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The Ecological Classification of Coastal Wet Longleaf Pine (*Pinus palustris*) of Florida from Reference Conditions

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ABSTRACT

Tropical storms, fire, and urbanization have produced a heavily fragmented forested landscape along Florida's Gulf coast. The longleaf pine forest, one of the most threatened ecosystems in the US, makes up a major part of this fragmented landscape. These three disturbance regimes have produced a mosaic of differently-aged pine patches of single or two cohort structures along this coastline. The major focus of our study was to determine reference ecosystem conditions by assessing the soil biochemical properties, overstory stand structure, and understory plant species richness along a patch-derived 110-year chronosequence in order to accurately evaluate on-going longleaf pine restoration projects. This ecological dataset was also used to classify each reference patch as mesic flatwoods, wet flatwoods, or wet savanna. All of the reference locations were found to have similar soil types with no significant differences in their soil biogeochemistry. Mean diameter-at-breast height (DBH), tree height, and patch basal area increased as mean patch age increased. Stand growth reached a plateau around 80 - 90 years. Shrub cover was significantly higher in the mature-aged patches (86 - 110 years) than in the young (6 - 10 years) or mid-aged (17 - 52 years) patches, despite prescribed fire. Plant species diversity as indicated by the Shannon-Wiener index decreased with patch age. Soil biogeochemical properties, forest structure, and understory species composition were effective for ecologically classifying our pine patches as 55% mesic flatwoods, 20% wet flatwoods, and 25% wet savanna. Florida's Gulf coastal wet longleaf pine flatwoods attain a structural and plant species equilibrium between 80 - 90 years.

Keywords: Forest Structure; Species Richness; Restoration; Pine Patches; Shannon-Wiener; Soil Biogeochemistry

1. Introduction

In recent years, there has been a great effort to restore longleaf pine (*Pinus palustris* Mill.) communities within the southeastern U.S. They are one of the most threatened ecosystems in the United States having less than 3% of its original extent remaining [1]. Restoration projects have been implemented in an effort to restore more than 405,000 ha of longleaf pine in the Southeast during the past decade alone [2]. This effort continues with the goal to restore an additional 1,900,000 ha by 2015 [3].

Although many past studies have focused on the understory plant communities of longleaf pine ecosystems [4-7], less information exists on the spatial-temporal patterns of understory plant species as they relate to the soil biogeochemical properties and forest structure specifically situated within Florida's Gulf coastal flatwoods zone [8-10].

In addition, many researchers have classified longleaf pine sites along the lower Gulf coastal plain utilizing understory vegetation composition to separate one longleaf pine site from another [4,11,12]. A few have used fluvial vs. upland descriptions, climatic conditions, soil drainage patterns, and differences in soil texture to classify differently structured longleaf pine stands [13-15].

Coastal Wet Flatwoods

Most of Florida's wet pine flatwoods are concentrated along the 1240 km Gulf coastline, which contains marshes, bays, and offshore islands. This coastal landscape is continuously shaped by active fluvial deposition and weather processes which promote and maintain the formation of beaches, swamps and wet mineral flats. The topographic relief ranges from 0 to 20 m, the annual precipitation from 1300 - 1600 mm, while the average annual temperature ranges between 19˚C - 21˚C. Growing seasons are long, lasting 270 - 290 days [16]. Soil parent material consists of marine deposits containing limestone, marl, sand, and clay. The dominant suborders are Aquods, Aquents, and Aquepts, which are highly acidic poorly drained sandy soils having thermic and hyperthermic temperature regimes and an aquic moisture regime [17-19].

In Florida, plant species richness increases with soil moisture until an ecotone between mesic pine flatwoods and *Taxodium distichum* swamps is reached [5,12,20,21]. This ecotone is occupied by wet flatwoods and wet savanna subtypes of the coastal pine flatwoods [14,22,23]. Their overstories are dominated with varying mixtures of *Pinus palustris*, *Pinus elliottii*, *Pinus clausa* var. *immuginata*), and/or *Pinus serotina* [24,25]. The herbaceous ground cover of longleaf pine flatwoods is very diverse due to the warm temperatures and high rainfall. *Andropogon virginicus*, *Serenoa repens*, *Aristida stricta* var. *beyrichiana*, *Dichanthelium* spp., *Solidago odora*, *Rhexia alifanus*, and *Aster adnatus* are found throughout all of the flatwoods types [26,27]. Where fire is restricted, *Smilax pumila* can be a prevalent vine species, especially on mature mesic sites [14]. Mesic longleaf pine flatwoods are also occupied by greater populations of oak species (*Quercus pumila* or *laurifolia*). Wet flatwoods have a greater presence of *Lyonia lucida*, *Cliftonia monophylla*, *Nyssa sylvatica* var. *biflora*, and *Ilex glabra* or *coriacea*. Wet pine savannas are distinguished from wet flatwoods by fewer overstory trees, and a greater abundance of *Lachnanthes caroliniana*, *Cyperus*, *Scleria*, *Sarracenia*, and *Calopogon* or *Platanthera* [23,26,27]. Wet pine flatwoods and wet savannas are defined as pine-dominated, poorly drained, broad plain wetlands [14,28, 29], and represent more than one million ha in the Southeast [30]. There are almost 200 rare vascular plant taxa found in the various longleaf pine habitats of the Southeastern U.S. [5,12], with the majority of them being native to Florida where they are located in these wet pine flatwoods and their associated wetlands [5,12,14, 21,31].

Three disturbance regimes are important when identifying any pattern of structure or composition within coastal longleaf pine [9,10,32,33]. Hurricanes directly affect the canopy structure of longleaf pine stands through gale-forced winds, opening up large tracts to sunlight and simplifying the structure and composition of the flora that occupy them [8]. The extensive flooding that accompanies the wind causes significant changes in both the above and below ground site productivity [8,9,34]. Fire impacts longleaf pine forests by reducing vegetative competition on regeneration through the removal of shrub size oaks and hickories [35]. Finally, anthropogenic effects from urban development, grazing, prescribed fire, and plantation forestry can reduce the structural complexity of forests and promote fragmentation within the landscape, reducing soil productivity and plant species diversity [36,37].

The objectives of this study were to determine reference ecosystem conditions by assessing the soil biochemical properties, overstory stand structure, and understory plant species richness along a patch-derived 110-year chronosequence in order to accurately evaluate ongoing longleaf pine restoration projects [15,38]. This ecological dataset was also used to classify each reference patch as mesic flatwoods, wet flatwoods, or wet savanna; while verifying similarities between each patch and conditions at restoration sites of the zone. The importance of this work centers on our ability to distinguish between the varieties of longleaf pine habitats found along Florida's Gulf in order to accurately assess their condition. We hypothesized that stand diameter-at-breast height (DBH), height, basal area (BA), and volume would increase while stand density and plant species richness would decrease when comparing younger pine patches with older ones. We also expected the majority of these parameters to reach a threshold ("plateau") as measured from within the older-aged patches [39].

2. Materials and Methods

2.1. Study Sites

Three reference locations were established within 3 kilometers of Florida's Gulf coastline. A strict coastal stratification was required to insure all of the reference locations would be exposed to similar weather conditions, specifically addressing the fact that Florida's Gulf lies within a very active hurricane zone [8,15,40]. The locations were Topsail Hill State Park, St. Marks National Wildlife Refuge, and the Chassahowitzka Wildlife Management Area of the Florida Fish and Game Commission (**Figure 1**). In addition to their coastal locations, these sites were selected because of the presence of certain plant communities, containing similar soil conditions, and having active longleaf pine restoration programs [15].

This narrow zone makes up the majority of the Natural Resource Conservation Service's Eastern Gulf Coast Flatwoods ecoregion (MLRA 152A) and the National Oceanic and Atmospheric Association's Panhandle Coast unit of the Louisianan reserve (National Estuary and River Reserve System). In addition, the Environmental Protection Agency (EPA) classifies this area as the Southern Coastal Plain (75) ecoregion, which was recently subdivided into the Gulf Coast Lowlands (75-01) and the Big Bend Karst (75-06) [41,42]. All of these federal designations make this coastal zone unique from an ecological as well as hydrological perspective.

All three sites have a soil moisture gradient as represented by mesic pine flatwoods, wet pine flatwoods, wet pine savannas, and *Taxodium distichum* swamps. Their common soils are described as sandy, siliceous, thermic, aeric, acidic, and poorly drained. All three sites have active longleaf pine restoration programs where fire has

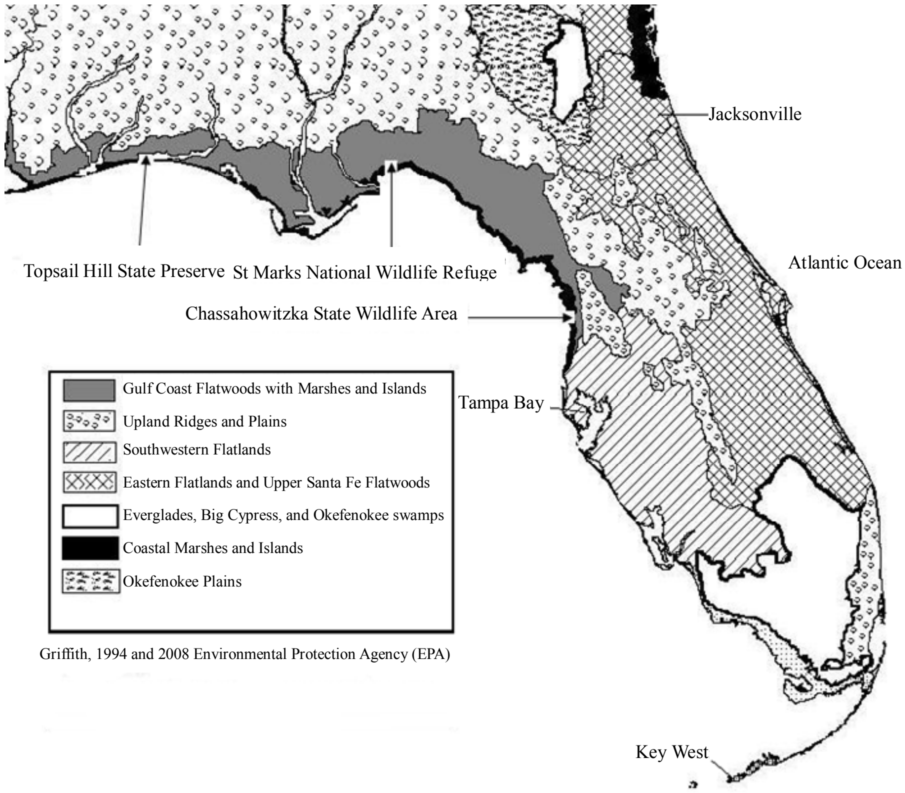

Figure 1. Locations of the three reference sites within the Gulf Coast Flatwoods subecoregion of Florida (Griffith *et al*. 1994, 2008).

been prescribed for more than 25 years at approximately a three-year-return interval. All of the sites are managed by a state or federal agency to enhance habitat for threatened species associated with longleaf pine ecosystems.

The southern reference site on the spatial gradient is the Chassahowitzka Wildlife Management Area (28˚78′47″N, 82˚34′26″W) in Hernando County, FL. It is approximately 12,140 ha, and the soils are dominated by Myakka fine sands (sandy, siliceous, hyperthermic, aeric, alaquods) and Basinger fine sands (sandy, siliceous, hyperthermic spodic Psammaquents) [17,43]. Even though this site is found within the Big Bend Karst (75-06) subecoregion, its coastal location contain vegetation and soils with greater similarity to the other study sites located within the neighboring Gulf Coast Lowlands (75-01) subecoregion [42,43]. The St. Marks National Wildlife Refuge (30˚6′18″N, 85˚11′7″W) in Wakulla and Jefferson Counties, FL consists of 25,900 ha with the major soils being the Leon series (sandy, siliceous, thermic, aeric, alaquods) and the Scranton series (sandy, siliceous, thermic, humaqueptic, Psammaquents); [19,44]. Topsail Hill State Park (30˚22′15″N, 86˚16′20″W) in Walton County, FL, contains 610 ha of some of the oldest longleaf pine stands in Florida. The park also contains important dune lake habitat. The soils are the Leon series and the Pickney sand series (sandy, siliceous, thermic, cumulic, humaquepts) [18,45].

Pine patches representing differently aged cohorts up to 110-years of longleaf pine succession have been included as the temporal scale applied in this study. The reference site and chronosequencial scale were only determined after an in-depth field survey of stand conditions along Florida's Gulf Coast Flatwoods zone.

2.2. Patch Age-Tree Size Classes

The 110-year patch-derived chronosequence is based upon measuring the selected longleaf pine patches starting from six years after stand replacement to the oldest patches (cohort) measured within our reference sites. Each reference location contained three distinctly-aged pine forests (one-hectare blocks) where four randomly placed 400 m^2 pine patches were measured from within each block. The patch size was based upon earlier longleaf pine flatwoods research which found the average gap size (cohort) to vary from 335 - 410 m^2 within natural pine stands [46]. The three following age-tree size class descriptions based upon collected field data provided a means of tying patch age to stand structure [39,47].

The young age-tree size class: A young age pine patch exists when at least 70% of the stocking is found as seedlings and saplings. Any minor pole component should have an average DBH less than 20 cm. The mid-age-tree size class: The mid age pine patch exists when at least 70% of the stocking is dominated by a mixture of poles and small sawlog size trees (10 - 30 cm DBH). The mature age-tree size class: A mature pine patch exists when at least 70% of the stocking is dominated by sawlog size trees (30 - 45 cm DBH). For this study, a seedling is defined as a woody plant that is generally less than 91.5 cm in height, while a sapling is a woody plant with a diameter-at-breast height (DBH) of less than 10 cm but greater than 2.5 cm. Finally, a tree is defined as a woody plant with a DBH of greater than 10 cm [48].

2.3. Data Collection

In order to examine natural phenomena as they exist, we conducted a non-experimental comparative survey of the ecological attributes from within the three reference locations. Therefore, field data collection utilized a modified nested approach to correspond with the average pine patch size found in Florida's coastal natural longleaf pine flatwoods [46,49]. Each reference location had three one-hectare blocks, representing each of the three previously defined patch age-tree size classes. Each one-hectare block contained four randomly placed 400 m^2 patches (cohort) used to take measurements [39]. Patch size was based on earlier longleaf pine flatwoods research that found the average gap size to vary from 335 to 410 m^2 in natural pine stands [46]. Tree height and DBH were measured on all trees greater than 10 cm. All saplings were measured for height and diameter (root collar). Patch density (trees/ha), basal area (BA) (m^2/ha) and standing volume (m^3/ha) were calculated from these data. At least 30% of the representative trees were cored at breast height to determine patch age. The equation used for tree volume was: Volume (V) = $(0.000078539816 * (DBH^2)) *$ tree height [48].

Each 400 m^2 measurement patch contained four 1-m^2 plots randomly nested within the larger patch for understory plant sampling. Stem counts and percent cover of each plant species were assessed using a modified Daubenmire method incorporating eight different coverages [49-51]. The list of species is found in the Species Code List (see **Appendix A**). Shannon-Weiner diversity values were calculated for each patch [52].

2.4. Soil Sampling and Preparation

Soil samples were taken from the top 10 cm within each 1 m^2 vegetation quadrat and stored at 4˚C until analysis. Sub-samples (20 g) were analyzed for soil pH by prepared slurries using a soil-to-water ratio of 1-to-2 [53], percent organic matter (SOM) content by the Walkley-Black method [54], and a sieved and dried (105˚C) sub-sample was used to determine gravimetric moisture content. Net nitrogen mineralization rates (N_{MIN}) were estimated from *in-situ* incubation of soil samples [55,56]. Soil microbial biomass carbon (C_{MB}) was determined by chloroform fumigation-extraction [57].

2.5. Statistical Analyses

A three-level balanced nested plot design was incorporated into a stratified random sample in order to integrate the different ecosystem attributes measured at different scales, and among sites. Patches previous grouped by the three age-tree size classes were further stratified using the specific ages of the cohorts they contained into five distinct time intervals (6 - 10, 17 - 34, 36 - 52, 60 - 71, 86 - 110). This allowed us to analyze changes in forest structure and plant species composition from one time interval to the next [58,59].

Since we conducted a non-experimental comparative survey of the ecological attributes of each site, the sampling of these nine distinct reference sites produced a dataset where the normality assumption needed for the analysis of variance (ANOVA) was not justified. Therefore, trends over time and between variables were obtained from linear polynomial regression using the general linear model [60]. The 2nd order polynomial regression equation standard form is $y = a^0 + a^1x + a^2x^2 + \varepsilon$. Regression models were validated by comparing residuals with predicted values along normal Q-Q plots and comparing F-ratios to eliminate higher order terms. Models were also tested for multicollinearity by variance inflation factors and condition index numbers.

PC-ORD, a PC-based program [61] containing an algorithm for Canonical Correspondence Analysis (CCA) was used to examine the overall spatial structure of the individual reference patches by identifying the understory plant species along vectors (gradients) for soil chemical, net nitrogen mineralization, and soil microbial biomass values found among the study sites [62]. Linear combinations of the environmental variables were used to maximize the separation of plant species along four biplot axes. Site scores were derived from the weighted averages of the associated species scores. Community structure was illustrated by the influence of different environmental variables upon plant species ordination [63].

Plant species indicator analysis (IndVal) was used to measure the level of relationship between a given plant species to categorical units such as pine flatwoods subtypes or patch age intervals. It was also used to attribute different plant species to particular soil biogeochemical conditions based on the abundance and occurrence of those species within the selected group. Indicator values range from 0 to 100, with "100" being a perfect indicator and "0" a no affiliation score. Because indicator species analysis is a statistical inference, the Monte Carlo permutation test procedure (1000 iterations) was used to establish significance of a p-value as determined by the number of random runs greater than or equal to the inferred value ($\alpha = 0.10$). Accuracy was defined from the binomial 95% confidence interval [64,65]. Hypothesis testing for differences between field data grouped by two soil drainage classes was accomplished by using two-sample t-test with an alpha of 0.05 and a two-tailed confidence interval. A Mixed model REML with F-ratios was used to determine the power of each collected field variable within the nested design along spatial and temporal scales [60].

3. Results and Discussion

3.1. Soil Types

All three sites contained taxonomically similar soil types. All of the soils had similar soil properties (sandy, acidic, thermic, aquic, and poorly drained). The soils were also found to be functionally equivalent (N_{MIN}, C_{MB} and BA); even when compared by drainage class (**Table 1**). The only significant difference was soil organic matter content between poorly drained and very poorly drained soils.

3.2. Overstory Stand Structure

A total of 36 measured pine patches resulted in 26 differently aged cohorts along the chronosequence. Five distinct patch age intervals were identified by data analysis. They were Young (6 - 10 years), Young-Midaged (17 - 34 years), Midaged (36 - 53 years), Mid-Mature (60 - 71 years), and Mature (86 - 110 years). The mean patch DBH, height, BA, and volume increased significantly among the five time intervals (**Table 2**). For example, the mean DBH for patches between 6 - 10 years after establishment was approximately 6.0 cm, 20 - 25 cm for the patches 35 - 52 years, and greater than 30.0 cm for the patches greater than 85 years (mature age). Height, BA, and volume exhibited similar results, even though stand density was highly variable with no identifiable temporal patterns (**Table 2**).

Polynomial regression analysis revealed all of the stand variables, except for stand density, increased with patch age. Patch mean DBH and height increased with age until they reached an asymptote at 85 - 90 yrs. Stand basal area and volume followed similar regression curves as with DBH and height (**Figure 2**). The diameter distribution of trees by patch age interval reflected the increase in diameter (**Figure 3**).

Table 1. Soil and stand properties between the three reference sites.

Location	Soil Great Group	Soil Texture (Top 10 cm)	Moisture Regime	Temperature Regime	Drainage Class
Chassahowitzka Wildlife Management Area					
	Psammaquent	Sandy	Aquic	Hyperthermic	Very poorly drained
	Alaquod	Sandy	Aquic	Hyperthermic	Poorly drained
St. Marks National Wildlife Refuge					
	Psammaquent	Sandy	Aquic	Thermic	Very poorly drained
	Alaquod	Sandy	Aquic	Thermic	Poorly drained
Topsail Hill State Preserve					
	Humaquept	Sandy	Aquic	Thermic	Very poorly drained
	Alaquod	Sandy	Aquic	Thermic	Poorly drained

Stand Basal Area and Soil Biochemical Properties (Mean Values*)

Drainage Class	Stand Basal Area (m^2/ha)	pH-log [H+]	Net Nitrogen Mineralization Rates (mg N/kg^{-1} soil/$month^{-1}$)	Microbial Biomass Carbon (mg C/kg^{-1} soil)
Very poorly drained	6.5a	4.4a	11.6a	374.3a
Poorly drained	8.3a	4.5a	9.9a	356.1a

*Means between drainage classes followed by the same lower case letters are not significantly different (alpha = 0.05).

Table 2. Stand attributes and species richness by patch age interval.

Patch Age Interval (years)	Patch Age Class	Mean Patch Diameter (cm)	Mean Patch Height (m)	Patch Density (trees/ha)	Patch Basal Area (m^2/ha)	Patch Volume (m^3/ha)	Shannon-Wiener Diversity H'
6 - 10	Young	5.1 (0.53)	2.5 (0.32)	258 (20.1)	0.12 (0.02)	9.3 (0.10)	1.96 (0.05)
17 - 34	Young/Mid	19.1 (0.77)	10.2 (0.25)	293 (20.0)	6.81 (0.48)	75.5 (5.59)	2.07 (0.05)
36 - 52	Mid-Age	25.5 (1.04)	15.4 (0.80)	211 (30.4)	8.56 (1.21)	138.3 (22.61)	1.75 (0.06)
60 - 71	Mid/Mature	29.6 (1.54)	15.4 (0.59)	229 (23.6)	11.59 (1.30)	186.9 (23.78)	1.75 (0.07)
86 - 110	Mature	29.9 (1.2)	16.6 (0.46)	190 (8.7)	11.83 (0.46)	214.3 (6.91)	1.44 (0.04)

The sample size for stand data by age class was $n \geq 6$; and for the vegetation-soils data $n \geq 12$.

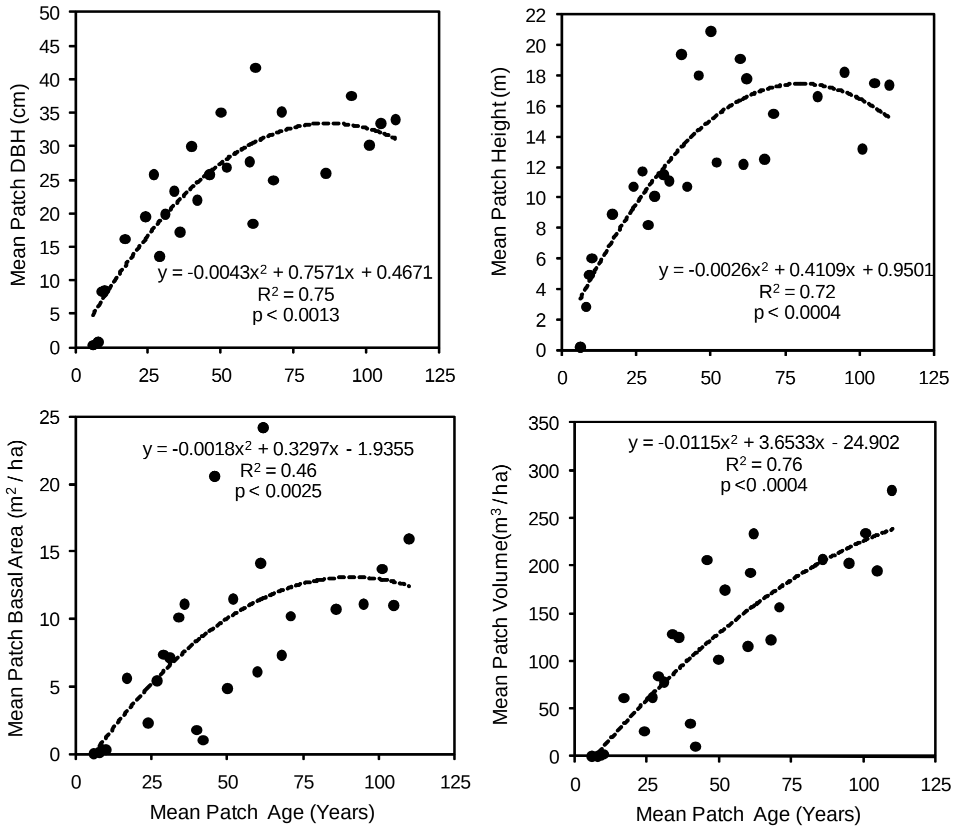

Figure 2. Mean stand DBH, height, BA, and volume along a 110-year longleaf pine chronosequence as measured from 26 differently aged pine patches.

3.3. Understory Plants

The three reference sites shared more than 45 plant species in common (**Appendix A**). The three most common understory species were *Ilex glabra*, *Quercus pumila*, and *Serenoa repens*. A species found in rare numbers among sites was *Xyris caroliniana*, a wetland indicator. The abundance of grasses and forbs decreased while the abundance of shrubs increased over the chronosequence ($p < 0.05$; **Figure 4**). The Shannon-Wiener diversity index decreased as patch age increased, while having a range from 2.07 - 1.44 for the dataset (**Table 2**; **Figure 5**).

3.4. Site Classification

Smilax pumila, *Hypericum hypericoides*, and *Gaylussacia frondosa* were the dominant plant species indicators for mesic flatwoods ($p \leq 0.038$), *Aristida stricta* var. *beyrichiana*, and *Dichanthelium ovale* were the dominant plant species indicators for the wet flatwoods subtype ($p \leq 0.001$), while *Lachnanthes caroliniana* and *Scleria cilliata* were the dominant plant species indicators for the wet savanna subtype ($p \leq 0.009$; **Table 3**). Twenty (20) patches were classified as mesic flatwoods, 7 patches as wet flatwoods, and 9 patches as wet savanna.

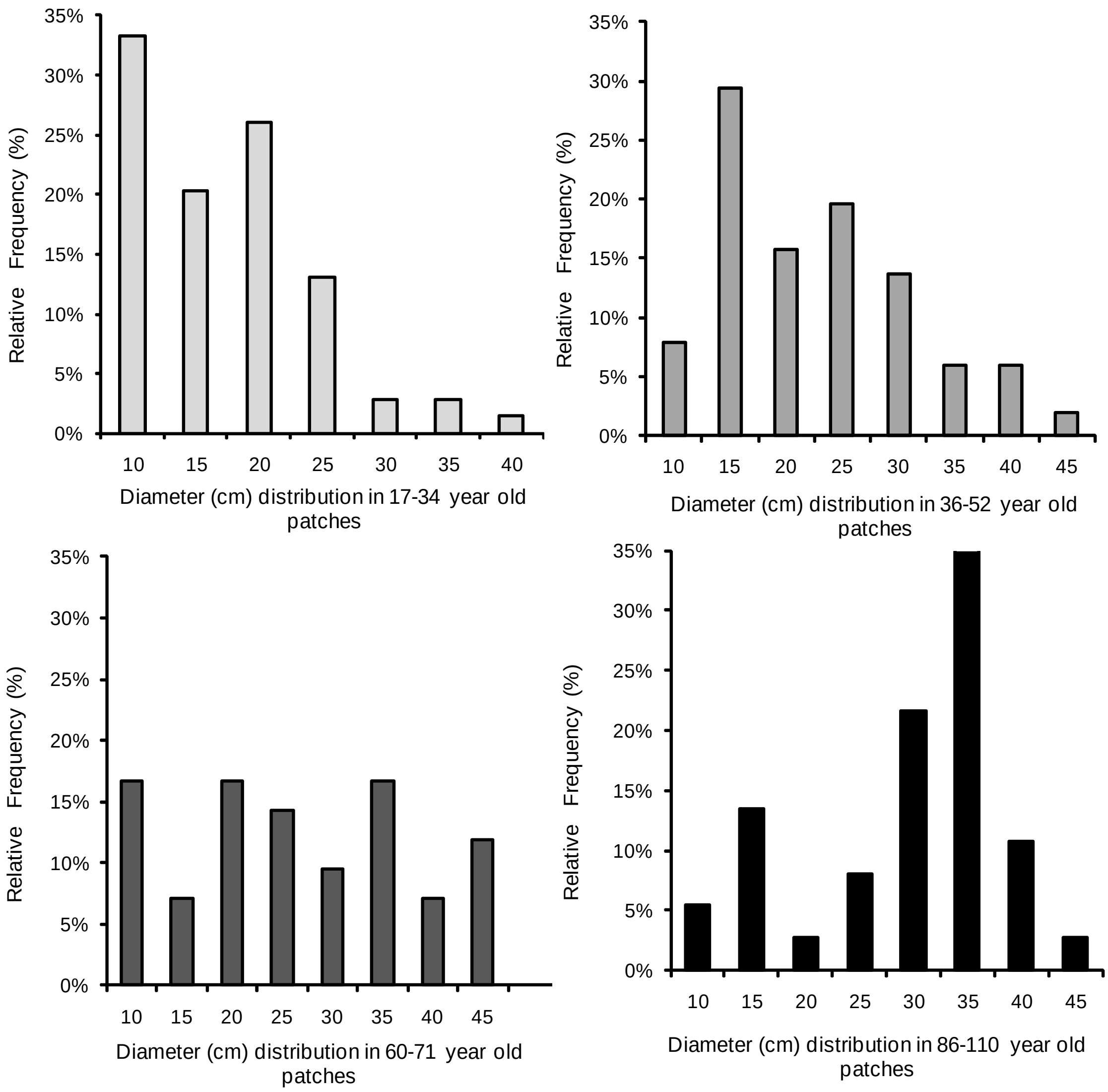

Figure 3. Diameter distribution of trees 10 cm d.b.h. and greater within the four patch age intervals as measured from 26 differently aged pine patches.

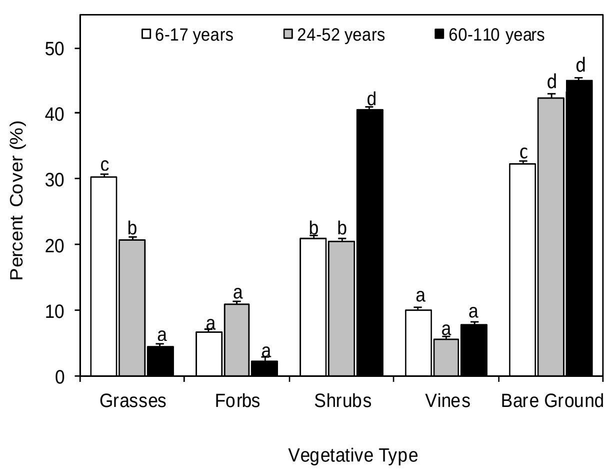

Figure 4. Composition of understory vegetation by patch age interval.

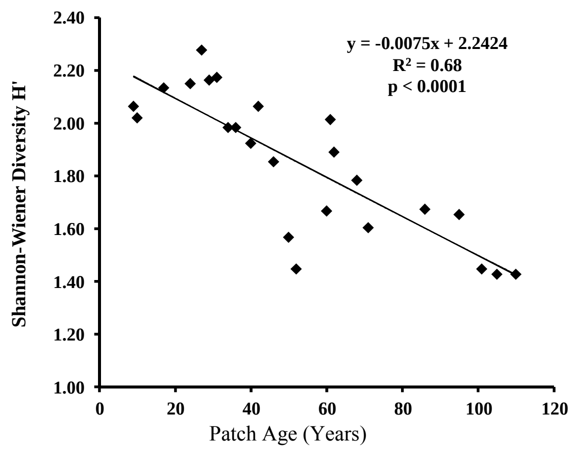

Figure 5. Shannon-Wiener Diversity index along a 110-year longleaf pine chronosequence as measured from 26 differently aged pine patches.

Table 3. Plant indicator values (IndVal*) (percent of perfect indication) with associated environmental variable by pine flatwoods type. P-values represent the proportion of randomized runs (1000) equal to or less than observed values ($\alpha = 0.1$).

Pine Subtype	Plant Species	Pine Subtype					
		Mesic	Wet Flatwoods	Wet Savanna	SD	P-Value	Veg Type
Mesic Flatwoods	*Smilax pumila*	25	1	5	4.69	0.038	Vine
	Hypericum hypericoides	17	1	0	3.08	0.024	Forb
	Gaylussacia frondosa	16	0	4	3.3	0.057	Shrub
	Pteridium aquilinum	12	0	1	3	0.066	Fern
Wet Flatwoods	*Lachnanthes caroliana*	0	52	4	3.57	0.001	Forb
	Arisitida beyrichiana	0	36	0	3.51	0.001	Grass
	Dichanthelium ovale	6	36	7	4.41	0.007	Grass
	Cyperus ssp.	1	11	1	2.67	0.088	Grass
Wet Savanna	*Ilex glabra*	19	13	38	3.55	0.009	Shrub
	Scleria ssp.	17	3	29	3.31	0.014	Grass

*INDICATOR VALUES (% of perfect indication based on combining the values for relative abundance and relative frequency) n = 48.

3.5. Discussion

There are four assumptions which must be met in order to insure the credible use of space-for-time substitutions (chronosequence) when studying ecosystem change [66]. They include having strong similarities in vegetative composition, soil properties, and climatic patterns, while sharing the same position in the landscape. There is also a need to have an extensive knowledge of the land-use history of each site. The use of a chronosequence to study secondary succession in coastal longleaf pine patches was justified given the close similarities (greater than 45 common species) in plant species composition, their almost identical soil properties found at each site, their location within the same climatic zone, their equivalent positions on the landscape, and the known 25 year land-use history of each reference site [67-69].

There were six major hurricanes which passed through our study sites during the 2004-2005 field seasons. The use of a strict coastline stratification proved to be effecttive at limiting the differences between the reference sites from the impacts of high winds and flooding on the forest canopies and soil properties of each site. The results on stand attributes, understory species diversity, and diameter distributions verify the effectiveness of the patch age intervals at stratifying the dataset (**Table 2**; **Figure 3**).

In response to criticisms against the use of the buried bag technique and the determination of field net mineralization rates instead of gross nitrogen fluxes [70,71], there was no need to determine the absolute (gross) levels of nitrogen uptake in this study. The wetland conditions of the sampled soils made the comparative measurement of ammonium more important then nitrate. When the purpose of the study is to compare similar forested wetland sites, it is perfectly justified to use polyethylene bags to determine the net nitrogen mineralization rates. The wetland conditions make the use of the ion exchange-resin bag technique very limited since the resin bags favor the collection of nitrate, and under estimate the levels of ammonium [70,72]. The use of polyethylene bags preserved the assessment of ammonium in saturated soils [73]. The plant uptake of nitrogen was less important since plants can compete for nitrate easier than they can for ammonium, which is the preferred source of nitrogen for microbes [74]. Wienhold (2007) found in-situ estimates are more reflective of field conditions than either anaerobic estimates or laboratory incubations [75].

The overstory variables of mean patch DBH, patch BA, volume, and to a lesser degree patch height exhibited strong positive relationships with the age of the pine patches between 6 - 110 years. But, patch tree density showed no clear pattern along the chronosequence, owing to the high variability found within the patches along Florida's Gulf. This is a reasonable result given the number of major hurricanes which impacted this landscape just prior to measurement. Patch tree density was continuously impacted by this disturbance regime during the life of the study. The ecological dataset showed most of the growth variables reaching an asymptote around 80 - 90 years. When the measured stand data from these pine patches was compared to growth and yield data from a group of thinned natural longleaf pine stands from across the eastern Gulf, our patches were found to have lower basal area (14 m^2 vs. 25 m^2) at age 30, but comparable stand volumes (150 m^3 vs. 130 m^3) at age 60 [76]. Our restoration threshold of 80-90 years was found to have a regional difference with the threshold age of 110 years for longleaf pine ecosystems in Texas, reported by Chapman (1909) [77].

Prescribed fire on a three year return-interval did not prevent shrub species from increasing or graminoid species from declining as the age of the pine patch increased. This result could be explained by lower intensive prescribed fires having less of an effect within the wet conditions encountered at our reference sites.

The vegetative and environmental variables collected from the reference sites were effective for ecologically classifying all of the patches. However, soil properties were stronger determinants of specific ecosystem conditions than were patch age determinations (**Table 1**; **Figure 6**).

4. Conclusions

All of the sites were found to have functionally equivalent soils and shared more than 40 plant species in common. Patch DBH, height, and basal area increased until 80 - 90 years when they reached a plateau. Shrub species were significantly higher in the mature-aged patches compared to either the young or mid-aged patches. These combined results infer that Florida's Gulf coastal wet longleaf pine flatwoods attain a structural and plant species equilibrium at approximately 80 - 90 years. Soil biochemical properties, forest structure, and understory species composition were effective for ecologically classifying our pine patches as 55% mesic flatwoods, 20% wet flatwoods, and 25% wet savanna within Florida's highly disturbed Gulf coast.

One area of this research warrants further attention. Our research found that plant species classified as "shrubs" dominated the mature-aged stands even with aggressive fire management programs. Many of these "woody" plant species do not have pioneer patterns similar to Ilex glabra, Serenoa repens, or Quercus pumila. They never dominated the site. There should be studies that focus on these lesser known woody species and their possible benefits to mature longleaf pine forest ecosystems.

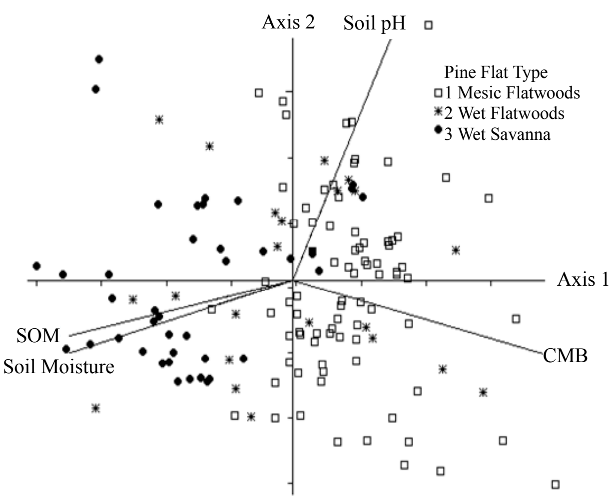

Figure 6. Pine flatwoods type determined by a four-dimensional ordination biplot derived from Canonical Correspondence Analysis (CCA) of 144 plots using understory plant species abundance and soil biogeochemical data (SOM, soil organic matter; CMB, microbial biomass carbon) from the three reference sites.

5. Acknowledgements

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Appendix A

Species Code List

Table A-1. Species list.

Scientific name	**Code**	Common name
Shrubs		
Asiminaincana	Asin	Wooly paw paw
Cyrillaracemiflora	Cyra	Titi
Gaylussaciadumosa	Gadu	Drawf huckleberry
Gaylussacia frondosa	Gafr	Dangleberry
Ilex coriacea	Ilca	Large gallberry
Ilex glabra	Ilgl	Gallberry
Ilex vomitoria	Ilvo	Yaupon
Kalmia hirsuta	Kahi	Hairy wicky
Licaniamichauxii	Limi	Gopher apple
Lyonia lucida	Lylu	Fetterbush
Magnolia virginiana	Mavi	sweet bay
Myricacerifera	Myce	Wax myrtle
Photiniapyrifolia	Phpy	Red choke berry
Quercus pumila	Qupu	Running oak
Serenoa repens	Sere	Saw palmetto
Stillangiasylvatica	Stsy	Queens delight
*Vaccinium*spp.	Vacc	Blueberry spp
Grasses		
Andropogon virginicus	Anvi	Bluestem grasses
Aristida stricta var. *beyrichiana*	Arbe	Wiregrass
Calamovilfacurtissii	Cacu	Curtis sandgrass
Cteniumaromaticum	Ctar	Toothache grass
Cyperus	Cype	Sedge spp
Eragrostisspectabilis	Ersp	Purple lovegrass
Dichanthelium ovale	Dich	Eggleaf witch grass
Panicum - Dichanthelium	Pani	Panicumspp
Dichantheliumerectifolium	Paer	Erect leaf witchgrass
Panicumlaxiflorum	Pala	Velvet Witchgrass
*Scleria*ssp.	Scle	Nutrushspp
Xyris caroliniana	Xyca	Yellow eyed grass
Forbs		
Asclepiasviridula	Asvi	Southern milkweed
Aster adnatus	Asad	Scaleleaf aster
Aster eryngiifolius	Aser	Thistleleaf aster
Aster reticulatus	Asre	White top aster
Aster tortifolius	Asto	Dixie aster
Carphephorouspseudoliatris	Caps	Bristleleafchaffhead
Carphephorusodoratissimus	Caod	Deer tongue
Chrysopsis	Chry	Silkgrassspp
Conyzacanadensis	Coca	Canadian horseweed

Continued

Coreopsis linifolia	Coli	Texas tickseed
Desmodiumrotundifolium	Dero	Tricklyfoil
Droseracapillaris	Drca	Pink sundew
Elephantopustomentosus	Elto	Devils grandmother
Eupatorium capillifolium	Euca	Dog fennel
Eupatorium compositifolium	Euco	Yankee weed
Eupatoriummohrii	Eumo	Mohr's thoroughwort
Eupatoriumpilosum	Eupi	Rough Boneset
Euthamiagraminifolia	Eugr	Flat top goldenrod
Gelsemiumsempervirens	Gese	Yellow jessamine
Gratiolahispida	Grhi	Rough Hedgehyssop
Hypericum hypericoides	Hyhy	St. Andrews cross
Hypoxissessilis	Hyse	Glossyseed yellow stargrass
*Hypoxis*spp.	Hypo	Stargrassspp
Lachnanthes caroliniana	Laca	Carolina redroot
Lachnocaulon anceps	Laan	Whitehead bogbutton
Lecheapulchella	Lepu	Leggett's pineweed
Liatrisgracilis	Ligr	Slender gayfeather
Liatristenuifolia	Lite	Shortleaf gayfeather
Mimosa quadrivalvis	Miqu	Sensitive brier
Oenotherafruticosa	Oefr	Evening primrose
Opuntiahumifusa	Ophu	Prickly pear
Pityopsisgraminifolia	Pigr	Silkgrass
Pterocaulonpycnostachyum	Ptpy	Blackroot
Rhexia alifanus	Rhal	Meadow beauty
Rhexiapetiolata	Rhpe	Fringed meadow beauty
Sabatiabrevifolia	Sabr	Shortleaf Rosegentian
Seymeriacassioides	Seca	Yaupon Blacksenna
Smilax laurifolia	Smla	Laurel green brier
Smilax pumila	Smpu	Green brier
Solidago odora	Sood	goldenrod
Stylismapatens	Stpa	Coastal plain dawn flower
Tragiaurens	Trur	Wavyleafnoseburn
Verbena brasiliensis	Vebr	Brazilian vervain
Viola septemloba	Vise	Blue violet
Vitisrotundifolia	Viro	Muscadine

