



Canopy disturbance and tree recruitment over two centuries in a managed longleaf pine landscape

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Abstract

Disturbance history was reconstructed across an 11300 ha managed longleaf pine (*Pinus palustris* Mill.) landscape in southwestern Georgia, USA. Our specific objectives were to: (i) determine forest age structure; (ii) reconstruct disturbance history through the relationship between canopy disturbance, tree recruitment and growth; and (iii) explore the relationship between canopy disturbance and climate. Age structure, canopy disturbance events and initial growth patterns at coring height were examined by randomly sampling 1260 trees in 70 1.3 ha plots. Principal component analysis was used to group plots with similar age structures to gain insight into the dynamics between canopy disturbance and recruitment. Disturbance events were detected by large and rapid increases in radial growth. We tested the following hypothesis to investigate whether these growth increases could have been triggered by improved climatic conditions: precipitation and drought are positively correlated to radial growth releases. Only four stands (comprising <6% of the study area) had an even-aged structure. Further, tree recruitment prior to European settlement indicates that longleaf pine naturally recruited into areas 1.3 ha or less, supporting early-20th century observations that the primary longleaf pine forest was uneven-aged. Contrary to our hypothesis, growing season precipitation and drought was significantly and negatively correlated with canopy disturbance (radial growth releases), which indicates that a reconstruction of disturbance history could proceed with some confidence. Most trees sampled were recruited at coring height from 1910 to 1935. Of the 67 canopy disturbances detected from 1910 to 1935, the average growth release ranged from 139 to 277% per half decade suggesting the occurrence of large canopy disturbances. Rapid initial growth patterns of young trees during these years show evidence of reduced overstory competition and support the detected disturbance intensity. Our reconstruction of stand dynamics is markedly similar to independent records of local oral and written history, which gives an additional set of evidence that the disturbance detection methodology used can be useful in open-canopied forests. Stands with multiple cohorts reveal a mix of continuous minor and major canopy disturbances leading to continual tree recruitment, suggesting their applicability as models for long-term forest management. The significant relationship between climate and disturbance in our data suggests that with the expected warming over the next 100 years, climatic impacts on stand dynamics should be incorporated into long-term longleaf pine forest restoration and management.

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1. Introduction

Reconstruction of forest history provides information on the patterns and processes of forest dynamics (e.g., Marshall, 1927; Heinselman, 1973; Swetnam and Betancourt, 1990; Villalba and Veblen, 1998; Orwig et al., 2001). Understanding disturbance

history, particularly reconstructing disturbance size, shape, frequency, and severity, is fundamental for development of models to guide natural forest management (e.g., Lindenmayer and Franklin, 1997; Palik et al., 2002; Varner et al., 2003). The response of forests to both natural (i.e., wind, flooding, fire) and anthropogenic (i.e., timber harvesting, land abandonment) disturbances can provide the mechanisms responsible for current stand development, composition, and structure.

Several methods exist to reconstruct forest disturbance history, including tree-ring, sediment core, forest floor and soil charcoal based analyses (e.g., Henry and Swan, 1974; Arno and Sneek, 1977; Lorimer, 1985; Swetnam et al., 1985; Lorimer and

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Frelich, 1989; Parshall, 1999; Liu and Fearn, 2000). One technique to reconstruct forest disturbance history uses growth patterns of tree-rings to identify canopy disturbance events (Lorimer, 1985; Lorimer and Frelich, 1989; Nowacki and Abrams, 1997). Developed initially in the closed canopied *Acer-Tsuga*-northern hardwood forests of Wisconsin and Michigan, USA (Lorimer, 1985), this method takes advantage of the intense understory competition for light as well as competition for water, nutrients, and space. The method identifies increases in growth of surviving trees and interprets these increases as disturbances in the overstory. It is not apparent, however, that this method works in open-canopied forests (Nowacki and Abrams, 1997). This lack of verification for open-canopied ecosystems represents a major need in forest disturbance history research.

Southeastern USA forests, woodlands, and savannas dominated by longleaf pine (*Pinus palustris* Mill.) represent a landscape with a long record of intensive land-use and forest disturbance (Frost, 2006). Over the past 400 years, small- and large-scale conversion to agriculture, widespread 20th century fire exclusion, and the advent of industrial forestry in which longleaf pine forests were replaced by plantations of loblolly (*P. taeda* L.) and slash pine (*P. elliottii* Engelm.) have led to a 97.8% decline in the area of longleaf pine ecosystems (Frost, 2006). Despite the long record of both natural and anthropogenic disturbances in longleaf pine ecosystems, little work has been conducted to reconstruct the pattern of historic disturbances and their influence on current forest structure. This oversight, combined with the increased interest in the restoration and management of remnant longleaf pine ecosystems (Landers et al., 1995; Varner and Kush, 2004; Jose et al., 2006), underscores the need to understand the role of disturbance in the development and dynamics of current and future stand structure.

In addition to anthropogenic disturbances, there is a need to better understand the role of climate variability in forest history. Previous dendroecological studies have shown a relationship between drought and mortality in different forest types (e.g., Jenkins and Pallardy, 1995; Allen and Breshears, 1998; Villalba and Veblen, 1998). The degree to which large-scale climate patterns are related to stand dynamics (generation of canopy gaps, stimulation of seedling establishment and growth), especially in our understanding of longleaf pine forest development, remains unanswered.

Our primary objectives in this study were to: (i) determine age structure and disturbance history of a managed longleaf pine forest; (ii) reconstruct disturbance history by studying the relationship between canopy disturbance, tree recruitment and growth; and (iii) explore the relationship between canopy disturbance and climate. To reach these objectives, we had to determine whether the tree-ring based methodology developed in closed-canopied forests to reconstruct disturbance history is applicable in open, longleaf pine forests. Therefore, to help separate the influences of canopy disturbance and climate on radial growth we tested the hypothesis that precipitation and drought are positively correlated to tree growth releases. As longleaf pine growth in the Gulf Coast region is significantly

correlated to precipitation and drought between March and October of the current year (Lodewick, 1930; Coile, 1936; Schumacher and Day, 1939; Meldahl et al., 1999), it follows that these factors should be primary drivers of growth. A positive correlation between growth releases and precipitation and drought, therefore, would indicate that results rendered by the traditional method for closed-canopied forests might be confounded by other factors (i.e., climate) in open-canopied forests to give false-positive results.

2. Methods

This study took place at the J.W. Jones Ecological Research Center on the inner Coastal Plain of southwest Georgia, USA, an area formerly known as the Ichauway Plantation (hereafter Ichauway; Fig. 1). Details of the study area and sampling design are outlined in Palik and Pederson (1996). The 11300 ha property, created over the course of a decade beginning in 1928 with consolidation of local farms and land parcels to form a quail hunting plantation, contains 7500 ha of second-growth, naturally regenerated longleaf pine forest. Typical quail hunting plantation management included salvage logging of all pine mortality, occasional harvesting of large pines, and dormant season (December to March) prescribed burns every 2–3 years to reduce hardwood growth and maintain open stand structure (Neel, 1971).

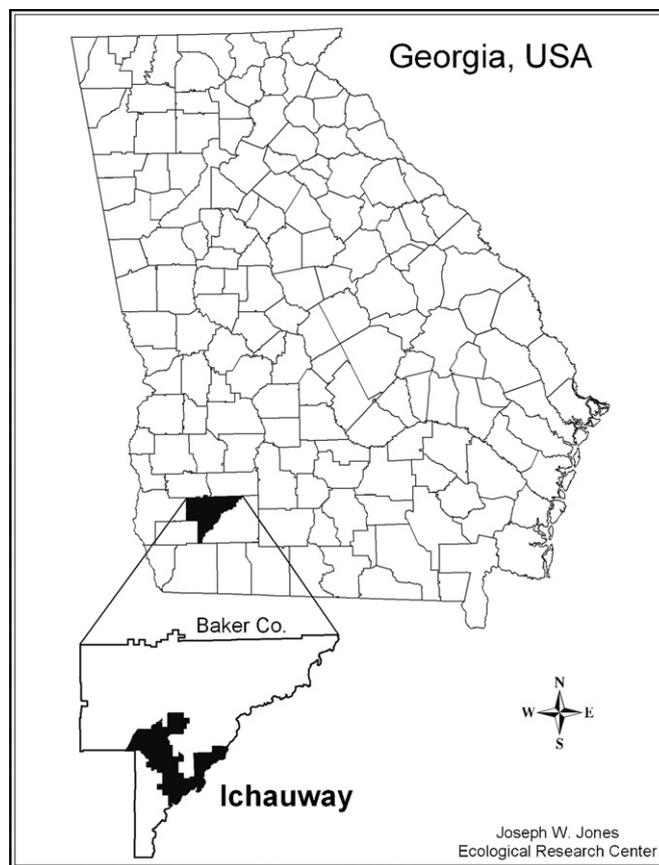


Fig. 1. Location of the study site at Ichauway Plantation, Baker County, Georgia, USA.

Seventy 1.3 ha (115 m × 115 m) plots were established in large tracts of forest dominated by longleaf pine to assess age structure and disturbance history. Plots were randomly located, but moved up to 100 m to exclude the effects of the inclusion of soil disturbance from plowing, fire breaks, etc. or maintain homogeneous conditions (Palik and Pederson, 1996). Two plots were on more mesic sites and were dominated by slash pine. There were also a few scattered shortleaf pines (*P. echinata* Mill.) among the plots. Overstory pines (i.e., trees ≥ 2.5 cm DBH with full crown exposure) were randomly selected for sampling. In total, 1260 trees (16–21 trees per plot) were cored between 0.5 and 1.0 m above ground level. One core per tree was removed and prepared using standard tree-ring analysis techniques (Stokes and Smiley, 1968). Samples were mounted, air dried and sanded with progressively finer sandpaper from 180 to 400 grit. Cores were visually cross-dated and aged (Stokes and Smiley, 1968; Yamaguchi, 1991). Crossdating and, thus, final ages were checked using the quality control program COFECHA (Holmes, 1983).

2.1. Age structure and recruitment history

Age structure was characterized by quantifying the following age attributes for each plot: age diversity (using the Shannon–Weiner's diversity index; Gauthier et al., 1993); average tree age; tree age range, minimum and maximum tree ages; skewness; kurtosis; standard deviation and covariation of plot age (following Muir, 1993); and the number of modal ages. We looked for similarity of age characteristics among plots using principal components analysis (PCA) ordination (ter Braak, 1988). PCA was used to reduce the complexity of the 10 age characteristics so the common variance among the 70 plots is isolated.

The year at which each tree reached coring height was placed in 5-years periods (i.e., 1930–1934, 1935–1939, ...) to reconstruct the recruitment history at the plot and landscape-scale. Because all samples were crossdated, the age assigned to each tree at coring height has no uncertainty (Stokes and Smiley, 1968; Fritts, 1976). The grass stage of longleaf pine, however, makes absolute tree age determination impossible. Longleaf pine seedlings can persist in the grass stage for 3–15 years after germination, during which no height growth occurs (Boyer, 1990) and no annual rings are produced (Pessin, 1934). Although coring height likely only misses 1–2 years after the grass stage because of rapid growth during 'bolting' (Boyer, 1990), 3–15+ years could be missed following germination, which should lead to a lag in reconstructed recruitment.

Two patterns of early tree growth were observed during ring analysis that suggested the initial competitive environment for each tree could be inferred as it reached coring height. Trees were placed in two categories based on ring patterns over the first 12 years, the first two 'bolt rings' and the following 10 years of growth (The first two rings at coring height were often wide regardless of the inferred competitive environment and ignored in this analysis). If a tree averaged 2.5 mm year⁻¹ or more for 10 years following the two 'bolting yrs' and showed an exponential decay or a negative linear decline in ring widths typical of open-grown conifers (Fritts, 1976; Cook, 1985)

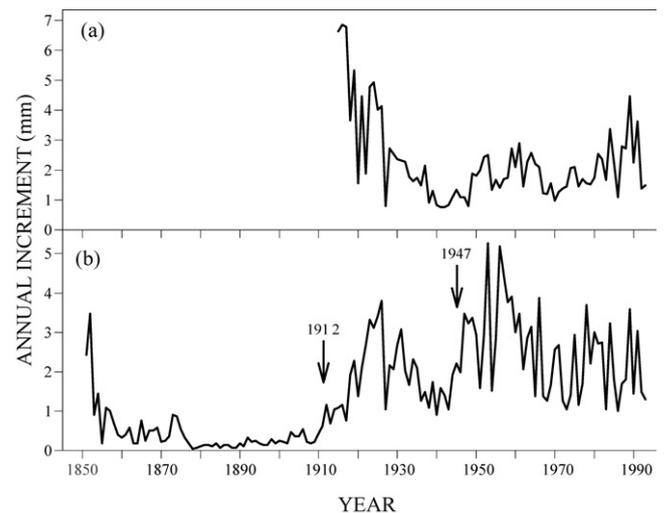


Fig. 2. Two longleaf pine radial growth patterns: (a) a pine established in a non-suppressed canopy position; (b) a pine established in a suppressed position. Note the rapid growth of the first 2 years in both cases, the 'bolt' rings. Arrows indicate growth releases in 1912 and 1947.

(Fig. 2a), it was interpreted as recruited in a reduced competitive environment. Such trees were then classified as being in a 'dominant' or open crown condition. Trees were interpreted as being suppressed if their average radial growth averaged less than 2.5 mm year⁻¹ or did not exhibit patterns of open-grown conifers (Fig. 2b). This level of radial increment, 2.5 mm year⁻¹, qualitatively appeared to be a dividing line for early growth between trees with the negative exponential or negative linear declines in radial increment in our sample. The number of trees recruited in the suppressed or dominant position was quantified and an estimation of the competitive environment was qualitatively observed for each 5-year interval at the plot and landscape level.

2.2. Disturbance history reconstruction

Each core was analyzed for canopy disturbance history following the methods of Lorimer (1985). A minor growth releases was defined as a 50–99% increase in growth over 15 years versus the preceding 15 years. A major release was defined as a 100% or more increase in growth over 15 years versus the previous 15 years (Fig. 2b). The number of release events for each age group was summed to identify their disturbance histories. The number of these events provides an estimate of the frequency of canopy disturbances. Average size of release (% increase in growth) was used to determine the relative intensity of canopy disturbance. Like recruitment history, the date of a disturbance has no uncertainty at coring height because of crossdating. To handle dating uncertainty caused by grass stage longleaf pine annual rings or a potential lag in response to canopy disturbance, we assigned events to 5-years periods. For clarification, we refer to intervals like "1900–1940s for all 5-years periods beginning in 1900 and including 1940 (i.e., 1900–1904, 1905–1909, etc. ...). Likewise, periods such as "after 1960" refer to time after the 1960 half-decade (i.e., 1960–1964, 1965–1969, etc. ...). The last

half-decade included in this analysis spans the period 1990–1994. Quantification of canopy disturbance and recruitment patterns through time aided in the interpretation of historical stand dynamics.

2.3. Disturbance history and climate

An interaction between tree growth and climate could cause false positives in disturbance detection and confound disturbance history interpretation. A favorable period of climate for tree growth, triggering a rapid increase in growth, could be interpreted as a canopy disturbance. Therefore, we tested whether detected increases in growth could have been caused by better climatic conditions for longleaf pine growth. As the radial growth of longleaf pine is limited by the moisture balance during the growing season, we used simple linear correlation analysis to determine the relation between 5-year averages of June through September total precipitation, average monthly temperature and Palmer Drought Severity Index (PDSI; Palmer, 1965) from the Albany, GA meteorological station (ca. 50 km north of the study site; Georgia's Climate Division 7 PDSI values from the National Climatological Data Center) to the number of disturbances and the average growth release per half-decade. We tested this relation for two time periods (1940–1984 and 1950 and 1984) to investigate whether the relation between climate and disturbance were influenced by intense tree-to-tree competition during stand development following intense canopy disturbance (Borman and Likens, 1979; Oliver and Larson, 1996). Correlations were considered significant when $\alpha < 0.05$.

3. Results

3.1. Landscape-level recruitment pattern

The oldest tree in our sample reached coring height in 1806, while the youngest tree reached that height in 1991 (Fig. 3). There was nearly continuous tree recruitment across the

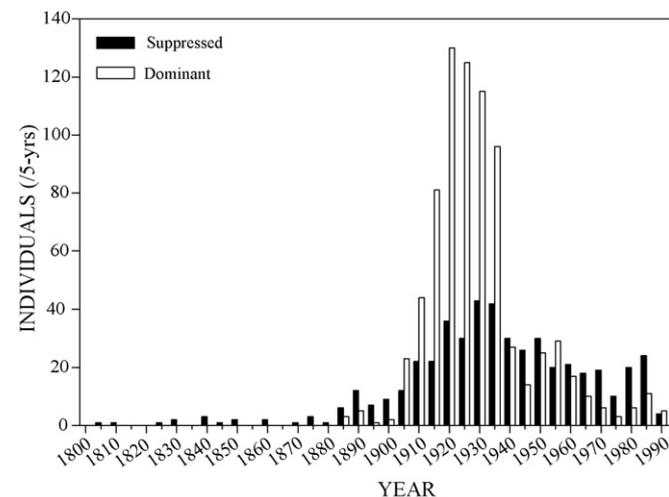


Fig. 3. Longleaf pine recruitment (individuals/5 year) across the Ichauway Plantation landscape over the last 200 years. Black bars = suppressed recruitment. Empty bars = recruitment in a dominant position.

Ichauway landscape over the last 150 years, with only two 5-year periods lacking recruitment from 1850 to 1994 (Fig. 3). Pine recruitment peaked between 1920 and 1924 and then leveled off to ca. 60 trees per 5-year period. Most tree recruitment (61.8%) occurred between 1910 and 1935 with the majority of these trees (74.8%) in a dominant position upon reaching coring height. All regeneration prior to 1885 was recruited in a suppressed position (Fig. 3). More trees were established in a suppressed position prior to 1899, 1940–1954, and 1960–1989.

3.2. PCA age group delineation

Sixty-six plots were delineated by PCA into eight age structure groups; four plots could not be clearly categorized and were not used in subsequent age group analyses. PCA explained 60.5% of age structure variation between plots with the first two axes and an additional 15.7% with the third axis (Fig. 4).

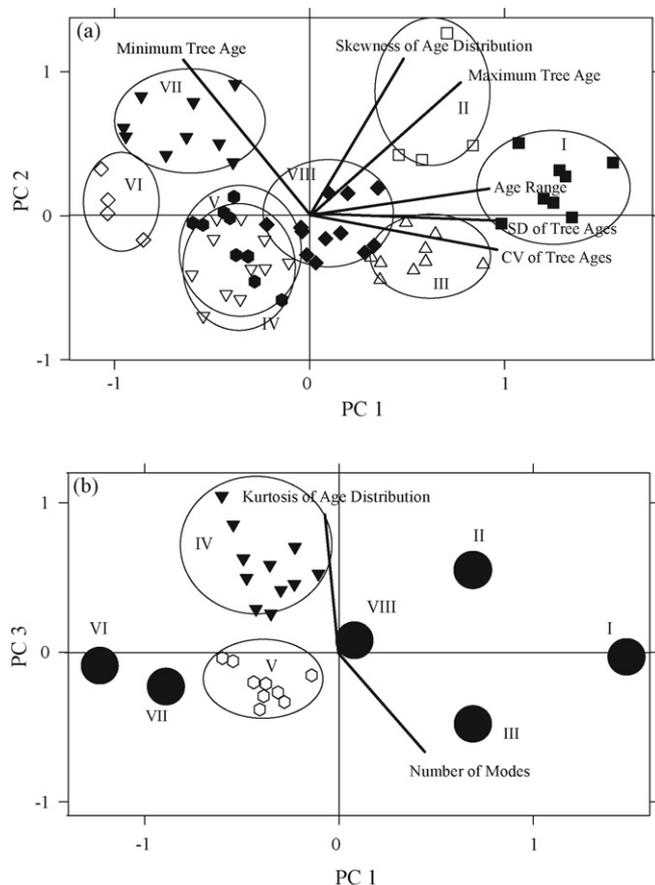


Fig. 4. (a) Plot of Axis 1 and 2 of principal components analysis (PCA) of second-growth longleaf pine stand age characteristics. Stands are represented by: Group I = black squares; Group II = open squares; Group III = open, upright triangles; Group IV = open, downward pointing triangles; Group V = black hexagons; Group VI = open diamonds; Group VII = black, downward pointing triangles; Group VIII = black diamonds. The ovals define each age group. (b) Plot of Axis 1 and 3 of PCA of stand age characteristics. Stands I, II, III, VI, VII, VIII are well-defined and represented by solids black circles for figure clarity. The vectors represent the eigen score loading for stand age characteristics.

Vectors in the ordination biplots reflect the age characteristics most important for distinguishing groups. PCA Axis 1 was defined by age range, standard deviation of age, maximum age, and coefficient of variation (Fig. 4a). Age skewness and minimum tree age define Axis 2. Axis 3 was defined by the kurtosis of age distribution and number of modal ages (Fig. 4b). Of the age groups delineated by PCA, only one group (Group VI) was essentially even-aged.

Each age group was comprised of 8–12 plots, with the exception of Groups II and VI, each with only four plots. An example of how age groups were delineated is best illustrated by Groups II and IV and Groups IV and V. A few old individuals of Group II (not shown) resulted in a skewed age distribution with higher maximum tree ages than other Groups IV and V. Age Groups IV and V overlap on Axis I and II, but separate clearly on Axis 3 (Fig. 4b). Inspection of recruitment patterns showed Group IV to be a slightly older and more even-aged than Group V (not shown).

3.3. Relationship between climate and tree growth releases

Climate was significantly correlated with growth releases (as interpreted as canopy disturbance) across the Ichauway landscape at the half-decade time step between 1940 and 1984 ($p < 0.05$) (Fig. 5; Table 1). Precipitation was negatively correlated with size of growth release (disturbance intensity; $r = -0.759$; $p = 0.018$; Fig. 5). Temperature was positively correlated with size of growth release for the same period ($r = 0.713$; $p = 0.031$). Precipitation, temperature and PDSI were not significantly correlated with each other over this period (Table 1).

The relationship from 1950 to 1984 between climate and growth releases was similar to the 1940–1984 period, although the relations were slightly stronger versus precipitation and temperature and much stronger versus PDSI (Table 1). The relation between number and size of growth release and PDSI is negative and becomes much stronger ($r = -0.806$; $p = 0.028$

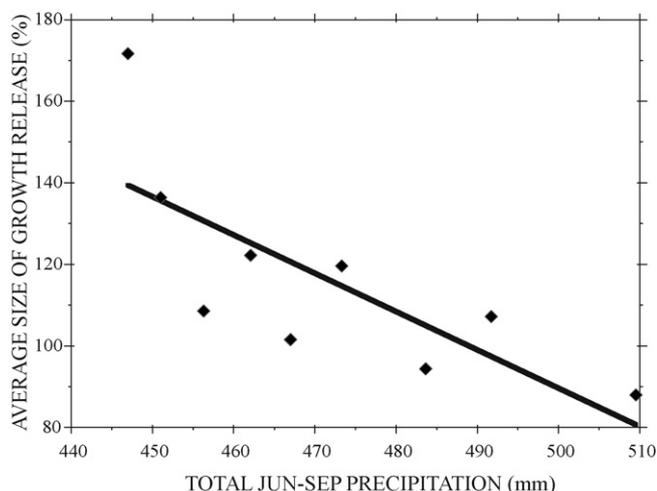


Fig. 5. The relation between average size of growth release (inferred to be canopy disturbance) and total June through September precipitation for each 5-year time step from 1940 through 1984. Each point on the graph represents a 5-year time step (1940–1944, 1945–1949, ...).

Table 1

Correlations between June–September precipitation, temperature and Palmer Drought Severity Index (PDSI) and the frequency and intensity of disturbance and between precipitation, temperature and PDSI

Correlation (p level)			
	Precipitation	Temperature	PDSI
1940–1984			
Frequency	-0.550 (0.125)	0.560 (0.117)	-0.598 (0.089)
Intensity	-0.759 (0.018)	0.713 (0.031)	-0.502 (0.169)
Climate variables			
Precipitation	-	-	0.485 (0.162)
Temperature	-0.526 (0.146)	-	-0.560 (0.117)
1950–1984			
Frequency	-0.676 (0.096)	0.654 (0.111)	-0.806 (0.028)
Intensity	-0.783 (0.037)	0.764 (0.045)	-0.856 (0.014)
Climate variables			
Precipitation	-	-	0.592 (0.162)
Temperature	-0.429 (0.336)	-	-0.917 (0.004)

and $r = -0.856$; $p < 0.014$, respectively). Only the correlation between temperature and PDSI becomes significant ($p < 0.004$) during the 1950–1994 period (Table 1).

3.4. Landscape-level disturbance history

Between 1885 and 1980, 472 radial growth releases (canopy disturbances) were detected. More than 80% (80.9%) of these disturbance events were detected since 1940 (Fig. 6). There were four distinct patterns of canopy disturbance across the Ichauway landscape (Fig. 6) (See Supplementary Material). First, no major ($\geq 100\%$ release) or large-scale canopy disturbances were recorded by sampled trees before 1855 with only a few minor disturbances identified prior to 1890. Second, 1890–1919 was characterized by major canopy disturbance, occurring synchronously across the landscape (See Supplementary Material). Third, a second period of major canopy disturbance occurred between 1940 and 1969. Lastly, peaks in the frequency of canopy disturbance across the landscaped occurred during the 1950s and early-1980s (Fig. 6) (See Supplementary Material).

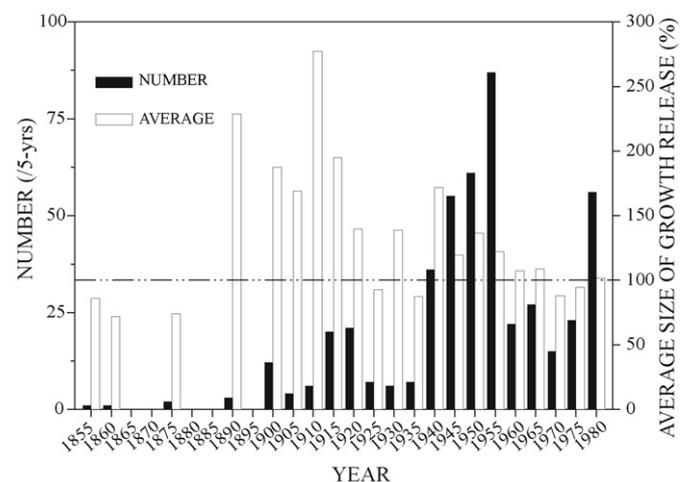


Fig. 6. Reconstructed canopy disturbance history across the Ichauway Plantation. Black bars represent the number of growth releases per half decade. Empty bars represent the average percent increase in growth per half decade.

Following the widespread canopy disturbance between 1890 and 1919, the frequency and intensity of releases decreased from 1925 to 1934 (Fig. 6). Canopy disturbance increased again starting in 1940 and peaked from 1955 to 1959 when there were 87 identifiable canopy disturbances. The 1955–1959 period is characterized by major canopy disturbance; the average growth release over this period was 122%. Recruitment following 1960 reflects major canopy disturbance as more trees established into a dominant canopy position (Fig. 3). Canopy disturbance decreased in frequency and intensity between 1960 and 1974. In turn, recruitment was reduced between 1960 and 1974 and more trees were established in a suppressed condition. A second peak in the number and intensity of canopy disturbances occurred from 1980 to 1984. Recruitment increased following this peak, but more pines were still recruited into a suppressed canopy position through 1990 (Fig. 6).

3.5. Disturbance history of PCA age groups

With a few differences, patterns of disturbance in each group generally follow the landscape pattern (See Supplementary

Material). For brevity, we report on only the age groups with the most distinct patterns of stand dynamics. Group I generally paralleled the Ichauway landscape disturbance history; plots in this group had minor canopy disturbances before 1890, major disturbances between 1890 and 1915 and increasing intensity of disturbance after 1940 (Fig. 7a). Recruitment was suppressed before 1890 and after 1960 (Fig. 7b), with a pulse of dominant recruitment from 1920 to 1930.

Plots in Group III, with trees younger than Group I, had a different pattern of stand dynamics. Major disturbance events in Group III occurred from 1900 to 1920, 1940 to 1960 and 1980, intermixed with fewer minor disturbances (Fig. 8a). Recruitment was continuous since 1915, with most pines establishing in suppressed condition from 1890 to 1894 and after 1945 (Fig. 8b).

The plots in Group VII had the narrowest range of tree ages of age groups delineated. Major disturbances in Group VII occurred 1900–1930, 1940 and 1955–1970, with minor disturbances in 1945–1950 and 1980 (Fig. 9a). Recruitment in Group VII was suppressed in the half-decades beginning with 1900, 1910, 1920 and after 1945 (Fig. 9b). Recruitment

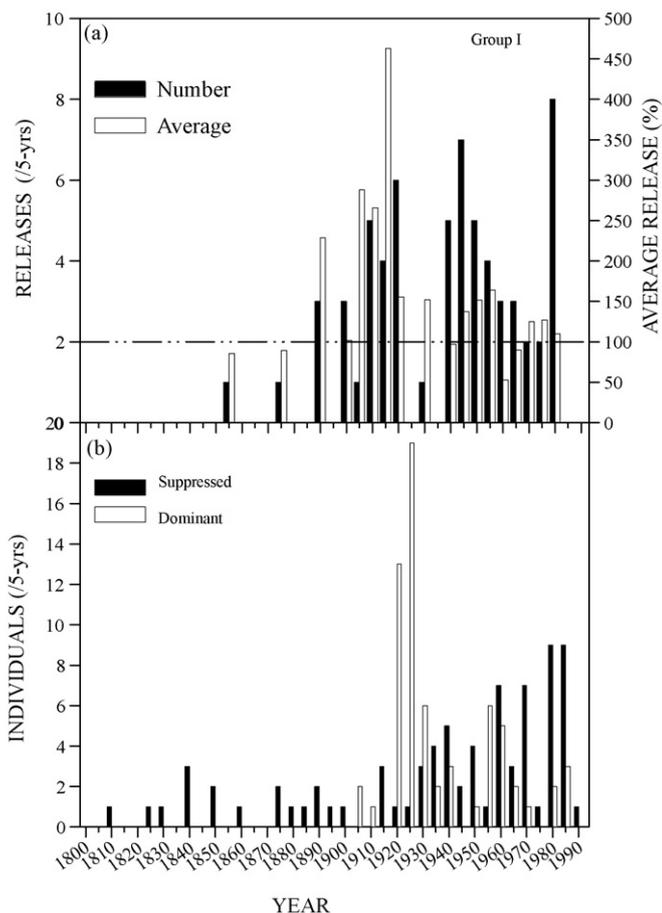


Fig. 7. Disturbance and recruitment patterns for age Group I. (a) Disturbance history—releases in the figure represent growth releases and are inferred to be canopy disturbance. Black bars = number of growth releases per half decade. Empty bars = average percent increase in growth per half decade. (b) Tree recruitment—Black bars = suppressed recruitment. Empty bars = recruitment in a dominant position.

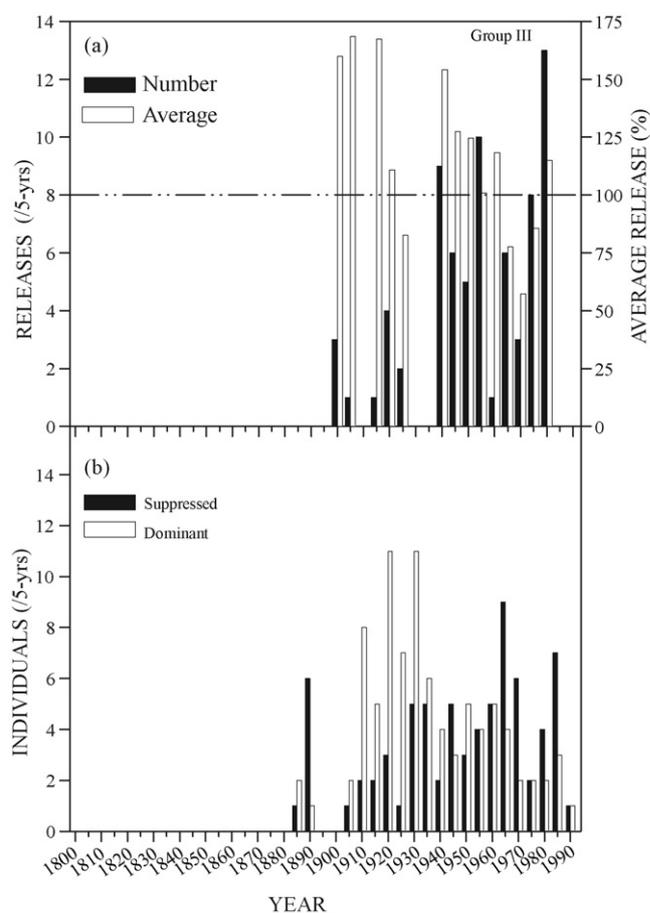


Fig. 8. Disturbance and recruitment patterns for age group III. (a) Disturbance history—releases in the figure represent growth releases and are inferred to be canopy disturbance. Black bars = number of growth releases per half decade. Empty bars = average percent increase in growth per half decade. (b) Tree recruitment—Black bars = suppressed recruitment. Empty bars = recruitment in a dominant position.

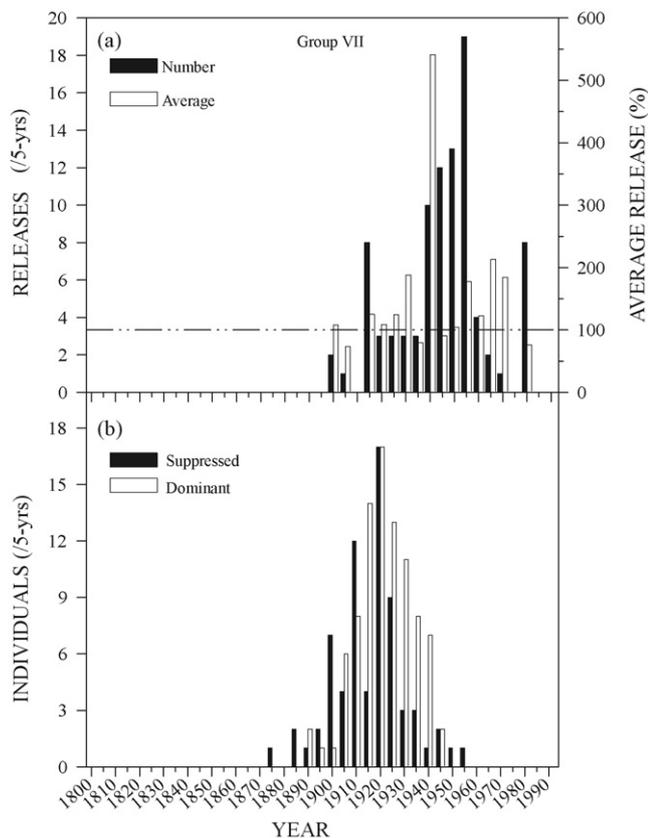


Fig. 9. Disturbance and recruitment patterns for age group VII. (a) Disturbance history—releases in the figure represent growth releases and are inferred to be canopy disturbance. Black bars = number of growth releases per half decade. Empty bars = average percent increase in growth per half decade. (b) Tree recruitment—Black bars = suppressed recruitment. Empty bars = recruitment in a dominant position.

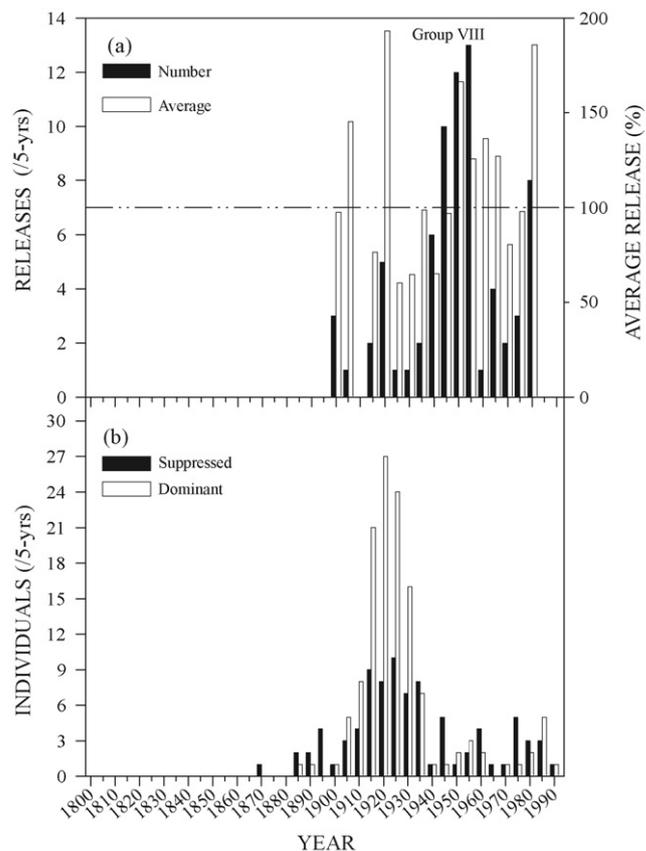


Fig. 10. Disturbance and recruitment patterns for age Group VIII. (a) Disturbance history—releases in the figure represent growth releases and are inferred to be canopy disturbance. Black bars = number of growth releases per half decade. Empty bars = average percent increase in growth per half decade. (b) Tree recruitment—Black bars = suppressed recruitment. Empty bars = recruitment in a dominant position.

occurred in a dominant position in 1905, 1915 and from 1925 to 1940. There was no recruitment in Group VII plots after 1955.

Age structure of the plots in Group VIII was similar to Group VII except for continuous recruitment over the last four decades, revealing a different pattern of stand dynamics. Plots in Group VIII typically had intense disturbances from 1900 to 1920, 1950 to 1965 and in 1980 (Fig. 10a). The majority of the disturbances occurred between 1935 and 1955. Most of the recruitment occurred between 1910 and 1935 and was typified by dominant trees (Fig. 10b). Trees were recruited into a suppressed state before 1900 and from 1935 to 1980.

4. Discussion

4.1. Landscape-level age structure

At the landscape scale, age structure analysis revealed nearly continuous tree recruitment across Ichaaway over the last two centuries. This pattern of recruitment was sustained during eras of natural and anthropogenically influenced stand dynamics (discussed in next section). Further, of the 91 ha studied, most plots (94.3% of the 70 plots) had two or more age cohorts; only the four plots that comprised Group VI (5.7%) had age structures that could be considered even-aged (See

Supplementary Material). During the era of presettlement stand dynamics (pre-1890), recruitment was periodic and resulted in an uneven-aged age structure. These results provide support that longleaf pine can be recruited in multiple age cohorts at scales of less than 1 ha (Grace and Platt, 1995; Palik et al., 1997; McGuire et al., 2001) and help explain the structural heterogeneity in remnant old-growth (Platt and Rathbun, 1993; Noel et al., 1998; Varner et al., 2003) and those described in characterizations of primary longleaf pine forests (Reed, 1905; Schwarz, 1907; Forbes, 1930).

4.2. Climate and growth releases

The average size of growth releases, a proxy for disturbance intensity, was significantly and negatively correlated with growing season precipitation, while growing season temperature was positively correlated with disturbance intensity (Fig. 5; Table 1). Correlations of the opposite sign between temperature and precipitation to tree growth are commonly found in dendroclimatological studies and likely represent the evaporative demand of trees (i.e., Fritts, 1976; LeBlanc and Terrell, 2001). Mortality was greater during dryer, warmer seasons, supporting the concept of an inciting stress leading to tree mortality (Manion, 1981; Pedersen, 1998). Even though PDSI

is primarily a combination of temperature and precipitation (Palmer, 1965), it is peculiar that PDSI is not strongly correlated with the average size of growth release. The significance of PDSI's poor relationship with disturbance is underscored in the comparison of climate and disturbance from 1940 to 1984 to 1950 and 1984 (Table 1). The relation between disturbance and precipitation and temperature remains essentially unchanged while the relation between PDSI and disturbance and PDSI and temperature becomes stronger. This relationship suggests that the PDSI of Georgia's climate division 7 may not be reliable for analysis at Ichauway or that the influence of precipitation and temperature on disturbance functions differently than how it might be captured in the PDSI. Regardless, our results indicate that precipitation and temperature play strong roles in longleaf pine canopy disturbance as reflected in growth releases of surviving trees.

Contrary to our hypothesis, detected growth releases were not correlated with a favorable climate. In fact, our findings indicate the opposite: the average size of a growth release increased during drier and hotter periods of climate, which is in opposition to prior research on the radial growth of longleaf pine (Lodewick, 1930; Coile, 1936; Schumacher and Day, 1939; Meldahl et al., 1999). The method of detecting disturbances is designed such that relative increases in growth over an extended period would only rarely be a false-positive result, i.e., that the release would not be caused by climate. Therefore, the detected growth releases most likely represent a reduction in tree-to-tree competition. The immediate implication of these results suggests is that interpretation of the disturbance history of the open-canopied Ichauway forest through tree ring analysis can be made with some confidence. This finding has important implications for the longleaf pine ecosystem of the Ichauway landscape and, perhaps, longleaf pine ecosystems in general.

4.3. Growth releases and climate linkages

The significant relation between climate (reduced precipitation and increased temperatures) and increased ring widths (inferred to be reduced tree-to-tree competition) suggests climatic variations may play an important role in stand dynamics. Previous studies have shown similar connections between drought and mortality in different forest types (e.g., Jenkins and Pallardy, 1995; Allen and Breshears, 1998; Pedersen, 1998; Villalba and Veblen, 1998). Our results and others at Ichauway (Palik and Pederson, 1996) indicate that drought exacerbates longleaf pine mortality. One mechanism for this phenomenon may be that increased evaporative demand reduces vigor, which then predispose trees to subsequent agents of mortality (Manion, 1981; Pedersen, 1998; Allen and Breshears, 1998). Data collected on tree mortality at Ichauway for the 1990–1994 period suggests such a relation: lightning-killed trees were more likely to occur on drier sites (Palik and Pederson, 1996). Alternatively, warmer, drier periods cause peaks in fire intensity and severity in frequently burned ecosystems, exacerbating overstory pine mortality. Increased overstory mortality reduces the competitive environment by

increasing resources for surviving pines and subsequent recruitment. Of course, it is probable that these and other factors act in concert on overstory mortality rates.

The positive correlation between temperature and mortality has important implications in the face of warming of the next 100 years, especially as it seems highly likely that future warming is expected to be greater than what has occurred over that last 100 years (Meehl et al., 2005). If our findings hold true across the greater longleaf pine landscape, it suggests that the increased warming will likely increase the mortality rate of overstory trees, especially if warming is accompanied by increased drought frequency or severity. If future climate is characterized by more warm and dry periods, individual canopy mortality would be expected to increase. The relationship between tree mortality and climate should be considered as seasonal and multi-annual management plans are developed.

4.4. Two centuries of landscape-level disturbance history

Despite nearly continuous recruitment over the last two centuries, there were considerable differences in the amount and periodicity of recruitment as well as the competitive environment before and after 1890. Tree recruitment increased in the 1890s and was considerably greater between 1910 and 1939 than before 1890 (Fig. 3). The crown position of recruited trees also changed from being primarily suppressed prior to 1905 to being primarily in a dominant position between 1905 and 1939. This change in quantity and crown position of tree recruitment corroborates the reconstructed of large-scale canopy disturbances between 1890 and 1934 (Figs. 6–10). The apparent lag between canopy disturbance and tree recruitment is most likely caused by longleaf pine's grass stage. As longleaf pine produces seed irregularly (Boyer, 1987), the lag may also be related to the variability in years between masting and seed bed availability. Regardless of the cause for the lag, our results point to an abrupt transition in land-use eras across the Ichauway landscape ca. 1890.

The contrast in tree recruitment and canopy position around 1890 reflects changes in land-use at Ichauway specifically, and southwest Georgia in general. Local and regional oral and historical reports indicate that the turpentine industry began ca. 1890 with the initial harvest and conversion of regional upland forests (Livingston, 1995a,b). Turpentine primarily used rail systems in the forests of northern Florida and southwestern Georgia (Livingston, 1995a). Abandoned narrow gauge rail beds were found near a few study plots and scattered trees on the Ichauway landscape still had turpentine collection buckets and other turpentine-related equipment attached or the "cat-face" scarring typical of turpentine. The period of initial entry into forests of the Ichauway region coincides with an increase in canopy disturbance between 1890 and 1930 (Fig. 6) and precedes an increase in longleaf pine recruitment in a dominant canopy position between 1905 and 1935 (Fig. 3). The number and intensity of growth releases at Ichauway decreased from 1925 to 1935, coinciding with the consolidation of farms and land (Elliott, 1974). Increases in canopy disturbance beginning in the 1940s (Fig. 6) were likely the result of typical

quail plantation management (Neel, 1971): stand thinning for wildlife habitat, timber harvesting, and salvage of diffuse natural pine mortality. Pairing reconstructed canopy disturbance history with recorded land-use history illustrates two different periods of stand dynamics: natural stand dynamics prior to 1890 and anthropogenically mediated stand dynamics after 1890. Also, the striking similarity between reconstructed and recorded history provides a second set of evidence that the disturbance detection methodology in closed-canopied forests has utility in open-canopied forests.

4.5. Inferring competitive environment

Radial growth patterns of the first 12 years in each tree were helpful in evaluating the competitive environment of small pines. For example, recruitment ring patterns before 1900, from 1925 to 1945 and 1960 to 1975 revealed that recruitment was predominantly suppressed (Fig. 3). Following major canopy disturbance (e.g., 1905–1920), ring patterns of recruitment indicated that most trees grew in a dominant position. Hypothetically, the ratio of dominant versus suppressed recruitment may be tracking stand density at scale of small, single-tree to large, multiple tree gaps. This hypothesis is based on earlier results that an average of 1.4 trees were killed per mortality event in these same 70 plots from 1990 to 1994 (range = 1–5 trees; Palik and Pederson, 1996). Larger mortality events and canopy openings were also dominant features of longleaf pine landscapes (Platt and Rathbun, 1993; Noel et al., 1998; Varner et al., 2003), but likely occurred infrequently following hurricanes, large-scale beetle outbreaks, and high intensity fires.

4.6. Age group level disturbance history

Examination of age-group level age structure and disturbance histories reveals the influence of different disturbance regimes on tree recruitment. Group I illustrates a history of canopy disturbance that allowed nearly constant tree recruitment over the past 100 years with spikes in tree recruitment followed major canopy disturbance (Fig. 7). Groups III and VIII exhibited similar pulses in tree recruitment (Figs. 8b and 10b) and had frequent, moderate to major canopy disturbances from 1940 to 1980 that coincided with constant tree recruitment (Figs. 8a and 10a). In contrast, Group VII plots experienced numerous minor and major canopy disturbances after 1945 and yet had no pine recruitment after 1955 (Fig. 9). The mechanism of recruitment limitation is unclear for plots of Group VII. Further investigations of contrasting successes and failures in tree recruitment should provide models for successful long-term management of longleaf pine ecosystems.

4.7. Management implications

Plots in age Groups I, III and VIII appear to be good models for long-term management of naturally regenerated second-growth longleaf pine forests. These groups had: (1) continuous recruitment; (2) a population of saplings ready for canopy

ascension following timber removal; and (3) a wide range of tree ages. Over time these stands should develop into a forest approximating the rotated sigmoid diameter distribution and patch structure of remnant old-growth longleaf pine forests (Noel et al., 1998; Varner et al., 2003). The primary longleaf pine forest was all-aged and composed of small patches of even-aged trees (Reed, 1905; Schwarz, 1907; Wahlenberg, 1946). The disturbance regime of Groups I, III, and VIII may provide an effective foundation upon which to base a long-term forest management model.

Growth histories revealed here show that longleaf pine can respond with increased growth with a change in its competitive environment and is capable of responding to disturbance more than once (Fig. 2a). Multiple growth releases were also identified in an old-growth longleaf pine forest in southern Alabama (Meldahl et al., 1999). These results are also consistent with research showing strong competitive response of longleaf pine seedlings to overstory competitors (Palik et al., 1997; McGuire et al., 2001). Together, these findings indicate that longleaf pine can survive during periods of overstory competition, responds strongly to a reduction in competition, and can be successfully recruited at small spatial scales. These life-history traits are further evidence that longleaf pine can be managed in a manner that makes large-scale canopy disturbance unnecessary (Farrar, 1996; Palik et al., 1997; Palik et al., 2002). Long-term restoration and management of longleaf pine ecosystems should take into consideration these life history traits as well as the emerging understanding of the relationship between climatic variability and stand dynamics.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2007.07.030.

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