Age, Composition, and Stand Structure of Old-growth Oak Sites in the Florida High Pine Landscape: Implications for Ecosystem Management and Restoration

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Natural Areas Journal 19:30–40

ABSTRACT: We sampled tree age, species composition, and stand structure of four high pine sites composed of old-growth sand post oak (Q. *margaretta* Ashe), old-growth turkey oak (*Quercus Zaevis* Walt.), and young longleaf pine (*Pinus palustris* Mill.) in north and central peninsular Florida. The oldest turkey oak sampled was 123 years old, and the oldest sand post oak was 230 years old. Turkey oak exhibited the greatest diameter variation in relation to age. The median number of rings found in rotten and/or hollow turkey oaks was 63 and the corresponding number for sand post oak was 105. Age reconstruction indicated that in 1900 minimum oak tree ($\geq$ 5 cm diameter at breast height) density ranged from 10 to 60 trees ha^{-1} among sites. This study demonstrates that sandhill oak trees historically were an integral component of at least some phases of the high pine ecosystem. These data support the hypothesis that spatial patchiness and variability in fire frequency, season, and intensity historically permitted oaks to reach and maintain tree size in varying densities over time and across the high pine landscape.

Index terms: old growth, sandhills, high pine, ecosystem management, fire ecology

INTRODUCTION

The "high pine" ecosystem once was common throughout the Atlantic Coastal Plain from Virginia to east Texas (Myers 1990). In Florida community types commonly referenced as high pine are sandhill, clayhill, longleaf pine-turkey oak, upland longleaf pine-wiregrass, turkey oak barrens, and upland pine forest (Myers 1990). These community types tend to fall out along an upland soil moisture-fertility gradient ranging from xeric infertile (sandhills) to moister, more fertile (clayhills) soils. Longleaf pine-wiregrass flatwoods is a distinct community type that occurs on hydric soils and, although it is sometimes confused as being part of the high pine ecosystem, it is not included in our definition of high pine.

Throughout most of its range, the high pine ecosystem is dominated by longleaf pine (*Pinus palustris* Mill.) mixed with varying densities of several oak species. In the southeastern United States, wiregrass (*Aristida stricta* Michaux) is the dominant groundcover and herbaceous plant species diversity is high (Myers 1990). Since the late 1800s the high pine ecosystem has been reduced from the estimated 25 million ha it occupied before European settlement to less than 1 million ha today (Myers 1990, Outcalt and Sheffield 1996). Most large remnants, totaling about 33% of this endangered ecosystem (Means and Grow 1985), are in public ownership (Outcalt and Sheffield 1996).

Palynological evidence suggests that the relative dominance of oak and pine has shifted many times within the past 20,000 years in the southeastern United States. This shift is probably the result of climatic and sea level changes that affected soil moisture and fire frequency (Watts 197 1). In recent millennia this "fire climax" vegetation was maintained by frequent spring and summer groundtires ignited by lightning, by Native Americans to increase game forage and facilitate hunting, and by Europeans to increase cattle forage (Komarek 1974; Means and Grow 1985; Frost et al. 1986; Platt et al. 1988, 1991; Waldrop et al. 1992).

Since its adoption in the 1930s (Heyward 1939), widespread fire suppression has resulted in degradation of remaining remnants of the high pine ecosystem by increasing the presence of sandhill oaks and other hardwood species not commonly occurring in high pine (Myers 1990). Increased shading and leaf litter suppress the ground vegetation, thereby reducing plant diversity as well as habitat quality for many vertebrates.

As interest in high pine ecosystem restoration grows, so does the need to define restoration objectives. For this, many look to vegetation descriptions by early naturalists and surveyors. Most early descriptions depict high pine as open, savanna-like forests dominated by an open canopy of scattered longleaf pine trees with a thick groundcover of grass and herbaceous plants and no other undergrowth except around water bodies (e.g., Vignoles 1823, Williams 1837, Harper 1911, Myers 1990).

Landers et al. (1990) suggested that these descriptions overstate the frequency of occurrence of this one pine variant because it was more easily, hence more commonly, traveled through than stands with higher oak densities. These authors also noted that soil moisture and fertility, factors that dramatically influence oak tree density, are rarely included in historic descriptions. The nearly pure longleaf pine flatwoods that once occupied much of the coastal plain may actually have been the subject of many descriptions now interpreted as depicting the historic structure of longleaf pine uplands.

In fact, numerous descriptions by early naturalists distinguish between phases of high pine, that is, between stands varying in structure (i.e., tree density, diameter, and height, and strata and groundcover) and in species composition (see Myers 1990). Harper (19 15) distinguished three types of high pine land: (1) open, savanna-like pine woods; (2) pine with turkey oak (*Quercus laevis* Walt.) on the driest sites; and (3) pine with bluejack oak (Q. *incana* Bartr.) sometimes mixed with turkey oak. Romans (1775: 11) wrote: "Some high pine hills are so covered with two or three varieties of the *quercus* or oak as to make an underwood to the lofty pines; and a species of dwarf chestnut is often found here . ." Vignoles (1823: 77) noted "another kind of land, are the ridges of white sand covered with the small black or post oak, commonly called black jacks [turkey oak]. These are sometimes so thick as to exclude the pines, and when this is the case there is scarcely any grass found on the sand hills." Williams (1837: 76) recorded "high willow oak" [bluejack oak] growing on barren hills, and black jack oak [turkey oak] on the poorest sand ridges. Garren (1943: 630) wrote of a "distinct type of forest ... found in scattered patches in the typical longleaf forest" having a "prominent understory of small sprouting scrub oaks [such as turkey oak, sand post oak, bluejack oak, sand live oak, southern red oak, and blackjack oak]." William Bartram (1791) similarly described this type in 1791.

Smith (1884: 201-202) identified three classes of upland longleaf "pine-land" soils and associated vegetation. Vegetation of first-class soils was "longleaf pine, with Spanish and red oaks [Q. *fulcutu* Michx.] and hickories." Second-class pine-land soil, where "the natural timber is chiefly longleaf pine, to which are added occasionally high-ground willowoak [bluejack oak], black-jack [turkey oak], and post oaks [sand post oak (Q. *murguretta* Ashe)]." Third-class soils were associated with sandy ridges that alternate with better quality pinelands where "natural growth is indicative of the poverty of the soil, and consists of long-leaf pine, mostly small and worthless for timber, shrubby oaks [running oak (Q. *pumila* Walt.), bluejack oak, southern red oak (Q. *fulcutu)*, turkey oak, and others], occasionally small hickories [*Carya* spp.], sour-wood *(Andromeda* sp.), and whortleberries *(Vuccinium* sp.)." Heyward (1939) estimated that the regional extent of such "oak ridges," or sand hills (composed of sand post oak, blackjack oak, turkey oak, bluejack oak, and southern red oak in various combinations) composed about 11% of the longleaf type.

Additional evidence suggests that tree-sized (defined as ≥ 5 cm diameter at breast height) turkey, bluejack, and sand post oak constitute an integral component of the high pine ecosystem. Except for turkey oak, which also occurs in xeric sand pine scrub, they occur only in this vegetation association. They have the ability to reach tree size and reproduce sexually (as well as clonally), suggesting that they reach acorn-bearing size with sufficient frequency to retain the trait (Landers et al. 1990, Myers 1990, Berg and Hamrick 1994). Unlike oaks of closed hardwood forests, even small young stems of turkey and sand post oaks of the high pine ecosystem have thick, fire-resistent bark (Simons, pers. obs.), which facilitates survival to tree size. And finally, several high pine denizens, such as Sherman's fox squirrels *(Sciurus niger shermani)* and red-headed woodpeckers (*Melanerpes erythrocephalus*), rely upon acorns as an important food supply.

It appears that the commonly described savanna-like high pine ecosystem represents one end of the high pine gradient; oak-dominated sand hills represent the other end. Historically, topography, soil moisture and fertility, and fire frequency, intensity, and spatial patchiness influenced oak density in high pine. Nonetheless, an oak-free, savanna-like high pine habitat remains the prevalent paradigm among many ecologists and land managers (e.g., Platt et al. 1991, Means 1996), resulting in a sometimes over-zealous effort to remove tree-sized oaks during restoration efforts.

We gathered field data to improve our understanding of the historical structure and composition of the Florida high pine ecosystem. Specifically, our objectives were (1) to determine the historical presence and minimum density of turkey oak and sand post oak trees in high pine; (2) to describe tree age, species composition, and stand structure of high pine sites having old-growth turkey oak and sand post oak; (3) to gather information on turkey oak and sand post oak longevity; and (4) to establish allometric relationships between tree age, diameter at breast height (dbh), and height for turkey oak, sand post oak, and young longleaf pine. We sampled tree age, species composition, and stand structure of four high pine sites composed of sand post oak, turkey oak, and longleaf pine in north and central peninsular Florida. Because we wished to obtain information on the density of tree-sized (at least 5 cm diameter at breast height) oaks in this ecosystem before effective fire suppression, we selected high pine sites that contained several old-growth (defined here as > 100 years old) sandhill oaks. Because our selection criteria were subjective, we do not suggest that this reconstruction represents the historic forest composition of the entire high pine landscape. However, it does represent one variant of this ecosystem. We believe that our results can be used by land managers and restoration ecologists who employ historical models of high pine to define their management objectives.

METHODS

Study Sites

We sampled four high pine sites in north and central peninsular Florida (Figure 1). Church Lake is located within the Ocala National Forest in Marion County and managed by the U.S. Forest Service. Ichetucknee Springs State Park is in Suwannee County and managed by the Florida Department of Natural Resources. Jennings State Forest is in Clay County and managed by the Florida Division of Forestry. The Katherine Ordway Preserve is in Putnam County and is owned and managed by the University of Florida. Soils at all sites are moderately to excessively well drained sand and include the Candler (Church Lake) (U.S. Soil Conservation Service 1975), Blanton (Ichetucknee) (U.S. Soil Conservation Service 1965), Ortega and Penny (Jennings) (U.S. Soil Conservation Service 1989a), and Candler and Apopka (Ordway) (U.S. Soil Conservation Service 1989b) series.

Site selection criteria included (1) no evidence (based on records and visual inspection) of logging or recent understory manipulation within the past 50 years in the near vicinity of plots (with the exception of Church Lake, where some firewood cutting had occurred near plots in recent years), (2) the presence of sand post oak, and (3) the presence of either sand post oaks or turkey oaks older than 100 years.

Information on fire and other disturbance histories of the study sites is sketchy, especially at the scale of our plot locations. Since 1988 Church Lake, Ichetucknee Springs, and the Ordway Preserve have been prescription-burned in the vicinity of our plots in spring or summer at least three times, and Jennings Forest has been burned at least once. Before 1988 sites were burned in winter or not at all. A hurricane in 1896 destroyed the nearby town of High Springs and may also have affected the Ichetucknee Springs study site (L. Duever, Conway Conservation, Inc., Micanopy, Florida, unpubl. data; Chen and Gerber 1990). Longleaf pine had been harvested from all sites within the past 100 years. While logging and postlogging fire (or fire suppression) have almost certainly influenced present tree densities, they do not affect the validity of reconstructing minimum prelogging tree density.

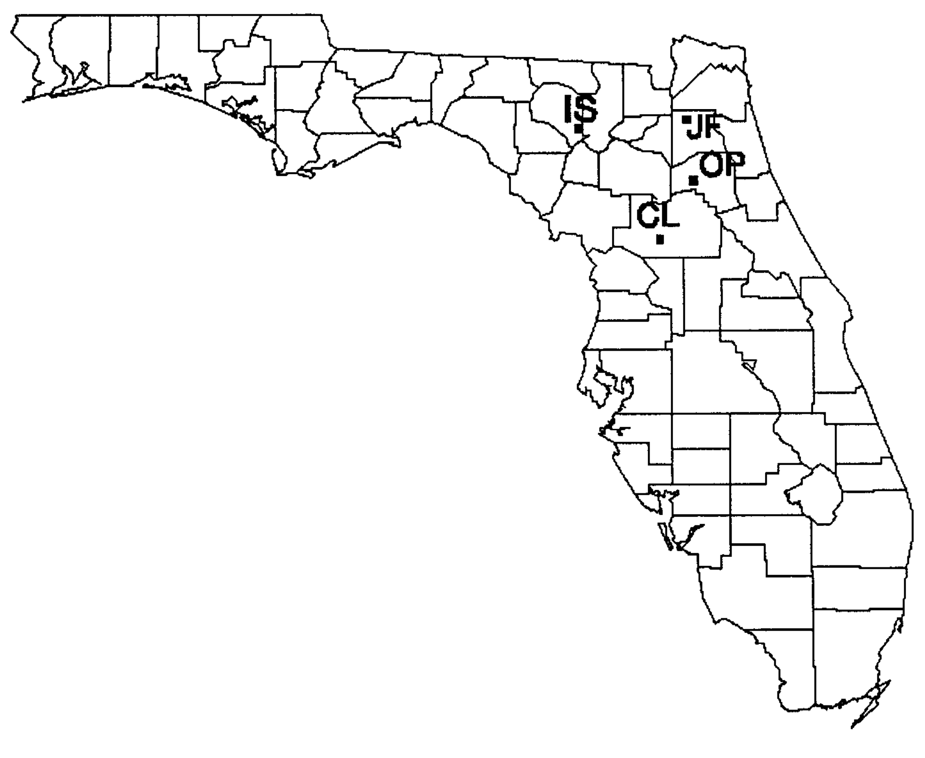

Figure 1. Location of study areas (CL=Church Lake in the Ocala National Forest, IS=Ichetucknee Springs State Park, JF=Jennings State Forest, OP=Katherine Ordway Preserve) in northern and central Florida.

Field and Laboratory Methods

We randomly established four 20-m x 50-m (O.l-ha) plots at each study site. We measured height (to top of the crown) and dbh of all live trees and snags $\geq$ 5 cm dbh within plots. Longleaf pine stems < 5 cm dbh within plots were counted individually. All other woody stems < 5 cm dbh were identified as to species, recorded as present or absent (regardless of how many occurred within a square meter) in each square meter within the O.l-ha plot, and converted to percent frequency. Hence values for all species except longleaf pine represent an index of abundance and dispersion within plots.

All live trees $\geq$ 5 cm dbh within plots were cored at 1.4 m above the ground (breast height). At each site we also cored one or more subjectively selected off-plot oaks that appeared to be very old based on tree form. Trees were cored above breast height if necessary to obtain a sound core. By coring a subsample of oaks (n=15 for four species combined) at 7.6 cm and 1.4 m above ground, we determined the average height growth rate of young oaks to be 0.3 m yr^{-1} during early growth. Hence, we added five years to the age of oaks cored at breast height or adjusted the age according to the height at which the tree was cored. We underestimated the age of any oaks that had lived as sprouts or seedlings for years before initiating height growth. Similarly, oak rootstocks might have been considerably older than any tree-sized oaks, but were not considered in this study. Because it was impossible to determine how long an individual remained in the grass

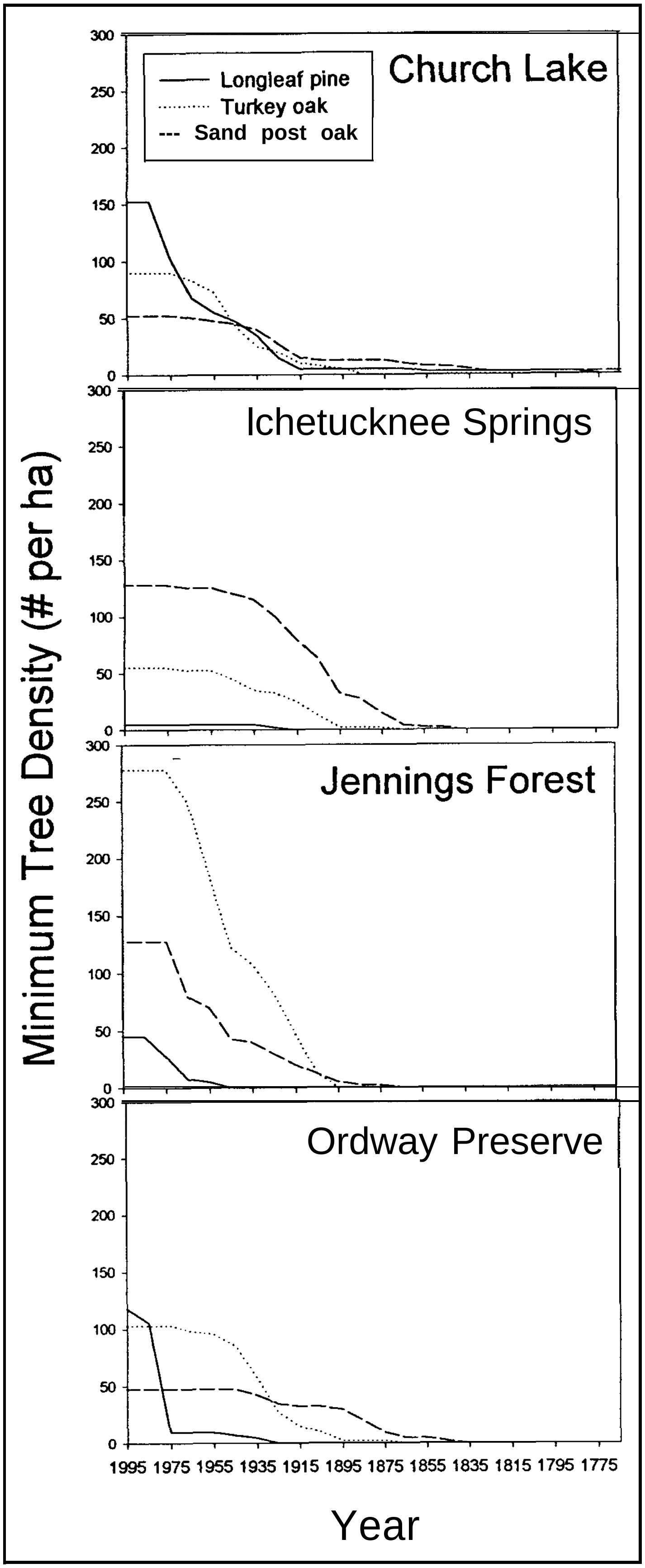

Figure 2. Minimum number of living longleaf pine, turkey oak, and sand post oak trees per year from 1765 through 1995 at four Florida high pine sites.

stage, age estimates of longleaf pine were based on growth after the grass stage.

Growth rings were counted using a dissecting microscope. Cores that were difficult to read were sliced with a sharp knife and/or stained with a solution of phloroglucinol 2-hydrate in 95% ethanol and then briefly immersed in 50% HCL solution. We did not estimate numbers of illegible rings or those that were missing because a tree center was missed during coring or a tree was hollow. Hence, estimates of tree age are conservative.

Data Analysis

We used linear and polynomial regression (SAS 1989) to model the relationships between age and dbh, age and height, and dbh and height for the three dominant tree species. Data were pooled across sites and included measured off-plot trees to maximize the sample size. We deleted the two oldest, outlier longleaf pine trees from regressions because they skewed the data. Only within-plot data were used for all other analyses and discussion. Polynomial regression reflected a biologically meaningful relationship between age and size (height and dbh) and slightly improved coefficients of determination; however, equations are useful only within the range of data modeled.

We reconstructed minimum oak densities since 1765 (the date of origin of the oldest tree cored) in each study area, using tree ages to determine the number of tree-sized oaks that were present during each given year. Estimates represent a minimum, because many trees that were living in those years probably have died.

RESULTS

A total of 556 trees were cored within the plots. The maximum age of cored turkey oaks (n=2 15) ranged rom 98 years old at the Jennings Forest site to 123 years old at the Ordway Preserve site (Figure 2). Maximum sand post oak age (n=146) ranged from 126 years old at the Jennings Forest site to 230 years old at the Church Lake site. Except for two old trees 138 and 212 years old at Church Lake, no longleaf pine (n=129) exceeded 78 years of age at any site (Figure 2). Young (≤ 50 years old) turkey oak and sand post oak stems were abundant at all study areas (Figure 2).

Young stems ≥ 5 cm dbh of other woody species not commonly occurring on high pine sites, such as laurel oak ***(Quercus hemisphaerica*** Bartr.), sand live oak (Q. *geminata* Small), and sparkleberry (*Vaccineum* ***urboreum*** Marsh.), were abundant at Jennings Forest (Figures 3 and 4). Bluejack oak and persimmon (*Diospyros* ***virginiana*** L.) comprised many of the young ≥ 5 cm dbh stems at the Ordway Preserve. No woody stems ≥ 5 cm dbh other than longleaf pine, turkey oak, and sand post oak were recorded at Ichetucknee springs; an old southern red oak (Q *falcata* Michx.) was the only other species ≥ 5 cm dbh recorded at Church Lake (Figures 3 and 4).

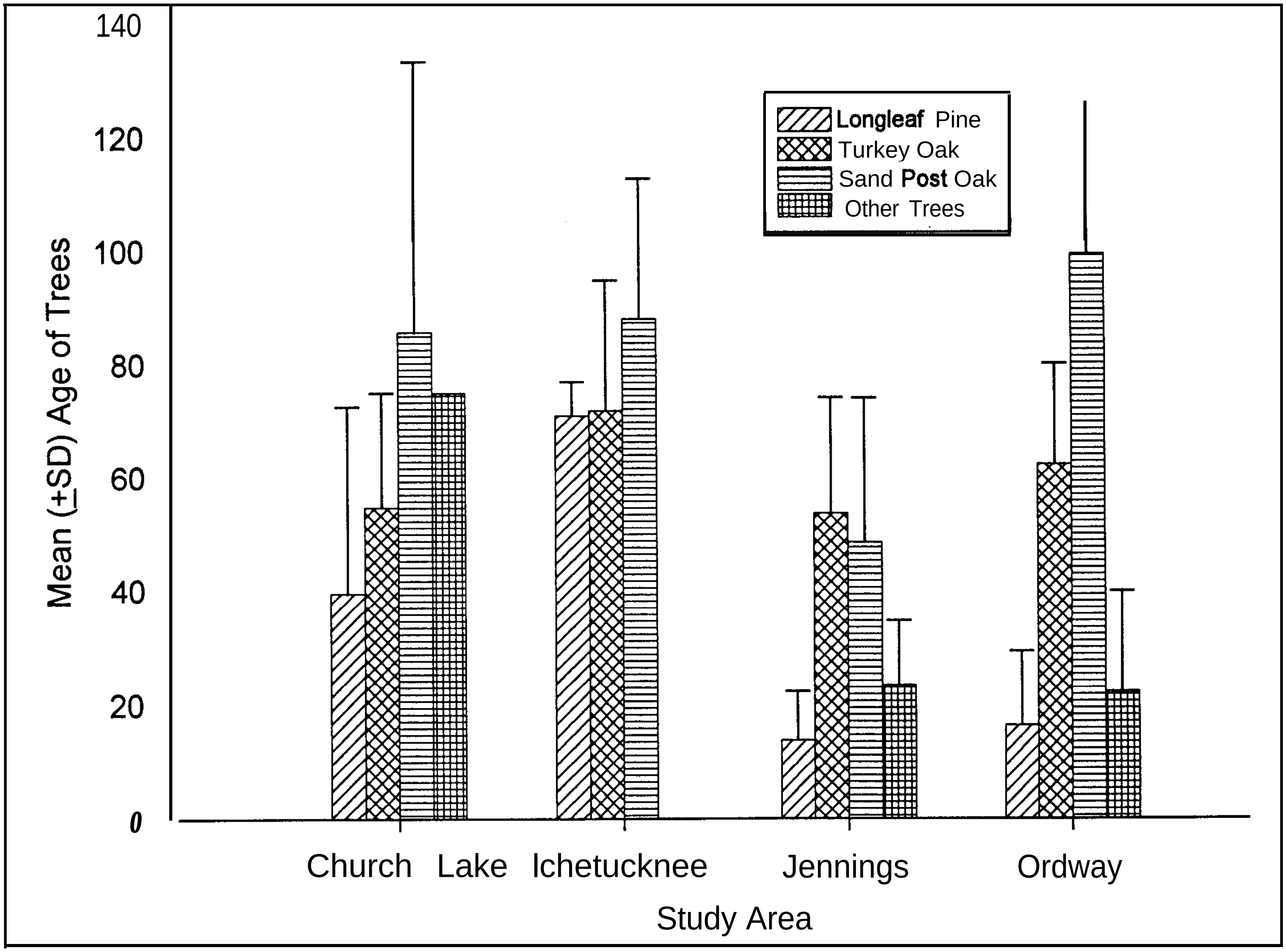

Figure 3. Mean (± SD) age of trees (≥ 5 cm dbb) at four Florida high pine sites.

Age and height were weakly but significantly ($p \leq 0.0001$) correlated for both turkey and sand post oak ($r^2 < 0.35$) and were strongly correlated for longleaf pine ($r^2 = 0.82$) (Figure 5). Most oaks in our study exceeded 3 m in height by age 20. Many of the short trees had bent trunks, decreasing their measured height. Tree diameter and height exhibited a strong, positive relationship ($p \leq 0.0001$) for both oak species ($r^2 \geq 0.55$) and, especially, for longleaf pine ($r^2 = 0.87$) (Figure 6).

The relationship between age and dbh was significant ($p \leq 0.0001$) for all three tree species, but both oaks exhibited greater dbh variation in relation to age than did longleaf pine, especially at older ages (Figure 7). Some turkey oaks as old as 80 years were ≤ 10 cm; the largest (51.3 cm dbh) was only 56 years old, whereas the oldest (123 years old) was 50 cm dbh. The age-dbh relationship was stronger for sand post oak. The smallest diameter (5.2 cm dbh) sand post oak tree was 23 years old, whereas the youngest tree (21 years old) was 5.4 cm dbh. However, the largest dbh sand post oak (46.1 cm) was 156 years old, while the oldest (230 years old) was 21.6-cm dbh. The youngest longleaf pine tree was also the smallest (5 cm dbh); the oldest (212 years old) was 41.2 cm dbh, while the largest was 52 cm dbh at 78 years of age (Figure 7).

None of the longleaf pines cored were hollow or rotten. Ten percent of turkey oak trees were hollow, rotten, or both. Since rings in very rotted heart wood or hollow trees could not be counted, ring counts represent the minimum age at which rot began. However, rings were usually all visible even in rotten wood of younger trees, permitting a fairly accurate estimation of their age. Rot occurred in trees with as few as 35 rings (Table 1). The median number of rings recorded for rotten and/or hollow trees was 63; for all sampled turkey oaks it was 54 (sites combined). In contrast, 22.5% of sand post oaks were hollow, rotten, or both, and rot occurred in one tree with as few as 27 rings. The median number of rings recorded for rotten and/or hollow sand post oak trees was 105; for all sampled sand post oaks it was 74 (Table 1).

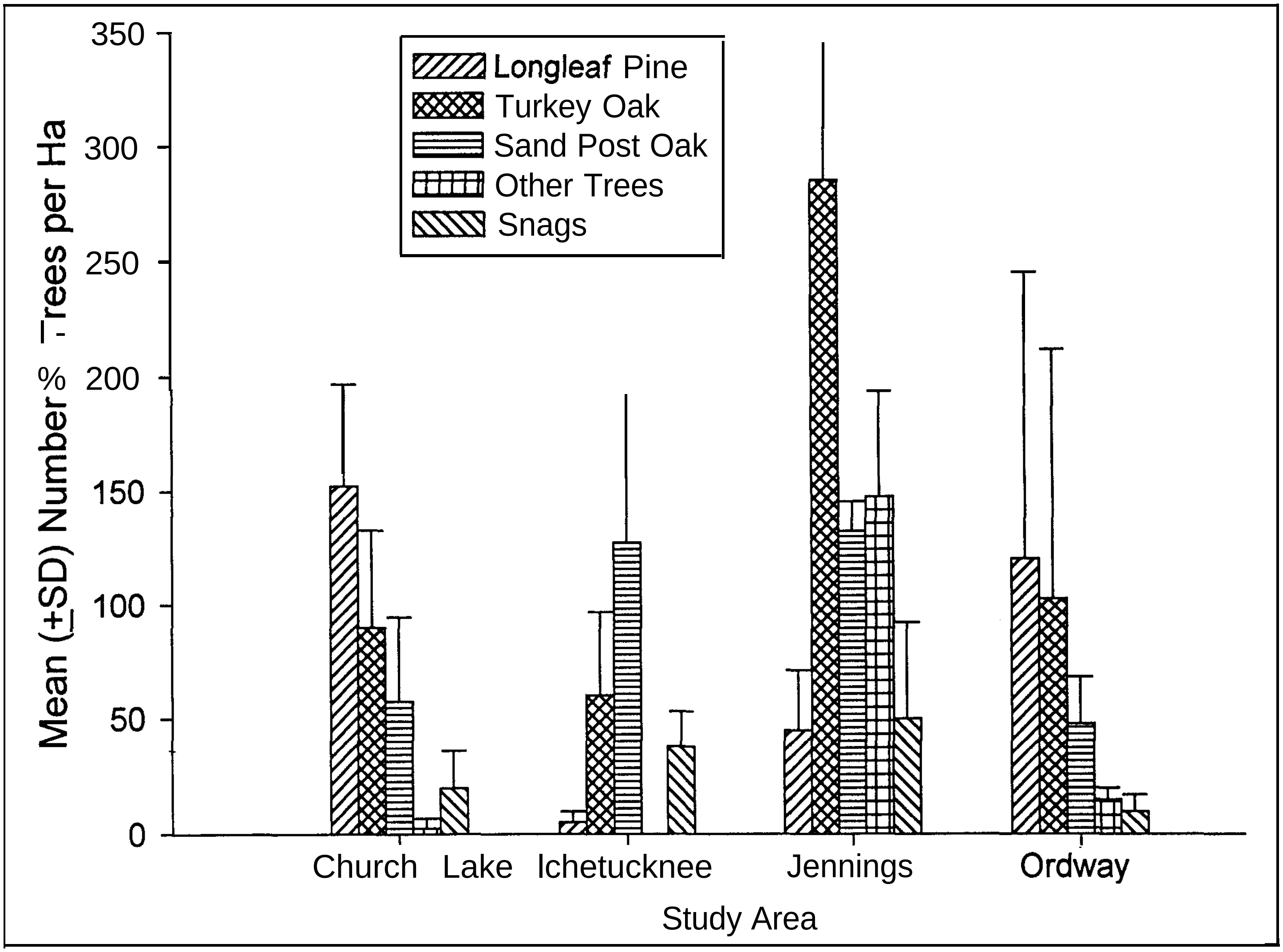

Figure 4. Mean (± SD) density (per ha) of trees (≥ 5 cm dbh) at four Florida high pine sites.

At least some of the snags (Figure 4) resulted from recent topkill by fire. Up to 67% of turkey oaks and 82% of sand post oaks sampled at Ichetucknee Springs had visible single or multiple fire scars.

Stand Composition, Tree Size, and Age Structure

Church Lake

Mean tree density at Church Lake was 303 trees ha^{-1} (Figure 4). Longleaf pine composed about one-half of total tree density. Turkey oak was dominant, exceeding sand post oak by about 50%. Snag density averaged 20 trees ha-‘.

Except for two old trees (138 and 212 years old) left by loggers, all longleaf pine at Church Lake were ≤ 78 years old. Longleaf pine stems < 5 cm dbh averaged 1,778 stems ha^{-1} (Table 2). The oldest sand post oak was 230 years old, and the oldest turkey oak was 100 years old. Stand reconstruction indicates that in 1900 there were at least 20 oak trees (with trees defined as being ≥ 5 cm dbh) per hectare (7.5

Table 1. Tree ring counts for hollow and/or rotten (first line) and for all (second line) turkey oaks and sand post oak sampled at four Florida high pine sites.

		Tree Ring Count		
Species	**N**	**Mean (±SD)**	**Range**	**Median**
turkey oak	**21 (10%)**	69.1±23.0	**35-123**	**63**
	210	57.4±21.3	**21-123**	**54**
sand post oak	**32 (22.5%)**	105.8±37.5	**27-230**	**105**
	142	75.0±36.3	**21-230**	**74**

turkey oaks and 12.5 sand post oaks), and in 19 15 there were at least 25 oak trees ha-[1] (10 turkey oaks and 15 sand post oaks) at Church Lake (Figure 2).

Ichetucknee Springs

Mean tree density at Ichetucknee Springs was 193 trees ha^{-1} (Figure 4). Only two longleaf pine trees, aged 65 and 77 years, occurred in the 0.4 ha that we sampled. Longleaf pine regeneration (< 5 cm dbh) also was virtually nonexistent within plots (Table 2). Sand post oaks were twice as abundant as turkey oaks (Figure 4). Snag density averaged 38 stems ha^{-1} (Figure 4).

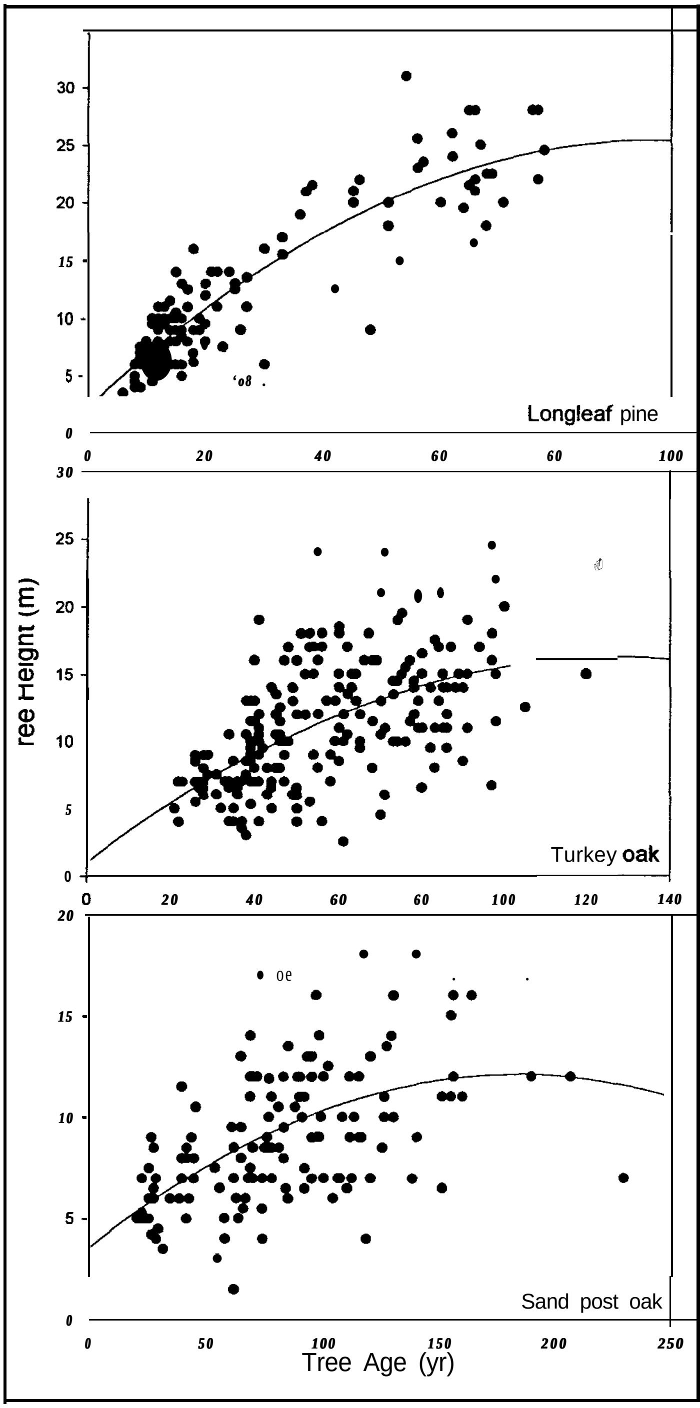

Figure 5. Regression of tree age on height for three tree species across four Florida high pine sites combined ($p \leq 0.0001$): **longleaf** pine (ht = 2.27 + **0.48(age)** + **(-0.002)(age^2)**, r^2**=0.82)**; turkey oak (ht = 1.00 + **0.24(age)** + **(-0.0009)(age^2)**, r^2 = 0.34); and sand post oak (ht = 3.55 + **0.09(age)** + **(-0.0003)(age^2)**; r^2 = 0.31).

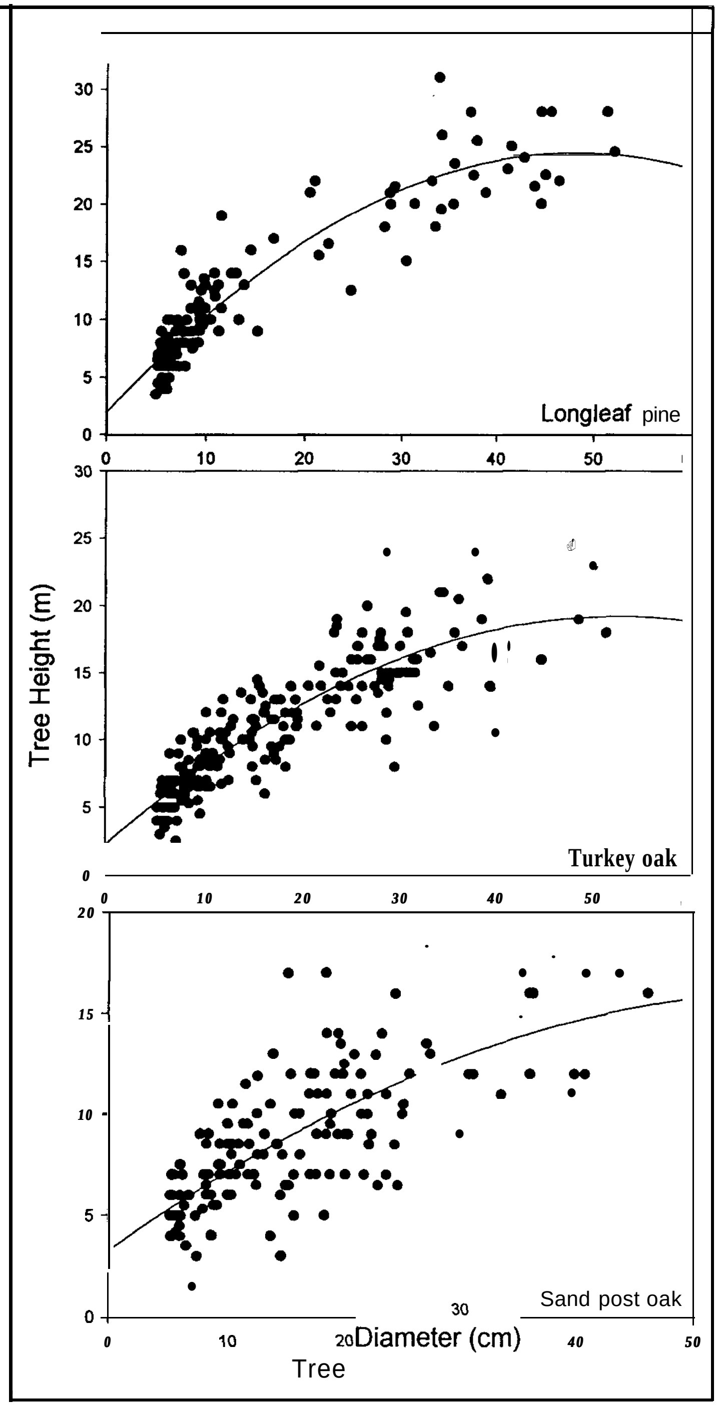

Figure 6. Regression of tree diameter on height for three tree species across four Florida high pine sites combined ($p \leq 0.0001$): **longleaf** pine (ht = 1.94 + **0.93(dbh)** + **(-0.01)(dbh^2)**, r^2**=0.87)**; turkey oak (ht = 2.26 + **0.65(dbh)** + **(-0.006)(dbh^2)**, r^2 = 0.76); and sand post oak (bt = 3.27 + **0.42(dbh)** + **(-0.003)(dbh^2)**, r^2 = 0.55).

The oldest sand post oak at Ichetucknee Springs was 15 1 years old. The oldest turkey oak was 120 years old. Stand reconstruction indicates that in 1900 there were at least 60 oak trees ha^{-1} (7.5 turkey oaks and 52.5 sand post oaks), and in 1915 there were at least 105 oak trees ha^{-1} (25 turkey oaks and 80 sand post oaks) at Ichetucknee Springs (Figure 2).

Jennings Forest

Mean tree density at Jenning Forest was 610 tres ha^{-1} (Figure 4). Longleaf pine density was low. Turkey oaks (mean 285 trees ha^{-1}) were twice as abundant as sand post oak. Tree-sized bluejack oak were also present, all $\geq$ 20 years old, and some $\geq$ 50 years old. Young stems of other pine and hardwood species such as laurel oak and sand live oak also were abundant. Snag density averaged 50 stems ha-' (Figure 4).

The oldest turkey oak at Jennings Forest was 98 years old, and the oldest sand post oak was 126 years old (Figure 2). The age of oaks indicates that in 1900 there were at least 10 oak trees ha^{-1} (5 turkey oaks and 5 sand post oaks), and in 1915 there were at least 68 oak trees ha^{-1} (47.5 turkey oaks and 20 sand post oaks) at Jennings Forest (Figure 2).

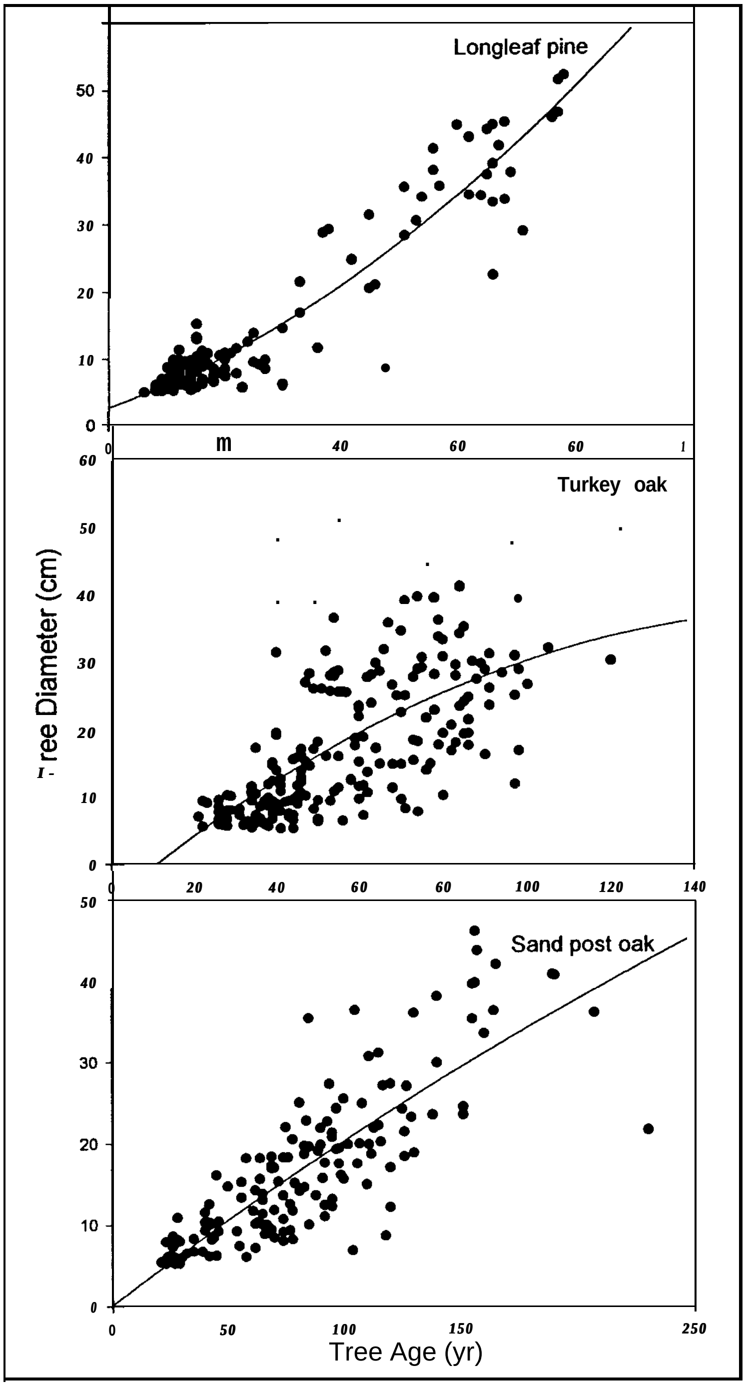

Figure 7. Regression of tree age on diameter for three tree species across four Florida high pine sites combined ($p \leq$ 0.0001): longleaf pine (dbh = 2.77 + 0.31(age) + (0.004)(age^2), r^2=0.90); turkey oak (dbh = -5.15 + 0.50(age) + (-0.001)(age^2), r^2 = 0.41); and sand post oak (dbh = 0.14 + 0.21(age) + (-0.0001)(age^2), r^2 = 0.68).

Ordway Preserve

Mean tree density was 285 trees ha^{-1} at the Ordway Preserve. Longleaf pine was abundant (Figure 4) but spatially patchy. Turkey oaks were more than twice as abundant as sand post oaks, and snag density averaged 10 stems ha-' (Figure 4).

Ages of longleaf pine trees at the Ordway Preserve ranged from 6 to 66 years old (Figure 2). An average of 177.5 longleaf pine seedlings and saplings occurred per hectare (Table 2).

The oldest turkey oak was 123 years old, and the oldest sand post oak was 156 years old (Figure 2). Stand reconstruction indicates that in 1900 there were at least 40 oak trees ha^{-1} (7.5 turkey oaks and 32.5 sand post oaks), and in 1915 there were at least 48 oak trees ha^{-1} (15 turkey oaks and 32.5 sand post oaks) at the Ordway Preserve (Figure 2).

DISCUSSION

Age reconstruction of four Florida high pine sites indicates that tree-sized turkey and sand post oaks historically were integral parts of the high pine ecosystem at some places and times. In 1900 minimum oak density ranged from 10 trees ha^{-1} (Jennings Forest) to 60 trees ha^{-1} (Ichetucknee Springs) among our study sites. Myers (1985) reported 34 turkey oak stems $\geq$ 5 cm dbh from a 1932 survey of a sandhill on the Lake Wales Ridge, Florida (most recent fire in 1927).

Although longleaf pine can live at least 450 years (Platt et al. 1988), such old trees were absent at our study sites. The age structure of longleaf pines at our study sites suggests that the large pines were harvested between the late 1890s (Ichetucknee) and the 1920s (Ordway Preserve).

Table 2. Mean (±SD) percent frequency (percentage of occupied 1-m² subplots per 1,000-m² plot)* of woody stems < 5 cm dbh in four Florida high pine sites.

Species	Site: Church Lake	Site: Ichetucknee Springs	Site: Jennings Forest	Site: Ordway Preserve
Asimina incana (Bartr.) Exe11		0.65±0.96	0.85±0.64	5.73±1.90
A. longijiolia Kral.		0.03±0.04		0.13±0.22
A. pygmaea (Bartr.) Dunal				0.30±0.25
Bumelia lanuginosa (Michx.) Pers.		0.08±0.13		
B. *tenax* (L.) Willd.	0.05±0.05			
Carya glabra (Mill.) Sweet		0.05±0.05		0.03±0.04
C. *tomentosa* (Poiret) Nutt.		0.03±0.04		
Castanea pumila (L.) Mill.		0.13±0.22		1.23±2.21
Ceratiola ericoides Michx.				0.03±0.04
Crataegus jloridana Sarg.	0.039.04			
Diospyros virginiana L.	0.18±0.15	2.53±1.49		3.20±1.34
Garberia heterophylla (Bartr.) Merr. & Harp.	0.03±0.04			
Hypericum hypericoides (L.) Crantz	——			0.05±0.09
Ilex opaca Ait.			0.05±0.09	
Juniperus silicicola (Small) Bailey			0.03±0.04	
Opuntia humifusa (Raf.) Raf.				0.10±0.17
Persea borbonia (L.) Spreng.		0.05±0.09	0.23±0.28	
Pinus clausa (Chapm. ex Engelm.) Vasey ex Sarg.				0.05±0.09
P. elliottii Engelm.				0.05±0.05
P. palustris Mill.[a]	177.75±44.53	4.75±4.97	28.25±27.13	70.50±63.20
P. taeda L.			0.03±0.04	
Prunus angustifolia Marsh.		0.03±0.04	0.034.04	
P. caroliniana Ait.			0.03±0.04	
P. *serotina* Ehrh.		1.10±1.31	0.05±0.05	
Quercus falcata Michx.		0.43±0.53		
Q. *geminata* Small	0.35±0.23		4.25±3.37	
Q. hemisphaerica Bartr.	0.08±0.08	0.18±0.15	0.28±0.37	3.08±2.47
Q. *incana* Bartr.	3.20±3.22	1.23±0.82	4.23±2.90	2.40±1.26
Q. laevis Walt.	6.70±1.00	13.93±7.55	5.05±1.03	16.70±3.01
Q. *margaretta* Ashe	3.00±0.94	14.05±5.04	4.90±1.90	2.45±1.35
Q. *myrtifolia* Willd.	0.03±0.04			
Q. *nigra* L.			0.15±0.26	
Rhus copallina L.	1.80±0.85	16.45±5.80	0.05±0.05	8.68±3.67
Rubus cuneifolius Pursh		0.25±0.38	0.38±0.41	0.03±0.04
Sabal etonia Swingle ex Nash				0.03±0.04
Sassafras albidum (Nutt.) Nees		1.38±0.87	0.08±0.13	
Serenoa repens (Bartr.) Small	0.03±0.04	0.10±0.17	0.65±0.42	
Vaccinium arboreum Marsh.		0.73±0.62	3.70±1.78	0.10±0.17
V. myrsinites Lam.		0.03±0.04	0.45±0.62	0.45±0.30
V. stamineum L.	0.10±0.12	1.389.74	9.15±1.11	0.20±0.19
Viburnum obovatum Walt.			0.03±0.04	
V. rufidulum Raf.		0.05±0.09		
Vitis aestivalis Michx.		1.55±1.56		0.034.04
V. rotundijolia Michx.		0.08±0.13		0.10±0.07

[a] *Pinus palustris* (only) stems < 5 cm dbh were counted individually; means represent the mean number of stems per 1,000-m² plot. (All other species were tallied as percent frequency, as described above.)

Turkey oak is considered to be a fast-growing, short-lived species (Harlow 1990). We suggest such conclusions were based on studies that sampled stands established after clearcutting or site preparation, followed by decades of fire suppression (e.g., Harlow and Eikum 1963). Our data confirm that turkey oaks can live up to 123 years, and commonly live in excess of 80 years. Robert Simons cored a 162-year-old turkey oak in a longleaf pine–turkey oak forest in southern Suwannee County, Florida. The turkey oaks sampled in our study exhibited highly variable dbh-growth rates, suggesting that dbh is not an accurate predictor of age.

Stahle and Chaney (1994) reported post oaks (Q. ***stellata*** Wangenh.) as old as 370 years old in Arkansas (many botanists consider sand post oak to be a subspecies of *Q. stellata*). Stahle (unpubl. data) cored a 175-year-old sand post oak at our Church Lake study site; the oldest we cored was 230 years old, also at Church Lake. Our data further suggest that sand post oak lives longer and degenerates at a greater age than turkey oak.

The abundance of young turkey and sand post oak stems at all study sites suggests that all sites have undergone a long period with either very cool burns or growing season burns. At Jennings Forest the relative abundance of young laurel oak, sand live oak, sparkleberry, and other woody species that are not indigenous to high pine further indicates a long absence of growing-season tire (Veno 1976, Myers and White 1987). The absence of bluejack oak trees (except at Jennings Forest) but presence of stems < 5 cm dbh suggest that it may once have been more abundant at our study sites.

Increases in oak density following the removal of longleaf pine were noted as early as 19 15 (Harper 19 15). Fallen pine needles contribute to the fuel and fire-carrying capacity of the ecosystem (Williamson and Black 1981, Rebertus et al. 1989a), and tall pines may serve as lightning rods that ignite the groundcover (K. Outcalt, Southern Research Station, U.S. Forest Service, Athens, Georgia, pers. corn.). Before the recent reintroduction of fire by prescribed burning, active fire suppression probably contributed to the proliferation of oaks.

Oak survival is affected by season, frequency, temperature, and patchiness of fire. Factors that affect fire temperature and patchiness, such as weather conditions, fuel load, leaf litter type, topography, landscape patterns, and microsite conditions indirectly affect oak survival (Williamson and Black 1981; Rebertus et al. 1989a, 1989b; Myers 1990; Platt et al. 1991; Glitzenstein et al. 1995). Glitzenstein et al. (1995) reported that sandhill oaks were susceptible to topkill from early growing-season burns regardless of size class, but that mortality from frequent burning was significant only in small diameter oaks. Rebertus et al. (1989b) found that large diameter turkey oaks survived mild surface fires better than small diameter turkey oaks probably due to the thicker bark of the larger trees. Williamson and Black (1981) demonstrated that the chances of a turkey oak surviving a sandhill fire increased with height (trees ≥ 3 m tall had the highest survival rates) and distance from longleaf pine crowns.

Only relatively short periods that are fire-free (Rebertus et al. 1993 suggest six to nine years), or include only low-intensity fires are required for an oak to attain a fire-resistant size (Rebertus et al. 1993). The presence of several large, old oak trees at our study sites suggests that even before the effective fire suppression and landscape fragmentation of the last two centuries, fires were sufficiently patchy, infrequent, and/or cool to permit the oaks' establishment and survival. In all probability, spatial patchiness and variability in fire frequency, season, and intensity permitted oaks to reach and maintain tree size in varying densities over time and across the high pine landscape.

MANAGEMENT IMPLICATIONS

This study demonstrates that tree-sized (≥ 5 breast height) sandhill oaks were historically an integral part of the high pine landscape, at least at some times and places in north and central penninsular Florida. Fire suppression in recent decades has resulted in increased sandhill oak density and invasion by other hardwood species not commonly occurring in high pine. Hence in many cases removal of hardwoods, including some sandhill oaks, is a justified goal of ecosystem restoration efforts.

Managers and restoration ecologists attempting to restore and maintain the stand and landscape structure of high pine as it was historically may be misguided in removing all tree-sized sandhill oaks. By leaving turkey, sand post, and bluejack oaks in multiple age classes and densities across stands or compartments ranging from none to sixty or more, managers may achieve a realistic reconstruction of the historic high pine landscape. If old sandhill oaks occur within a stand, managers may wish to identify and preserve those, as well. In addition, by varying the season, intensity, frequency, and spatial coverage of fire, managers can create and maintain densities of tree-sized oaks that vary over time and across the high pine landscape.

ACKNOWLEDGMENTS

We thank the staff of the Florida Division of Forestry, Florida Department of Natural Resources, the Katherine Ordway Preserve, and the Ocala National Forest who granted permission to collect data and provided information or assistance in the field. Robert Hamlin, B. Wilbanks, J. Blanchard, R. Franz., G. Custer, S. Cole, W. Jones, and A. Nail were especially helpful. Special thanks to I. Williams, J. Buckner, M. Buckner, and M. Allen for field assistance. We also thank P. Outcalt for assistance with graphics and K. Outcalt, J. Walker, P. Bowman, and two anonymous reviewers for providing useful suggestions to improve earlier versions of this manuscript.

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