditions, coupled with favorable land use history, burn history, and less intensive agricultural practices have likewise created a better environment for herbaceous cover. Hardwood density was significantly higher in natural stands, but due to the large number of stems in the sapling (0-2.5 cm diameter) class, the data are somewhat misleading and inconclusive.

There were no significant differences in soil physical variables between plantations and natural stands on the mesic end of the gradient (Table 4.22). There were, however, significant differences among soil chemical variables between the two site types (Table 4.23). Natural stands on the mesic end of the gradient had a higher pH and contained considerably higher levels of nitrogen, calcium, magnesium, potassium, and sodium than plantation sites. Organic matter was significantly higher in natural stands, averaging 3.30 percent organic matter compared to 1.07 percent in plantations.

Tests for significant differences among physical variables between plantations and natural stands on the xeric end of the soil moisture gradient were also performed. Based on ordination and cluster analysis, the xeric end of the gradient showed the most similarity between plantation and natural stands. I analyzed and compared exact plot groupings identified through ordination (group III_A and group III_B, Figure 4.5) for xeric plantations and natural stands. There was a large significance difference in species richness between xeric plantations and natural stands. Natural stands had a mean species richness of 70.91 species per plot on xeric sites, considerably higher than plantations, which averaged 54.82 species per plot (Table 4.24). There were no significant differences found in mean basal area or density of hardwood stems between plantations and natural stands. There was, however, a significantly higher pine basal area on plantations averaging 16.75 m^2 per

Table 4.22. Mean A and B horizon soil physical property value of selected mesic plantation and natural sites for the Savannah River Site. Rows with same letter indicate insignificant difference at $\alpha = 0.05$. Mean values are presented as ± SE (standard error).

Soil Physical Variable	**Plantation Sites Group I (n=21)**	**Natural Sites Group IV (n=14)**
Percent sand A horizon (%)	89.09a±0.59	86.14b±1.27
Percent clay A horizon (%)	4.45a±0.51	6.13a±1.43
Percent sand B horizon (%)	64.53a±2.27	62.64a±4.52
Percent clay B horizon (%)	28.10a±2.55	27.85a±3.98

Table 4.23. Mean soil chemical values of selected mesic plantation and natural sites for the Savannah River Site. Rows with same letter indicate insignificant difference at $\alpha = 0.05$. Mean values are presented as ± SE (standard error).

Soil Chemical Variable	**Plantation Sites Group I (n=21)**	**Natural Sites Group IV (n=14)**
pH	4.66a±0.05	4.84b±0.08
Organic matter (%)	1.07a±0.07	3.30b±0.26
Nitrogen (kg/ha)	44.53a±1.79	88.71b±2.85
Calcium (kg/ha)	281.14a±24.30	448.95a±67.05
Magnesium (kg/ha)	54.26a±2.89	74.69b±7.68
Potassium (kg/ha)	29.51a±2.20	46.92b±2.75
Sodium (kg/ha)	19.95a±0.91	36.07b±2.45

Table 4.24. Mean values of structural variables for xeric plantation and natural sites at the Savannah River Site. Means in each row with different letter indicate significant difference at $\alpha = 0.05$. Mean values represented as ± SE (standard error).

Variable	**Plantation Sites III_A (n=17)**	**Natural Sites III_B (n=11)**
Species richness (# per plot)	54.82a±3.21	70.91b±4.42
Basal area pine (m^2 per hectare)	16.75a±1.55	10.94b±1.65
Basal area hardwood (m^2 per hectare)	3.21a±0.54	3.95a±0.99
Density pine (# stems per hectare)	814.70a±109.58	182.27b±24.95
Density hardwood (# stems per hectare)	2440.86a±498.53	1735.00a±347.95

hectare compared to 10.93 m^2 per hectare on natural stands. There was also a significantly higher density of pine on plantation sites with a mean of 815 stems per hectare compared to 183 stems per hectare on natural stands.

Soil physical variables between plantations and natural stands were constant. This is what we would expect given that these two groups occur on the most xeric end of the soil moisture gradient. There is very little variation in soil texture on such xeric sites and no significant differences were found in soil physical variables between the two groups (Table 4.25). Soil chemical variables between sites varied considerably. There were no significant differences found in soil pH, organic matter, or nitrogen between xeric plantations and natural stands (Table 4.26). Levels of soil calcium, magnesium, potassium, and sodium were all significantly higher in natural stands than in plantations.

In general, soil chemical variables were all higher on natural stands when compared to plantations for both mesic and xeric plots. This trend would indicate some type of disturbance-related problem to plantation sites that has resulted in leaching of soil nutrients. This reduction in soil nutrients may also be related to nutrient uptake by plantation sites.

Species Abundance--Plantation vs. Natural

Moisture class one (MC1) represents the most xeric sites sampled at the Savannah River Site. Soils representative of MC1 were generally coarse textured sands and sandy loams. These are excessively and somewhat excessively well-drained soils with a low water holding capacity. Herbs, grasses, legumes, shrubs, and vines, particularly *Vernonia angustifolia*, *Andropogon virginicus*, *Tephrosia virginia*, *Gaylussacia dumosa*, *Vaccinium stamineum*, and *Gelsemium sempervirens*, were for the most part more

Table 4.25. Mean A and C horizon soil physical property values of xeric plantation and natural sites for the Savannah River Site. Rows with same letter indicate insignificant difference at $\alpha = 0.05$. Mean values are presented as ± SE (standard error).

Soil physical variable	**Plantation sites III_A (n=17)**	**Natural sites III_B (n=11)**
Percent sand A horizon (%)	91.65a±1.87	93.27a±1.35
Percent clay A horizon (%)	3.21a±0.37	3.10a±0.18
Percent sand C horizon (%)	92.76a±0.31	88.91a±2.45
Percent clay C horizon (%)	5.06a±0.38	8.19a±2.27

Table 4.26. Mean soil chemical values of xeric plantation and natural sites for the Savannah River Site. Rows with same letter indicate insignificant difference at $\alpha = 0.05$. Mean values are presented as ± SE (standard error).

Soil chemical variable	**Plantation sites III_A (n=17)**	**Natural sites III_B (n=11)**
pH	4.64a±0.34	4.78a±0.05
Organic matter (%)	1.16a±0.06	1.35a±0.09
Nitrogen (kg/ha)	47.15a±1.55	51.69a±2.22
Calcium (kg/ha)	219.53a±12.42	275.73b±17.06
Magnesium (kg/ha)	44.97a±0.99	51.89b±1.51
Potassium (kg/ha)	21.57a±1.33	28.99b±1.45
Sodium (kg/ha)	17.63a±0.54	34.15b±2.66

Table 4.27. Comparison of mean species abundance of selected species on plantation and natural sites for moisture class 1 (MC1). Species reported were found to be significantly different at α = 0. 10. Mean values presented as ± SE (standard error).

Species	**Plantation Sites (n=25)**	**Natural Sites (n=13)**
Andropogon virginicus	0.56±0.06	1.27±0.30
Asclepias amplexicaulis	0.004±0.004	0.11±0.05
Asclepias humistrata	0.06±0.27	0.007±0.007
Aster tortifolius	0.14±0.04	0.33±0.06
Baptisia tinctoria	0.08±0.03	0.007±0.007
Bulbostylis capillaris	0.004±0.004	0.03±0.01
Carya pallida	0.11±0.06	3.66±1.75
Chrysopsis gossypina	0.07±0.03	0.22±0.07
Cnidoscolus stimulosus	0.19±0.04	0.32±0.06
Dichanthelium aciculare	0.37±0.04	0.10±0.05
Dichanthelium spp.	0.02±0.02	0.17±0.06
Diospyros virginiana	1.34±0.24	0.65±0.10
Dyschoriste oblongifolia	0.19±0.05	0. 52±0.13
Eupatorium album	0.04±0.03	0.12±0.06
Euphorbia curtisii	0.004±0.004	0.15±0.06
Euphorbia ipecacuanhae	0.21±0.04	0.36±0.06
Gaylussacia dumosa	1.84±0.49	4.46±1.32
Gelsemium sempervirens	0.05±0.02	3.35±1.77
Gyinnopogon brevifolius	0.20±0.05	0.07±0.04

Table 4.27. (Continued)

Species	Plantation Sites (n=25)	Natural Sites (n=13)
Liatris spp.	0.08±0.02	0.36±0.06
Nyssa sylvatica	0.02±0.02	0.65±0.28
Opuntia compressa	0.03±0.009	0.16±0.05
Physalis spp.	0.17±0.38	0.38±0.38
Pinus palustris	36.70±2.85	18.19±3.47
Poaceae spp.	0.02±0.02	0.17±0.06
Quercus incana	1.63±0.47	0.62±0.26
*Quercus laevis**	7.30±1.78	10.08±3.08
*Quercus marilandica**	0.06±0.03	1.51±1.33
*Quercus margaretta**	1.34±0.29	2.85±1.34
*Quercus nigra**	0.38±0.07	1.75±1.31
Rhynchspora grayi	0.07±0.03	0.21±0.07
Robinia pseudoacacia	0.004±0.004	0.12±0.06
Scleria triglomerata	0.05±0.27	0.32±0.07
Smilax bona-nox	0.10±0.02	0.23±0.06
Tephrosia virginiana	0.09±0.03	1.51±0.40
Vaccinium arboreum	5.37±1.75	1.08±0.56

*Abundance not significantly different statistically, but of importance ecologically.

Table 4.28. Comparison of mean species abundance of selected species on plantation and natural sites for moisture class 2 (MC2). Species reported were found to be significantly different at $\alpha = 0.10$. Mean values presented as ± SE (standard error).

Species	Plantation Sites (n=13)	Natural Sites (n=8)
Andropogon virginicus	0.50±0.00	1.62±4.40
Aster paternus	0.008±0.008	0.20±0.08
Aster tortifolius	0.06±0.04	0.51±0.16
Bonamia patens	0.05±0.04	0.39±0.07
Carphephorus bellidifolius	0.02±0.01	0.39±0.18
Carya glabra	0.34±0.13	0.06±0.06
Carya tomentosa	0.05±0.04	1.83±0.91
Coreopsis major	0.04±0.041	0.38±0.07
Crateagus spp.	0.12±0.05	0.38±0.07
Desmodium strictum	0.25±0.06	0.06±0.06
Dichanthelium aciculare	0.15±0.06	0.43±0.06
Dichanthelium angustifolium	0.10±0.05	0.31±0.09
Dichanthelium spp.	0.008±0.008	0.18±0.09
Gaylussacia dumosa	0.008±0.008	2.81±1.09
Hieracium gronovii	0.15±0.06	0.03±0.01
Liatris spp	0.10±0.05	0.32±0.08
Pinus palustris	31.25±7.29	11.44±2.98
Pinus taeda	1.27±0.64	16.32±6.53
*Quercus falcata**	0.30±0.12	1.44±0.96

Table 4.28. (Continued)

Species	Plantation Sites (n=13)	Natural Sites (n=8)
*Quercus laevis**	0.12±0.06	3.14±2.09
*Quercus marilandica**	0.10±0.05	4.75±2.78
*Quercus margaretta**	0.30±0.07	1.25±0.51
Rhus copallina	0.40±0.12	1.07±0.38
Silphium compositum	0.008±0.008	0.18±0.09
Solidago odora	0.25±0.06	0.45±0.05
Tragia urens	0.36±0.05	0.17±0.07
Vaccineum arboreum	0.25±0.12	1.20±0.38
*Vaccineum stamineum**	1.91±0.41	5.12±1.90
Vitis rotundifolia	3.85±1.87	1.70±0.85

*Abundance not significantly different statistically, but of importance ecologically.

Table 4.29. Comparison of mean species abundance of selected species on plantation and natural sites for moisture class 3 (MC3). Species reported were found to be significantly different at $\alpha = 0.10$. Mean values presented as ± SE (standard error).

Species	**Plantation Sites (n=16)**	**Natural Sites (n=9)**
Andropogon spp.	0.007±0.007	0.22±0.08
Andropogon virginicus	0.47±0.02	1.05±0.17
Aster linariifolius	0.01±0.009	0.44±0.05
*Aster paternus**	0.04±0.03	0.18±0.08
Bonamia patens	0.05±0.03	0.41±0.05
Carya pallida	0.30±0.11	5.91±2.40
Carya tomentosa	0.17±0.11	2.44±1.02
Clitoria mariana	0.07±0.05	0.25±0.07
Coreopsis major	0.007±0.007	0.41±0.06
Danthonia sericea	0.01±0.009	0.16±0.08
Desmodium glabellum	0.10±0.04	0.01±0.01
Desmodium strictum	0.21±0.06	0.05±0.05
Dichanthelium angustifolium	0.20±0.06	0.45±0.04
Dyschoriste oblongifolia	0.04±0.03	0.51±0.14
Eupatorium glaucascens	0.30±0.06	0.05±0.05
Galium hispidulum	0.22±0.06	0.05±0.05
*Gaylussacia dumosa**	0.03±0.03	3.27±1.85
Gelsemium sempervirens	0.48±0.15	2.94±0.94

Table 4.29. (Continued)

Species	Plantation Sites (n=16)	Natural Sites (n=9)
Gymnopogon brevifolius	0.23±0.06	0.05±0.05
Lespedeza repens	0.13±0.05	0.40±0.06
Liatris spp.	0.15±0.06	0.61±0.11
*Nyssa sylvatica**	0.04±0.03	2.51±1.91
*Pinus palustris**	33.39±5.86	20.66±5.54
Pityopsis aspera	0.20±0.06	0.40±0.06
*Quercus falcata**	0.20±0.11	2.94±1.99
Quercus hemisphaerica	0.03±0.03	0.27±0.08
Quercus marilandica	0.20±0.11	5.94±2.29
Quercus margaretta	0.13±0.05	1.62±0.82
*Quercus nigra**	2.64±0.66	1.34±0.54
Quercus stellata	0.04±0.03	5.67±2.45
Rhus radicans	0.33±0.14	0.02±0.14
Rubus spp.	0.41±0.045	0.20±0.07
Schrankia microphylla	0.03±0.03	0.29±0.08
Silphium compositum	0.04±0.03	0.30±0.08
Solidago odora	0.20±0.02	0.50±0.00
Tephrosia virginiana	0.007±0.007	1.05±0.33
Tragia urens	0.47±0.02	0.22±0.08

Table 4.29. (Continued)

Species	**Plantation Sites (n=16)**	**Natural Sites (n=9)**
Vaccinium arboreum	0.13±0.05	0.83±0.36
Vaccinium stamineum	2.08±0.68	6.83±2.25
Vernonia angustifolia	0.03±0.03	0.30±0.08
*Vitis rotundifolia**	1.25±0.34	2.27±0.76

*Abundance not significantly different statistically, but of importance ecologically.

Gaylussacia dumosa, *Tephrosia virginiana*, *Vaccinium stamineum*, *Nyssa sylvatica*, *Carya spp.*, and oaks (*Quercus falcata*, *Q. marilandica*, *Q. stellata*, *Q. margaretta*, and *Quercus hemisphaerica*).

CHAPTER V

DISCUSSION

Vegetation Variation and Community Patterns

The strongest compositional gradients in longleaf plantation and natural stands at the Savannah River Site are related to a soil moisture gradient. The same relationship has been demonstrated in other studies (Peet and Allard 1993, Walker and Peet 1983, Van Lear and Jones 1987, Jones 1991). The soil gradient this study sampled ranged from dry, sandy uplands to gently rolling transitional areas between pine uplands and pineland drainages.

Soil variables that would affect soil moisture had the most effect on the distribution of vegetation along environmental gradients for plantation sites, but additional variables influence vegetation among natural groups. Natural sites were not as homogenous as plantation sites. Differences in canopy structure and composition, fire regimes, and land use history, undoubtedly all contribute to the distribution of vegetation among natural groups. It would appear, however, that soil moisture controls the majority of this distribution along environmental gradients. The presence or absence of a B horizon was the most significant environmental variable discriminating among groups of both plantations and natural stands.

The sub-mesic community types of plantations and natural sites were more variable than on other site types. Plantation sites had a canopy dominated by *Pinus elliottii* with *P. taeda* and *P. palustris* common associates. Sub-mesic natural sites exhibited two different community types, one dominated by pine (*Pinus palustris* and *Pinus taeda*) and the other by hardwoods (*Quercus stellata*, *Q. marilandica*, and *Q. falcata*). Sites dominated by the hardwood component appeared to be in an older seral stage compared to pine dominated communities. These communities usually consisted of mature hardwood stems, often with one to a few old-growth *Pinus palustris* mixed in the canopy, revealing a successional pattern from pine to oak dominated communities typical of fire disclimaxes. Sub-canopy and mid-story species were fairly similar between plantation and natural stands. Notable differences were the presence of *Sassafras albidum* on plantation sites and of *Nyssa sylvatica* on natural stands. Both types had a thick vine layer composed mostly of *Vitis rotundifolia*, *Gelsemium sempervirens*, and *Smilax spp*. Herbaceous layers differed significantly, with natural stands maintaining a more diverse herb layer than plantations. This higher diversity, in large part, may be attributed to lower basal area and density of the overstory. In a study of longleaf plant communities on the Kisatchie National Forest in Louisiana (Haywood et al. 1997), it was found that current year herbaceous production was partly associated with overstory and midstory basal area, canopy coverage, and number and size of understory shrubs. It was determined that sites with the least amount of overstory and the fewest understory woody stems had the greatest herbaceous production. This finding is consistent with the results that decreased basal area and density of the overstory on natural stands has are associated with higher species richness.

Vegetative models of late-successional longleaf communities that tie in well to plantation sites of this project include models from Van Lear and Jones (1987), Jones et al. (1994), and Jones (1991). These models are ones that are most comparable in terms of locality and soil moisture. Sub-mesic management/successional types of the Hilly

Coastal Plain of South Carolina identified by Jones (1991) that are similar to the sub-mesic type presented here include the *Pinus elliottii—Prunus serotina—Quercus nigra* and the *Pinus elliottii—Sassafras albidum—Rhynchosia reniformis* associations.

Peet and Allard (1993) described "natural" vegetation on different longleaf site types along the Southern Atlantic and Eastern Gulf Coast Regions. Of those, the mesic longleaf pine woodland, Fall-line mesic longleaf woodland, Fall-line slope mesic longleaf woodland, and Southern mesic longleaf woodland are comparable to the natural sub-mesic community type identified at the Savannah River Site. Native longleaf flora common on natural sites shared by these two models include species such as *Aristida beyrichiana*, *Aristida purpurascens*, bluestem grasses (*Andropogon spp.* and *Schizachyrium spp.*), *Gaylussacia dumosa*, *Pteridium aquilinium*, many species of *Aster*, *Euphorbia*, and *Vaccinium*. They (Peet and Allard 1993) also noted that there are fewer natural mesic sites to sample because those favorable sites were cleared for agriculture, or fire has been excluded for so long that natural conditions disappeared long ago.

Canopies of sub-xeric plantation and natural stands were nearly identical. Both types were dominated by *Pinus palustris* with *Pinus taeda* as a common associate. The most notable difference between sub-xeric plantation and natural stands occurred in the sub-canopy and mid-story. The density of hardwood stems in the mid-story of natural stands was nearly seven times greater than that of plantations. Hardwood basal area between the two types does not indicate such a large discrepancy because a large proportion of stems in the 0-2.5 cm diameter class. Not only is hardwood density much greater, but there is also a greater mixture of hardwood species found in the mid-story of natural stands, especially of oak species. Dominant oak species found in the mid-story of natural stands were *Quercus laevis*, *Q. margaretta*, *Q. nigra*, and *Q. marilandica*. In contrast, the only abundant oak species on plantation sites was *Quercus nigra*. Overall species diversity was most similar between sub-xeric natural and plantation sites compared to sub-mesic and xeric sites. Dominant vine species occurring on both types was *Smilax bona-nox*, *S. glauca*, and *Vitis rotundifolia*. Shrub layers were nearly identical between the two types. Dominant species included *Vaccinium stamineum*, *V. arboreum*, *Rhus copallina*, and *R. toxicodendron*. One significant difference in the herbaceous layer was the high constancy of witchgrass (*Dichanthelium spp.)* and legume species (*Desmodium* and *Lespedeza spp.*) on plantation sites. Although a higher occurrence of these species did occur on plantations, it should be noted that their overall abundance was extremely low.

Sub-xeric community types of the Hilly Coastal Plain of South Carolina identified by Jones (1991) and Van Lear and Jones (1987) that are similar to the sub-xeric community type presented here include the *Pinus palustris-Sassafras albidum* association and the *Pinus palustris-Nyssa sylvatica-Carya pallida* association. The best comparison of community types for natural sub-xeric longleaf sites at the Savannah River Site are models from Peet and Allard (1993). They examined vegetation on several different longleaf site types along the Southern Atlantic and Eastern Gulf Coast Regions. Of those, the Fall-line sub-xeric longleaf woodland, the Atlantic sub-xeric longleaf woodland, and the Southern sub-xeric longleaf woodland are comparable to the natural sub-xeric community type identified at the Savannah River Site. Dominant native flora found on natural stands for both models include *Quercus laevis*, *Q. marilandica*, *Q. margaretta*, *Q. incana*, *Vaccinium arboreum*, *Aristida beyrichiana*, bluestem grasses (*Andropogon* and *Schizachyrium*), *Pityopsis aspera*, *Tephrosia virginiana*, and *Rhynchosia reneformis*.

Of all three site types identified, xeric plantation and natural stands appear to be most similar. Both xeric plantation and natural stands had an overstory dominated by *Pinus palustris*. As would be expected, the basal area pine on xeric sites for both groups is extremely low. This is especially true of natural stands, where the basal area of pine averages only 9.70 m^2 per hectare. Sub-canopy and mid-story species of xeric plantations and natural stands were nearly identical. Dominant species included *Quercus laevis*, *Q. margaretta*, *Q. incana*, *Q. nigra*, *Carya pallida*, *Diospyros virginiana*, and *Prunus serotina*. Hardwood densities of the two groups were also similar and the highest mean hardwood density of all three sites types within each respective group. Common shrub layer dominants shared by both groups include *Vaccinium stamineum*, *Rhus copallina*, and *Gaylussacia dumosa*. The differences in species richness between plantations and natural stands reflect differences in the herbaceous layers. Comparing species composition between the two site types can be somewhat misleading; though species composition may be similar, abundance may be extremely variable between the two site types. Herbaceous species dominating both plantation and natural sites were many native longleaf species such as *Eriogonum tomentosum*, *Stipulicida setacea*, *Euphorbia ipecacuanhae*, *Bonamia patens*, *Pityopsis aspera*, *Tragia urens*, *Cnidoscolus stimulosus*, *Solidago odora*, *Andropogon virginicus*, and *Sporobolus junceus*.

Xeric longleaf plantation sites that are fairly similar to models from Jones et al. (1984). They found that at the Savannah River Site, the most xeric plantation sites that were artificially planted or seeded formed the *Pinus palustris*-*Quercus laevis*-*Aristida stricta* community type. These stands are characterized by a low overstory of *Pinus palustris* and *Quercus laevis*. Diagnostic understory species include *Eriogonum* *tomentosum* and *Gaylussacia dumosa*. A difference in these models that should be pointed out is the absence of wiregrass in the understory of plantation sites we sampled at the Savannah River Site. Most likely, this is related to the extensive ground disturbance that these sites have undergone over the past century, a condition in which shallowly rooted, endemic species such as *Aristida stricta* and *Gaylussacia dumosa* do not fair well.

Peet and Allard (1993) described several natural, xeric longleaf community types that formed models similar to the natural communities on xeric sites at the Savannah River Site. These include descriptions from the Fall-line xeric longleaf woodland, the Atlantic xeric longleaf woodland, the southern xeric longleaf woodland, and the Atlantic maritime longleaf woodland. These models describe sites with widely scattered longleaf pine and a broad-leaved, deciduous sub-canopy composed mostly of scrub oak species, primarily *Quercus laevis*. A sparse to moderate cover of herbs and grasses is characteristic. Natural flora found on these xeric sites included species such as *Aristida beyrichiana*, *Eriogonum tomentosum*, *Cnidoscolus stimulosus, Pityopsis aspera*, and *Sporobolus junceus*. [Note: The two species of wiregrass mentioned here, *Aristida stricta* and *A. beyrichiana*, occur in two different regions of South Carolina. *Aristida stricta* is confined to northern portions of South Carolina, while the species found at the Savannah River Site, *Aristida beyrichiana*, is confined to the southern portions of the state.]

Fire and its Role in Structuring Vegetation

The role fire played in structuring vegetation communities described in this investigation is complicated. Numerous studies (Rebertus et al. 1988, Platt et al. 1988, Streng et al. 1993, Waldrop et al. 1992, Frost 1997) have investigated the role of fire and its effect on the structure and composition of vegetation in longleaf pine ecosystems. Fire frequency, intensity, and season-of-burn influence the structure of how longleaf communities are shaped.

In this study, fire history was used as a guideline when selecting sites to be sampled. The objective with regard to fire history was to sample stands that had experienced similar fire regimes over the past few decades. This goal was more reliably achieved for longleaf plantation sites compared to natural sites because of more precise records of plantation fire history. Plantation sites, despite similar fire histories, were quite variable in regard to vegetation structure and composition. The dominance of hardwood species, particularly scrub oak (*Quercus laevis, Q. margaretta,* and *Q. incana*) is often viewed as an indicator of lack of fire, but these fifty-seven plantation sites had fire frequencies ranging from one to five year intervals.

Determining fire regimes of natural longleaf communities at the Savannah River Site was challenging. Because the longleaf ecosystem is fire-maintained, only those few sites that have continued to experience chronic fire retain a strong resemblance to the natural longleaf communities of the Southeast (Peet and Allard 1993). Most of the natural stands had retained a fairly diverse understory of herbs and grasses. Due to the lack of natural longleaf stands available at the Savannah River Site, sampling included some less frequently burned sites. The most distinguishing characteristic of these sites, however, was the large proportion of hardwood stems found in the canopy and sub-canopy. Some natural stands were almost completely dominated by hardwood components. This would indicate that most of these sites, if not all, had experienced fire exclusion at some point through the history of their development. Examples of natural longleaf vegetation containing both old-growth trees and understory unaltered by fire exclusion are almost nonexistent. Fortunately, fire has continued to be a tool for land management in many longleaf areas with the result that examples of second-growth stands can be found with the understory vegetation still intact.

The role that fire has played in the development of these communities is beyond the scope of this investigation. Other factors, such as agriculture and previous land management, and more recent disturbances such as pine straw raking and mechanized timber removal, need to be assessed to fully understand the potential for restoring these areas.

Species Richness and Biological Diversity

One of the primary objectives of this project was to assess the vascular plant species diversity of longleaf pine sites at the Savannah River Site. Major factors that may negatively affect biological diversity include replacement of native species with non-native species, opening sites to invasion of exotics, conversion of wild areas to agriculture, industry and other human uses, pollution, global climate change, overuse of species by humans, and fragmentation of habitats and populations. Factors countering these potential negative affects on biological diversity include restoration of species and ecosystems and management of wild areas for sustainable uses of natural resources (Mejeur et al., submitted; Salwasser 1990).

Diversity is usually defined as a combination of species richness (total number of species) and species evenness (the distribution of individuals among species) (Hutto 1998). I focused on describing the species richness of longleaf plantations compared to natural stands. Even though species richness tends to be the dominant criterion for ecological restoration and conservation evaluation techniques (Usher 1986), overall ecological significance cannot be fully understood without considering the effects of relative species abundance and evenness.

In many forested ecosystems, species richness tends to increase with increasing soil moisture from xeric to mesic conditions. On longleaf plantation sites, species richness increased to a maximum with increasing soil moisture from xeric to sub-xeric sites, but then decreased slightly on mesic sites. This is most likely the result of increased stand density, primarily *Pinus palustris*, on the more productive mesic sites. Dense canopies of *Pinus palustris* are common on these moist sites, decreasing light penetration and increasing litter on the forest floor, consequently forming conditions unfavorable for herbaceous growth and ultimately limiting species richness.

Overall mean species diversity on natural stands increased slightly with increasing soil moisture from sub-xeric to sub-mesic sites, but was highest on xeric sites. This may be related, in part, to the extreme nature of xeric sites. As stated by Mejeur et al. (submitted), "Many native species on frequently burned xeric sites are slow growing and stress tolerant, with deep tap-roots and wide spreading rhizomes. Further, there are no fast growing ruderals, native or exotic, that capture disturbed patches and have the potential to completely dominate the stand, ultimately reducing species diversity". Also, there are many plant adaptions to xeric conditions such as (1) vertical orientation of leaves to reduce the impact of sunlight and heat, (2) succulent plant tissues that help retain soil moisture, (3) narrow leaves to help reduce water loss, and (4) vegetative growth early in the growing season when moisture availability is greatest (Porcher 1995).

Species of Important Ecological Significance

One of the more interesting aspects of this project was describing the flora on longleaf plantation and natural stands to determine which species have been eradicated from a particular site and which species have remained intact. This information can be used to help determine proper management objectives for conservation and to aid in ecological restoration of these areas. Table 5.1 contains a list of species restricted to either plantations or natural stands at the Savannah River Site. The presence or absence of a species from a particular area (plantation or natural site) can be used as a tool to evaluate the condition of a site and its potential for restoration. Species restricted to a particular site at the Savannah River Site are of particular interest to plant and forest ecologists. For instance, native plants endemic to longleaf pine communities found only on natural longleaf stands at the Savannah River Site include such species as *Aristida beyrichiana*, *Baptisia lanceolata*, and *Nolina georgiana*. These species, which have been found to be particularly sensitive to ground disturbance and fire suppression, are fairly good indicators of a herbaceous layer characteristic of natural longleaf pine communities.

Rare, Threatened or Endangered Species

Several vascular plant species found in longleaf ecosystems at the Savannah River Site are relatively uncommon to this region. These species are categorized by their population frequency (and health) and are of particular interest to plant and restoration ecologists across the southeast. Species found on longleaf plantations and natural stands at the Savannah River fall into several categories, ranging from infrequent populations at the Savannah River Site, to state and Federal listed species. Most of these species are

Table 5.1. Species restricted to longleaf plantation and natural sites at the Savannah River Site.

PLANTATION	NATURAL
Amphicarpa bracteata	*Agave virginica*
Andropogon gerardii	*Allium canadense*
Apios americana	*Amianthium muscaetoxicum*
Agrostris hyemalis	*Amorpha herbacea*
Aristida lanosa	*Andropogon ternarius*
Asclepias viridiflora	*Antennaria plantaginifolia*
Aster dumosus	*Aristida beyrichiana*
Aureolaria pedicularia	*Aristida purpurascens*
Campsis radicans	*Asclepias verticillata*
Cassia obtusifolia	*Aster undulosus*
Celtis laevigata	*Baptisia alba*
Celtis tenuifolia	*Baptisia lanceolata*
Chionanthus virginicus	*Bellis perennis*
Croton spp.	*Carphephorus bellidifolius*
Cynodon dactylon	*Chrysogonum virginianum*
Cyperus filiculmis	*Cocculus carolinus*
Cyperus rotundus	*Coreopsis verticillata*
Desmodium nutallii	*Cyperus plukenetii*
Dichanthelium meridionale	*Danthonia spicata*
Dichanthelium ravenelii	*Delphinium carolinianum*
Epigea repens	*Desmodium tortuosum*
Erigeron strigosus	*Dichanthelium chamaelonche*
Eupatorium aromaticum	*Dichanthelium scoparium*
Euthamia tenuifolia	*Dichanthelium tenue*
Galium circaezans	*Dichanthelium villosissimum*
Gaura filipes	*Dioscorea villosa*
Hamamelis virginiana	*Duchesnea spp.*
Helenium amarum	*Echinacea laevigata*
Helianthemum rosmarinifolium	*Erechtites hieracifolia*
Hypericum denticulatum var. reticulatum	*Eryngium yuccifolium*
Juglans nigra	*Fothergilla gardenii*
Lechea sessilifolia	*Galactia volubilis*
Lespedeza striata	*Gentiana spp.*
Onosmodium virginianum	*Helianthus hirsutus*
Penstemon australis	*Helianthus angustifolius*
Pinus elliottii	*Houstonia longifolia*
Piptochaetium divaraceum	*Hymenopappus scabiosaeus*
Platanus occidentalis	*Hypericum canadense*

Table 5.1. (Continued)

PLANTATION	NATURAL
Potentilla spp.	*Hypericum stans*
Scleria ciliata	*Hypericum gentianoides*
Scleria ciliata var. *glabra*	*Ilex decidua*
Scleria pauciflora	*Ilex vomitoria*
Seymaria cassioidies	*Ipomoea pandurata*
Solanum canadense	*Juniperus virginiana*
Solidago caesia	*Lespedeza stipulacea*
Sorghastrum nutans	*Ligusticum canadense*
Spiranthes grayi	*Magnolia virginiana*
Tephrosia spicata	*Malus angustifolia*
Trichostema dichotomum	*Marshallia obovata* var. *scaposa*
Trifolium incarnatum	*Nestronia umbellula*
Viburnum rifidulum	*Nolina georgiana*
Zornia bracteata	*Oenothera lacinata*
	Paspalum floridanum
	Passiflora lutea
	Persea borbonia
	Phlox carolina
	Physalis virginiana
	Potentilla canadensis
	Quercus coccinea
	Quercus phellos
	Rhexia lutea
	Robinia pseudoacacia
	Rosa carolina
	Rudbeckia fulgida
	Rumex hastatulus
	Sabatia angularus
	Silphium dentatum
	Smilax laurifolia
	Solidago fistulosa
	Strophostyles umbellata
	Thaspium trifoliatum
	Tillandsia usneoides
	Tragia urticifolia
	Vaccinium corymbosum
	Verbena canadensis
	Viola papilionaceae
	Viola septemloba

Table 5.1. (Continued)

PLANTATION	NATURAL
	Viola villosa *Wahlenbergia marginata* *Zigadensus densus*

considered rare or threatened to the Hilly Coastal Plain Region of South Carolina, in particular, the Savannah River Site.

Plantation sites are not generally noted for presence of rare species, due in part to the severe ground disturbance that most of these stands have been subjected to over the years. Severe ground disturbances, coupled with years of fire exclusion, have all but eliminated most rare and threatened species populations at the Savannah River Site under artificial conditions. Table 5.2 contains a list of species considered rare or threatened found in longleaf pine plantations at the Savannah River Site. Of these, only two species observed were state listed, *Paspalum bifidum* and *Dichanthelium aciculare*.

The presence of rare species increased tremendously from plantation to natural sites. Strictly from an ecological standpoint, there were many more interesting species found on natural stands when compared to plantations. On well-maintained sites, state listed species such as *Nolina georgiana*, *Baptisia lanceolata*, and *Dichanthelium aciculare* were observed regularly. The two least common species found on natural longleaf stands was the state listed Carolina larkspur (*Delphinium carolinianum*), and the Federally endangered smooth purple coneflower (*Echinacea laevigata*). The smooth purple coneflower is considered globally imperiled and was found on only one site. Refer to Table 5.3 for a complete list of rare, threatened, or endangered species found on natural sites at the Savannah River Site.

Table 5.2. Rare, threatened, and endangered species, and their status, found on longleaf plantation sites at the Savannah River Site.

Common Name	**Scientific Name**	**Status**[1]	**SRS**[2]	**GRANK**[3]	**SRANK**[4]
Sedge	Carex tenax	-----	Rare	-----	-----
Catbells, Gopherweed	*Baptisia perfoliata*	-----	Rare	-----	-----
Witchgrass	*Dichanthelium fusiforme*	-----	Rare	-----	-----
Low Stiff Witchgrass	*Dichanthelium ovale*	-----	Rare	-----	-----
Broomsedge	*Dichanthelium aciculare*	SC	Rare	G4G5	S?
Paspalum	*Paspalum bifidum*	SC	Rare	G5	S?
Smooth nutrush	*Scleria ciliata var. glabra*	-----	Rare	-----	-----
Wild Indigo	*Indigofera caroliniana*	-----	Rare	-----	-----

[1]Status – legal status of species
SC – of Concern, State
[2]SRS – Species of Concern at the Savannah River Site
[3]GRANK – The Nature Conservancy rating of degree of endangerment; Globally
G4 – Apparently secure globally, though may be rare in parts of its range
G5 – Demonstrably secure globally, though it may be rare in parts of its range
[4]SRANK – The Nature Conservancy rating of degree of endangerment; State
S? – Status unknown

Table 5.3. Rare, threatened, and endangered species, and their status, found on natural longleaf sites at the Savannah River Site.

Common Name	Scientific Name	Status[1]	SRS[2]	GRANK[3]	SRANK[4]
Whorled Milkweed	Asclepias verticillata	-----	R	-----	-----
Thick-Pod White Wild Indigo	*Baptisia alba*	-----	R	-----	-----
Baptisia	*Baptisia lanceoloata*	SC	R	G4?	S?
Catbells, Gopherweed	*Baptisia perfoliata*	-----	R	-----	-----
English Daisy	*Bellis perennis*	-----	R	-----	-----
Sedge	*Carex tenax*	-----	R	-----	-----
Carolina Larkspur	*Delphinium carolinianum*	SC	R	G5	S?
Broomsedge	*Dichanthelium aciculare*	SC	R	G4G5	S?
Carpet Witchgrass	*Dichanthelium chamaelonche*	-----	R	-----	-----
Witchgrass	*Dichanthelium fusiforme*	-----	R	-----	-----
Low Stiff Witchgrass	*Dichanthelium ovale*	-----	R	-----	-----
Smooth Coneflower	*Echinacea laevigata*	FE	E	G2G3	S1
Coastal Witch Alder	*Fothergilla gardenii*	-----	R	-----	-----
Eastern Longleaf Bluet	*Houstonia longifolia*	-----	R	-----	-----
Woolly White	*Hymenopappus scabiosaeus*	-----	R	-----	-----
Yaupon	*Ilex vomitoria*	-----	R	-----	-----
Wild Indigo	*Indigofera caroliniana*	-----	R	-----	-----
Nestronia	*Nestronia umbellula*	SC	R	G4	S2
Georgia Beargrass	*Nolina georgiana*	SC	R	G3G5	S?
Paspalum	*Paspalum bifidum*	SC	R	G5	S?
Meadow Parsnip	*Thaspium trifoliatum*	-----	R	-----	-----
Southern Woolly Violet	*Viola villosa*	-----	R	-----	-----

[1]Status – Legal status of species
FE – Federally Endangered
SC – Of Concern, State
[2]SRS – Species of concern at Savannah River Site
R – Rare
E – Endangered
[3]GRANK – The Nature Conservancy rating of degree of endangerment; Globally
G2 – Imperiled globally because of extreme rarity or because of some factor(s) making it especially vulnerable to extinction
G3 – Either very rare throughout its range or found locally in a restricted range, or having factors making it vulnerable
G4 – Apparently secure globally, though it may be rare in parts of its range
G5 – Demonstrably secure globally, though it may be rare in parts of its range
[4]SRANK – The Nature Conservancy rating of degree of endangerment; State
S1 – Critically imperiled state-wide because of extreme rarity or because of some factor(s) making it especially vulnerable to extirpation
S2 – Imperiled state-wide because of rarity or factor(s) making it vulnerable
S? – Status unknown

CHAPTER VI

CONCLUSIONS

While there is much interest in the structure and composition of vegetation on longleaf pine ecosystems, remarkably little has been subjected to rigorous ecological study (Peet and Allard 1993). This is especially true of compositional variation over limited ranges of soil conditions. This study focused not only on the structure and composition of vegetation on mature longleaf plantations at the Savannah River Site, but also described and compared vegetation structure and composition of plantations to that of natural stands of longleaf pine across a soil moisture gradient ranging from moist to dry soil conditions.

Three distinct vegetative communities were described for both longleaf plantation and natural sites across a soil moisture gradient at the Savannah River Site. Presence/absence of the B horizon, soil pH, and percent sand in the underlying soil horizons (B or C) were the most discriminating environmental variables separating plant communities on longleaf plantation sites. On natural stands, eleven discriminating variables were used to separate plant communities: the presence/absence of the B horizon, landform index, levels of soil magnesium, sodium, calcium, nitrogen, potassium, and organic matter, and percent sand in respective horizon (A, B, and C horizons). Variables controlling the distribution of vegetation among natural groups are not as clearly defined as plantation groups. The presence or absence of a B horizon was the most discriminating environmental variable discriminating among groups for both plantation and natural stands.

Plots were separated into two distinct associations based on origin (plantation or natural). Further, the most similar groups of plots between plantation and natural stands were those that occurred on the most extreme xeric end of the soil moisture gradient. Although overall species richness was significantly higher on natural stands, vegetation composition and structure on these sites were most similar for both xeric plantations and natural stands. This work suggests that well-burned xeric longleaf plantations that have undergone limited soil disturbance may not be as degraded as previously thought (Noss 1989; Abrahamson and Hartnett 1990; Mejeur et al., submitted).

Out of the 265 species found on plantation sites sampled, about 90 percent were judged to be species representative of natural or native longleaf pine sites. The lack of compositional differences between xeric plantation and natural stands suggests that restoration of the herbaceous layer of longleaf plantations may not be as complex as often thought. Restoration of plantation sites may require the reintroduction of only several native species to the landscape, as well as management practices best suited to maintain natural conditions, such as frequent burning and thinning of the canopy to restore herb vigor (Mejeur et al., submitted).

The findings presented in this study should provide reasonable encouragement for longleaf pine ecosystem restoration. Although data may suggest similarities in vegetation composition and structure occur mostly on extreme xeric sites, restoration on more mesic (and consequently more disturbed) sites appears attainable with more aggressive management practices.

APPENDIX

PHYLOGENETIC LIST OF VASCULAR PLANTS FOUND ON LONGLEAF PINE DOMINATED STANDS AT THE SAVANNAH RIVER SITE

LLP indicates species only occurring on longleaf plantation sites and LLN indicates species only occurring on natural longleaf sites.

ACERACEAE

Acer rubrum L., Red maple

POACEAE

Agrostris hyemalis (Walter) BSP., Bent grass
Andropogon gerardii Vitman, Big bluestem, Turkeyfoot (LLP)
Andropogon ternarius Michaux var. *ternarius**, Splitbeard bluestem (LLN)
Andropogon virginicus L., Broomstraw
*Aristida beyrichiana** Trinius & Ruprecht, Southern wiregrass (LLN)
Aristida lanosa Muhl. ex Ell., Woolysheath Three-awn grass (LLP)
*Aristida purpurascens** Poiret, Arrowfeather (LLN)
Cynodon Dactylon (L.) Persoon, Bermuda grass
Danthonia sericea Nuttall, Silky oat-grass
Danthonia spicata (L.) Beauvois ex R. & S. (LLN)
*Dichanthelium aciculare** (Desvaux ex Poiret) G. & C., Needle witch grass
*Dichanthelium acuminatum** (Swartz) G. & C., Woolly witch grass
*Dichanthelium angustifolium** (Elliott) Gould, Narrow-leaved witch grass
*Dichanthelium boscii** (Poiret) G. & C., Bosc's witch grass
*Dichanthelium species 6 (=chamaelonche)** Carpet witch grass (LLN)
*Dichanthelium commutatum** (Schultes) Gould, Variable witch grass
*Dichanthelium dichotomum** (L.) Gould, Forked witch grass
*Dichanthelium species 8 (=fusiforme)** Spindle- fruited witch grass
*Dichanthelium laxiflorum** (Lamarck) Gould, Open-flower witch grass
*Dichanthelium meridionale** (Ashe) Freckmann, Matting witch grass (LLP)
*Dichanthelium oligiosanthes** (Schultes) Gould, Few-flowered witch grass
Dichanthelium ovale (Elliot) G. & C. var *addisonii** (Nash) G & C, Low stiff witch grass
*Dichanthelium ravenelii** (Scribner & Merrill) Gould, Ravenel's witch grass (LLP)
*Dichantheliun scoparium** (Lamarck) Gould, Velvet witch grass (LLN)
*Dichanthelium sphaerocarpon** (Elliot) Gould, Round-fruited witch grass
*Dichanthelium species 7 (=tenue)** White-edged witch grass (LLN)

Dichanthelium villosissimum (Nash) Freckmann var. *villosissiumum** White haired witch grass (LLN)
Gymnopogon ambiguus (Michaux) BSP., Eastern beard grass
Gymnopogon brevifolius Trinius, Pineland beard grass
Panicum anceps Michaux, Beaked panic grass
Panicum spp. L., Panic grass
Paspalum bifidum (Bertolina) Nash
Paspalum floridanum Michaux (LLN)
Paspalum setaceum Michaux
*Schizachyrium scoparium** (Michaux) Nash, Common little bluestem
Sorghastrum nutans (L.) Nash, Yellow Indiangrass (LLP)
Sporobolis junceus (Michaux) Kunth, Sandhills dropseed

CYPERACEAE
Carex tenax Chapman.
Cyperus filiculmis Vahl. (LLP)
Cyperus plunkenetii Fernald (LLN)
Cyperus rotundus L., Nutsedge, Nutgrass (LLP)
Cyperus ovularis (Michaux) Torrey
Rhynchospora grayi Kunth Gray's beaksedge
Scleria ciliata Michaux, Hairy nutrush (LLP)
Scleria ciliata Michaux var. *glabra** (Chapman) Fairy, Smooth nutrush (LLP)
Scleria pauciflora Muhl. ex Willd., Pappilose nutrush (LLP)
Scleria triglomerata Michaux, Tall nutrush

VITACEAE
Ampelopsis arborea (L.) Koehne, Pepper-vine

FABACEAE
*Amorpha herbacea** Walter, Dwarf Indigo-bush (LLN)
Amphicarba bracteata (L.) Fernald, Hog peanut (LLP)
Baptisia alba (L) Ventenat var. *alba**, Thick-pod white wild indigo (LLN)
Baptisia cinerea (Raf.) Fernald & Schubert, Carolina wild indigo
Baptisia lanceolata (Walter) Elliott var. *lanceolata** (LLN)
Baptisia perfiolata (L.) R. Brown, Catbells, Gopherweed
Baptisia tinctoria (L.) R. Brown, Honesty-weed, Rattleweed
Cassia nictitans L., Wild sensitive plant
Cassia fasciculata Michaux, Partridge pea
Cassia obtusifolia L., Sicklepod (LLP)
Centrosema virginianum (L.) Bentham, Butterfly pea
Apios americana Medikus, Groundnut (LLP)
Clitoria mariana L., Butterfly pea
Crotalaria angulata Miller, Rattlebox
Desmodium canescens (L.) DC., Hoary tick-trefoil
Desmodium ciliare (Muhl. ex Willd.) DC.
Desmodium fernaldii Schubert, Fernald's tick-trefoil

Desmodium glabellum (Michaux) DC.
Desmodium laevigatum (Nuttall) DC.
Desmodium lineatum DC., Matted tick-trefoil
Desmodium marilandicum (L.) DC.
Desmodium nutallii (Schindler) Schubert (LLP)
Desmodium paniculatum (L.) DC.
Desmodium rotundifolium DC., Dollarleaf, Roundleaf tick-trefoil
Desmodium strictum (Pursh) DC., Pineland tick-trefoil
Desmodium vridiflorum (L.) DC.
Desmodium tortuosum (Swartz) DC. (LLN)
Galactia macreei M. A. Curtis
Galactia regularis (L.) BSP.
Galactia volubilis (L.) Britton
Indigofera caroliniana Miller, Wild indigo, Carolina indigo
Lespedeza capitata Michaux, Bush-clover
Lespedeza cuneata (Dumont) G. Don, Sericea Lespedeza
Lespedeza hirta (L.) Hornemann, Hairy Lespedeza
Lespedeza intermedia (Watson) Britton, Wand Lespedeza
Lespedeza procumbens Michaux, Downy trailing Lespedeza
Lespedeza repens (L.) Barton, Smooth trailing Lespedeza
Lespedeza stipulacea Maxim., Korean clover (LLN)
*Lespedeza striata** (Thunberg), H. & A., Japanese clover
Lespedeza stuvei Nuttall, Velvety Lespedeza
Lespedeza virginica (L.) Britton, Virginia lespedeza
Rhynchosia reneformis DC., Dollarweed
Robinia pseudoacacia L., Black locust (LLN)
Schrankia Microphylla (Solander ex Smith) Macbride, Sensitive briar
Stylosanthes biflora (L.) BSP., Pencil flower
Strophostyles umbellata (Muhl. ex Willd.) Britton (LLN)
Tephrosia spicata (Walter) T. & G. (LLP)
Tephrosia florida (Dietrich) C. E. Wood
Tephrosia virginiana (L.) Persoon, Goat's rue
Trifolium incarnatum L., Crimson clover
Zornia bracteata Walter ex J. F. Gmelin, Zornia

APOCYNACEAE
Amsonia ciliata Walter, Blue star

CARYOPHYLLACEAE
Arenaria caroliniana Walter, Sandwort

ARISTOLOCHIACEAE
Aristolochia serpentaria L., Turpentine root, Virginia snakeroot

ASCLEPIADACEAE
Asclepias amplexicaulis Smith, Milkweed

Asclepias humistrata Walter, Milkweed
Asclepias tuberosa L., Butterfly-weed, Pleurisy-root
Asclepias verticillata L., Milkweed (LLN)
Asclepias viridiflora Raf., Milkweed (LLP)

ASPLENIACEAE
Asplenium platyneuron (L.) Oakes, Ebony spleenwort

ASTERACEAE
Antennaria plantaginifolia (L.) Richardson, Pussy-toes (LLN)
Aster paternus Cronquist, White-topped aster
Aster patens Aiton, Clasping aster
Aster concolor L., Eastern silvery aster
Aster linariifolius L., Stiff-leaved aster
Aster dumosus L., Long-stalked aster (LLP)
Aster tortifolius Michaux., White-topped aster
Aster undulatus L., Aster (LLN)
Bellis perennis L., English daisy (LLN)
Berlandiera pumila (Michaux) Nuttall, Eastern green eyes
Carphephorous bellidifolius (Michaux) T. & G.
Chrysogonum virginianum L., Green-and-gold (LLN)
Chrysopsis gossypina (Michaux) Shinners
*Cirsium repandum** Michaux, Sandhills thistle
Coreopsis major Walter
Coreopsis verticillata L. (LLN)
Elephantopus tomentosus L., Elephant's foot
*Conyza canadensis** (L.) Cronquist, Common horseweed
Echinaceae laevigata (Boynton & Beadle) Blake, Smooth purple coneflower (LLN)
Erechtites hieracifolia (L.) Raf., Fireweed (LLN)
Erigeron strigosus Muhl. ex Willd., Daisy fleabane (LLP)
Eupatorium album L., White-bracketed thoroughwort
Eupatorium aromaticum L., Thoroughwort (LLP)
Eupatorium capillifolium (Lam.) Small, Common dog-fennel
Eupatorium compositifolium Walter, Coastal dog-fennel
*Eupatorium glaucascens** Elliott, Wedgeleaf Eupatorium, Broadleaf bushy Eupatorium
Eupatorium hyssopifolium L., Hyssopleaf Eupatorium
Eupatorium rotundifolium L., Common roundleaf Eupatorium
Euthamia tenuifolia (Pursh) Nuttall (LLP)
Gnaphalium obtusifolium L., Rabbit tobacco
Gnaphalium purpureum L.
Helianthus angustifolius L., Sunflower (LLN)
*Helenium amarum** (Raf.) H. Rock, Bitter-weed
Helianthus hirsutus Raf., Sunflower (LLN)
Helianthus spp. L., Sunflower

Hieracium gronovii L., Hawkweed
Hymenopappus scabiosaeus L'her., Wooly-white (LLN)
Krigia virginica (L.) Willd., Virginia dwarf-dandelion
Kuhnia eupatorioides L., False boneset
Lactuca graminifolia Michaux
Liatris tenuifolia Nuttall
Liatris spp. Schreber, Blazing star
Marshallia obovata var. *scaposa* Channell (LLN)
*Pityopsis aspera** (Shuttleworth ex Small) Small
Pyrrhopappus carolinianus (Walter) DC., False-dandelion
Rudbeckia fulgida Aiton (LLN)
Senecio aureus L., Ragwort
Silphium dentatum Ell. (LLN)
Silphium compositum Michaux
Solidago caesia L., Axillary goldenrod, Blue-stem goldenrod (LLP)
Solidago fistulosa Miller (LLN)
Solidago nemoralis Aiton, Southern gray goldenrod
Solidago odora Aiton, Licorice goldenrod
Vernonia angustifolia Michaux, Ironweed

SCROPHULARIACEAE
Aureolaria pectinata (Nuttall) Pennell, Southern oak-leach
Aureolaria pedicularia (L.) Raf., Appalachian Annual oak-leach (LLP)
Seymeria cassioides (J.F. Gmelin) Blake (LLP)

RHAMNACEAE
Berchemia scandens (Hill) K. Koch
Ceanothus americanus L., New Jersey tea

VERBENACEAE
Callicarpa americana L., French mulberry, Beauty-berry

BIGNONIACEAE
Campsis radicans (L.) Seeman, Trumpet-creeper, Cow-itch vine (LLP)

JUGLANDACEAE
Carya glabra (Miller) Sweet, Pignut hickory
Carya pallida (Ashe) Engler & Graebner, Pale hickory, Sand hickory
Carya tomentosa (Poiret) Nuttall, Mockernut hickory
*Juglans nigra** L., Black walnut

ULMACEAE
Celtis laevigata Willd, Sugarberry, Hackberry (LLP)
Celtis occidentalis var. *georgiana* L., Sugarberyy, Hackberry
Ulmus alata Michaux, Winged elm

CELTIDACEAE*

*Celtis tenuifolia** Nuttall, Dwarf hackberry, Georgia hackberry (LLP)

ERICACEAE

Chimaphala maculata (L.) Pursh, Spotted wintergreen, Pipsissewa
Epigea repens L., Trailing-arbutus (LLP)
Gaylussacia dumosa (Andrz.) T. & G., Dwarf Huckleberry
Vaccinium arboreum Marshall, Sparkleberry
Vaccinium corymbosum L., Highbush blueberry (LLN)
Vaccinium stamineum L., Common deerberry

OLEACEAE

Chionanthus virginicus L, Fringe-tree (LLP)

EUPHORBIACEAE

Cnidoscolus stimulosus (Michaux) Engelm. & Gray, Spurge-nettle, Tread-softly
Croton spp. L. (LLP)
Euphorbia corolatta L., Flowering spurge, Tramps spurge
Euphorbia curtisii Engelm., White sandhills spurge
Euphorbia ipecacuanhae L., Carolina ipecac
Stillingia sylvatica Garden
Tragia urens L., Southeastern noseburn
Tragia urticifolia Michaux (LLN)

COMMELINACEAE

Commelina erecta L., Dayflower

CORNACEAE

Cornus florida L., Flowering dogwood

EBANACEAE

Diospyros virginiana L., Persimmon

ACANTHACEAE

Dyschoriste oblongifolia (Michaux) Kuntze, Pineland Dyschoriste

POLYGONACEAE

Eriogonum tomentosum (Michaux), Dog-tongue, Wild-buckwheat
Rumex hastatulus Baldwin ex Ell. (LLN)

RUBIACEAE

Galium circaezans Michaux, Southern forest bedstraw (LLP)
Galium hispidulum Michaux, Bedstraw
Galium pilosum Aiton, Bedstraw
Houstonia longifolia Gaertner (LLN)
Mitchella repens L., Partridge berry

ONAGRACEAE

Gaura filipes Spach, Threadstalk Gaura

LOGANIACEAE

Gelsemium sempervirens (L.) Aiton f., Yellow jessamine

HAMAMELIDACEAE

Fothergilla gardenii Murray, Witch-alder (LLN)
*Hamamelis virginiana** L., Witch-hazel
Liquidambar styraciflua L., Sweet-gum

CISTACEAE

Helianthemum canadense (L.) Michaux, Canada frostweed
Helianthemum caroliniamm (Walter) Michaux, Carolina sunrose
Helianthemum rosmarinifolium * Pursh, Rosemary sunrose
*Lechea sessiliflora** Rafinesque (LLP)
Lechea minor L., Thymeleaf pinweed
Lechea villosa Ell.

HYPERICACEAE

Hypericum canadense L. (LLN)
Hypericum denticulatum var. *reticulatum** HBK.
Hypericum gentianoides (L.) BSP., Pineweed (LLN)
Hpericum hypericoides (L.) Crantz, St. Andrew's Cross
Hypericum stans (Michaux) P. Adams & Robson, St. Peter's-wort (LLN)

AMARYLLIDACEAE

Hypoxis hirsuta (L.) Coville, Yellow star-grass

AQUIFOLIACEA

Ilex decidua Walter, Possum haw (LLN)
Ilex opaca Aiton, American holly
Ilex vomitoria Aiton, Yaupon (LLN)

CONVOLVULACEAE

Ipomoea lacunosa L., White morning-glory
Ipomoea pandurata (L.) G. F. W. Meyer, Manroot (LLN)

JUNCACEAE

Juncus dichotomous Ell.
Juncus tenuis Willd., Path rush

CAPRIFOLIACEAE

Lonicera japonica Thunberg, Japanese honeysucke
Lonicera sempervirens L., Coral honeysuckle
Viburnum rifidulum Raf., Blue haw (LLP)

MYRICACEAE
Myrica cerifera L., Wax myrtle

NYSSACEAE
Nyssa sylvatica Marshall, Black gum

BORAGINACEAE
Onosmodium virginianium (L.) A. DC., Virginia marbleseed (LLP)

CACTACEAE
Opuntia compressa (Salisbury) Macbride, Prickly pear cactus

VITACEAE
Parthenocissus quinquefolia (L.) Planchon, Virginia creeper
Vitis rotundifolia Michaux, Muscadine grape
Vitis labrusca L., Fox grape
Vitis aestivalis Michaux, Summer grape

PASSIFLORACEAE
Passiflora incarnata L., Maypops

SCROPHULARIACEAE
Penstemon australis Small (LLP)

SOLANACEAE
Physalis angulata L., Smooth ground cherry
Physalis spp. L., Ground cherry
Physalis virginiana Miller, Ground cherry (LLN)
Solanum carolinense L., Horse-nettle, Bell-nettle

PINACEAE
Pinus palustris Miller, Longleaf pine
Pinus elliottii Engelm., Slash pine (LLP)
Pinus taeda L., Loblolly pine
Pinus echinata Miller, shortleaf pine

TURNERACEAE
Piriqueta caroliniana (Walter) Urban

PLATANACEAE
Platanus occidentalis L., Sycamore (LLP)

POLYGALACEAE
Polygala polygama Walter, Southern bitter milkwort

LOGANIACEAE

Polypremum procumbens L.

ROSACEAE

Duchesnea indica (Andrz.) Focke, Indian strawberry, Mock strawberry (LLN)
Malus angustifolia (Aiton) Michaux, Crab-apple (LLN)
Potentilla spp. L. (LLP)
Potentilla canadensis L., Five-fingers (LLN)
Prunus serotina Ehrhart, Black cherry
Prunus angustifolia Marshall, Chickasaw plum
Prunus caroliniana Aiton, Carolina laurel cherry
Prunus umbellata Ell., Hog plum
Crataegus spp. L., Hawthorn
Pyrus communis L., Common pear
Rosa carilina L., Wild rose (LLN)
Rubus cuneifolius Pursh, Sand blackberry
Rubus spp. L., Blackberry

PTERIDACEAE

Pteridium aquilinium (L.) Kuhn, Bracken fern

FAGACEAE

Quercus coccinea Muenchh., Scarlet oak (LLN)
Quercus phellos L., Willow oak (LLN)
Quercus falcata Michaux, Southern red oak
*Quercus hemisphaerica** Bartram ex Willd., Sand laurel oak
Quercus incana Bartram, Blue-jack oak
Quercus laevis Walter, Turkey oak
Quercus margaretta Ashe, Scrubby post oak
Quercus marilandica Muenchh., Black jack oak
Quercus nigra L., Water oak
Quercus stellata Wang., Post oak
Quercus laurifolia Michaux, Laurel oak
Quercus velutina Lam., Black oak

ANACARDIACEAE

Rhus copallina L., Winged sumac
Rhus toxicodendron L., Poison oak
Rhus radicans L., Poison ivy

LAMIACEAE

Salvia azurea Lam., Azure sage
Trichostema dichotom L., Blue curls (LLP)

LAURACEAE

Persea borbonia (L.) Sprengel., Red bay (LLN)
Sassafras albidum (Nuttall) Nees., Sassafras

Scutellaria elliptica Muhl., Skullcap

LILIACEAE

Allium canadense L., Wild onion (LLN)
Amianthium muscaetoxicum (Walter) Gray., Fly-poison (LLN)
Nolina georgiana Michaux, Georgia beargrass (LLN)
Smilax bona-nox L., Greenbriar, Catbriar
Smilax glauca Walter, Greenbriar, Catbrier
Smilax laurifolia L., Bamboo (LLN)
Smilax rotundifolia L., Greenbriar, Catbriar
Smilax smallii Morong, Greenriar, Catbriar
Zigadensus densus (Desr.) Fernald, Black snakeroot, Crow-poison (LLN)

ORCHIDACEAE

Spiranthes grayi Ames, Little ladies' tresses (LLP)

CARYOPHYLLACEAE

Stipulicida setacea Michaux, Wire plant

STYRACACEAE

Styrax grandifolia Aiton, Bigleaf snowbell, Bigleaf styrax

SYMPLOCACEAE

Symplocos tinctoria (L.) L'her., Sweet leaf, Horse sugar

COMMELINACEAE

Tradescanthia rosea Vent., Spiderwort

VIOLACEAE

Viola pedata L., Bird-foot violet
Viola spp. L., Violet, Pansy
Viola papilionacea Pursh, Violet (LLN)
Viola septemloba House, Violet (LLN)
Viola villosa Walter, Violet (LLN)

AMARYLLIDACEAE

Agave virginica L., Agave (LLN)

MENISPERMACEAE

Cocculus carolinus (L.) DC., Coralbeads (LLN)

RANUNCULACEAE

*Delphinium caroliniamum** Walter, Carolina larkspur (LLN)

CANNACEAE

Dioscorea villosa L., Wild yam (LLN)

APIACEAE

Eryngium yuccifolium Michaux, Button snakeroot, Rattlesnake master (LLN)
Ligusticum canadense (L.), Britton, Lovage (LLN)
Thaspium trifoliatum (L.) Gray, Meadow parsnip (LLN)

GENTIANACEAE

Gentiana spp. L., Gentian (LLN)
Sabatia angularus (L.) Pursh, Rose pink, Bitter-bloom (LLN)

CUPRESSACEAE

Juniperus virginiana L., Red-cedar (LLN)

MAGNOLIACEAE

Magnolia virginiana L., Sweet bay (LLN)

SANTALACEAE

Nestronia umbellula Raf., Nestronia (LLN)

ONAGRACEAE

Oenothera laciniata Hill, Evening primrose (LLN)

PASSIFLORACEAE

Passiflora lutea L., Passion-flower (LLN)

POLEMONIACEAE

Phlox carolina L. (LLN)

MELASTOMATACEAE

Rhexia lutea Walter, Meadow-beauty (LLN)

BROMELIACEAE

Tillandsia usneoides L., Spanish moss (LLN)

VERBENACEAE

Verbena canadensis (L.) Britton (LLN)

CAMPANULACEAE

Wahlenbergia marginata (Thunberg) DC (LLN)

Nomenclature follows Radford et al. except where noted with an *, in which case nomenclature follows Weakley.

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