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Effects of long-term fire exclusion on tree species composition and stand structure in an old-growth *Pinus palustris* (Longleaf pine) forest

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Abstract

Frequent fire is an integral component of longleaf pine ecosystems, creating environmental conditions favoring survival and growth of juvenile pines. This study examined stand structure, species composition, and longleaf pine regeneration in an old-growth tract of longleaf pine forest (Boyd Tract) experiencing long-term (>80 yr) fire exclusion in the Sandhills of North Carolina. Sampling of woody stems (i.e., ≥2.5 cm diameter at breast height) and tallies of longleaf pine seedlings were carried out in plots established randomly on upland, mesic areas and lowland, xeric areas within the Boyd Tract. Dominant woody species in mesic plots were black oak, hickories, and large, sparse longleaf pines. Xeric plots had high densities of turkey oak with the large longleaf pines, as well as higher frequencies of smaller longleaf stems. These differences between areas were associated with higher clay content of upland soils and higher sand content of lowland soils. Age-class frequency distributions for fire-suppressed longleaf pine following the last wildfire at the Boyd Tract approximately 80 yr ago contrasted sharply with data from an old-growth longleaf tract in southern Georgia (Wade Tract) that has been under a long-term frequent fire regime. Post-burn recruitment for the Boyd Tract wildfire appears to have been initially high on both site types. Longleaf pine recruitment diminished sharply on the mesic site, but remained high for ∼60 yr on the xeric site. Currently, longleaf pine regeneration is minimal on both site types; several plots contained no seedlings. Sharp contrasts in longleaf pine dominance and stand structure between the Boyd and Wade Tracts demonstrate the importance of large-scale disturbance, especially hurricanes and fire, in shaping the structure and function of longleaf pine ecosystems of the southeastern United States. In particular, long-term exclusion of fire on the Boyd Tract has altered stand structure dramatically by permitting hardwoods to occupy at high densities the characteristically large gaps between longleaf stems that are maintained by fire and other disturbances.

Nomenclature: Radford et al. (1968); Godfrey (1992).

Introduction

Habitat loss commonly results from drastic physical alteration of natural ecosystems (e.g., agricultural practices and urban development). Loss of habitat, however, also can result from manipulation of natural processes responsible for maintaining ecosystem integrity. One such process that frequently has been manipulated is that involving fire and southeastern savannas dominated by *Pinus palustris* Mill. (longleaf pine). Although *P. palustris* ecosystems once covered 25-35 million ha throughout the southeastern United States, at the current time less than 3% is still extant and much of what remains is degraded (Noss 1989; Frost 1993). Such losses have been due to intensive human alterations, such as turpentine operations and logging after railroads were constructed in the southeast, and to an effective fire suppression effort that began in the region around 1920 (Frost 1993).

Fire has been component of ecosystems of the southeastern Coastal Plain throughout the Quaternary (Gilliam 1991a), resulting in the selection for plant species that are both fire tolerant and fire dependent (Mutch 1970). There is a strong relationship between fire and *P. palustris* (Platt 1997). It has been recognized for almost a century that regeneration of *P. palustris* depends on fire (Andrews 1917; Chapman 1932a; Heyward 1939; Wahlenberg 1946; Croker & Boyer 1975; Platt et al. 1988; 1991). Fire exposes the mineral soil, which is needed for successful seedling establishment (Bruce 1951). Fires also remove litter and above-ground vegetation, enhancing establishment and growth of juveniles (Pessin 1938; Boyer 1993). Juveniles are fire resistant as early as two years after germination (Grace & Platt 1995), but tend to have very low survival in the absence of fire (Chapman 1932b; Gilliam 1991b). Once in the 'grass stage,' juveniles tend to have low mortality from fire (Croker and Boyer 1975; Rebertus et al. 1993). Although juveniles that are initiating height growth may be susceptible to hot fires (Rebertus et al. 1993), large *P. palustris* stems tend to be very resistant to most fires (Glitzenstein et al. 1995).

Stands of *P. palustris* occur throughout the fall-line sandhills, a physiographic region in the southeastern U.S. occurring along the juncture between the Piedmont and Coastal Plain provinces from North Carolina to northern Alabama (Christensen 1988). The characteristic deep, coarse-textured sandy soils of the region create xeric conditions that historically resulted in a fairly uniform tree dominance in true sandhills – *P. palustris* in the overstory and *Quercus laevis* Walter (turkey oak) in the understory (Wells 1928; Wells & Shunk 1931). Land use changes and fire exclusion have resulted in a marked decline of the *P. palustris* ecosystem in the fall-line sandhills over the past half-century.

The Weymouth Woods-Sandhills Nature Preserve in Moore County, North Carolina contains the Boyd Tract, a 66-ha old-growth stand of *P. palustris*. This is the largest old-growth stand in the state and in the entire fall-line region of the southeast. Field observations and historical records indicate that the Boyd Tract has not burned for more than 80 years (Gilliam et al. 1993). In this paper we document the effects of long-term fire exclusion on the tree community of the Boyd Tract. First, we describe composition and structure of the upland and lowland sections of the Tract. Second, we use age-size relationships derived from tree cores taken on the Boyd Tract to describe the structure of *P. palustris* populations in these two sections. Finally, we compare the composition and structure of tree communities, as well as the structure of the *P. palustris* population of the Boyd Tract to those of the Wade Tract, an old-growth site that has not experienced prolonged fire suppression.

Table 1. Soil characteristics from upland and lowland sites of the Boyd Tract, North Carolina. Note: pH_W is water-extractable pH, pH_{KCl} is 1N KCl-extractable pH, and O.M. is organic matter.

Site type	pH_W	pH_{KCl}	O.M. (%)	Texture (%)		
				Sand	Clay	Silt
Upland	4.66*	4.07**	4.07***	84.1*	10.5**	5.4
Lowland	4.56	3.94	3.09	85.5	8.9	5.5

*Indicates significant difference between site types at $p < 0.10$.
**Indicates significant difference between site types at $p < 0.05$.
***Indicates significant difference between site types at $p < 0.01$.

Site descriptions

Boyd Tract

The Boyd Round Timber Natural Area (Boyd Tract) is located in Moore County in the sandhills region of south central North Carolina (35°N, 79°W). The tract is approximately 200-km northwest from the coastline of the Atlantic Ocean. Parent materials for much of this area of the state are Cretaceous sediments that form unconsolidated sand and clay layers (Sechrist & Cooper 1970). Soils are predominantly sands of the Blaney series, sandy siliceous thermic Arenic Fragiudults; the 50–100 cm thick A horizons tend to be uniform and acidic (U.S.D.A. 1972).

There are two distinct site types on the Boyd Tract. These site types, of approximately equal area, differ in elevation; uplands are 165–180 m and lowlands are 137–165 m above mean sea level (Gilliam et al. 1993). Uplands and lowlands also differ in soil characteristics (Table 1). Soils of the uplands are mostly loamy sands with higher percentages of clay than those of the lowlands. Soils of the lowlands are generally very coarse-textured sands. Although differences in soil texture between site types were significantly different (Table 1), there is substantial variation in soil texture within uplands and lowlands (Gilliam et al. 1993). Upland soils also tend to be less acidic and have higher organic content than those of the lowlands (Table 1).

The Boyd Tract was part of the Weymouth Estate, purchased by James Boyd at the turn of the century. The tract was never logged, and otherwise appears to have had minimal anthropogenic impact on the trees (Gilliam et al. 1993). The oldest known *P. palustris* on the tract are >400 years old (Gilliam et al. 1993), similar to maximum ages in other old-growth stands (Platt et al. 1988). In the 1970's, the Boyd Tract became part of the Weymouth Woods-Sandhills Nature Preserve. The last recorded fire prior to the initiation of this study occurred in the spring of 1909, as part of a wildfire that was widespread in much of the immediate area (Huttenhauer 1980). Subsequent to our study, no fires, or other large-scale disturbances have been recorded for the Boyd Tract.

Wade Tract

The Wade Tract is an 80 ha old-growth *P. palustris* stand located on Arcadia Plantation in the Tallahassee Red Hills region (Thomas County) of southern Georgia (30°N, 83°W). The tract is 100 km from the coastline of the Gulf of Mexico. In the region of the Wade Tract, the topography is rolling and extends from about 120–130 km above mean sea level. Parent materials for much of this region are Cretaceous sediments that were uplifted during the late Oligocene-Miocene and now form unconsolidated sand and clay layers (Myers 1990; Platt & Schwartz 1990). Soils are predominantly sands that overlie clays; A horizons are 50–100 cm thick and tend to be uniform and acidic. Unlike the Boyd Tract, there are no distinct site types on the Wade Tract; changes in elevation are more continuous on the Wade Tract, varying a total of about 15-m from lowest to highest elevations.

As with the Boyd Tract, the Wade Tract is recognized as an old-growth stand. Cores of trees have revealed a number of trees greater than 300 years (West et al. 1993); the oldest known tree was killed by lightning in 1978 when it was about 500 years old. There are no records that indicate logging on the Wade Tract, although there was very selective cutting in the region in the early 1800's when the region was settled initially by humans of European and African origins. The plantation, including the Wade Tract, has been burned frequently (annually/biennially) for as long as plantation records exist. At the current time, the Wade Tract is managed by Tall Timbers Research Station as part of a conservation easement with the owners.

Methods

Boyd Tract

Sixty circular 0.04-ha sample plots (11.3-m radius) were established on the Boyd Tract in 1989. Thirty each were located randomly in upland and lowland sites. All stems ≥2.5 cm diameter at 1.3 m (hereafter, dbh) within each plot were identified, and dbh was recorded. In addition, all juvenile *P. palustris* were counted in each plot. Most hickories were *Carya tomentosa* (Poiret) Nuttall, although some *C. pallida* (Ashe) Engler & Graebner were present also. In this study, the two species were grouped.

A subsample of measured trees was cored with an increment borer in 1994. Thirty trees, representing the full range of sizes (10–76 cm dbh) on the Boyd Tract, were selected in each site type (upland and lowland), for a total of 60 cored trees. Annual rings were counted and used as an estimate of age. No corrections were made for cores that did not contain the pith. The dbh and age of the 60 aged trees were used to construct age-diameter regressions.

Wade Tract

Data for the Wade Tract were obtained from the original sampling of a 40-ha mapped plot established in 1979 (Platt et al. 1988). Procedures, outlined in Platt et al. (1988), involved mapping of all trees > 2 cm dbh. Species and dbh also were recorded at this time. We used the 1979 data in the current study. We calculated the basal area and density of all woody species based on data within the entire 40 ha plot. The relative basal area and density, expressed as percentages of totals within the plot, were added to obtain importance values for each species. The six species of which the importance value was ≥1 were considered separately; the other 15 woody species were grouped together as 'other' species.

Results

Boyd Tract

The basal area, density, and importance values of *P. palustris* and the more prominent hardwoods in the Boyd Tract are presented for the upland, lowland, and both combined in Table 2. Overall, *P. palustris* comprised the vast majority of the basal area, but there were fewer stems of pines than of hardwoods.

As a result, importance was shared with hardwoods; about one-third of the total importance value was represented by *P. palustris* on the Boyd Tract. Although basal area of *P. palustris* was similar in the uplands and lowlands, the presence of more stems resulted in a higher importance value in the lowlands. Larger numbers of stems of *P. palustris* in lowlands compared to uplands resulted primarily from higher densities of (especially) small and intermediate-sized trees in the lowlands (Figure 1a); for large trees (>50 cm dbh), there were similar numbers of trees in uplands and lowlands. In addition, the density of juvenile *P. palustris* (<2.5 cm dbh) ranged from 50–70 per hectare on both uplands and lowlands; densities were not significantly different between site types.

When the upland and lowland areas were separated, local differences in species composition and abundance became evident. Different species of hardwoods were most abundant in the uplands as compared to the lowlands (Table 2). In the upland, a number of *Q. velutina* of all sizes, but especially those <50 cm dbh (Figure 1b), were present, resulting in importance values equivalent to those of *P. palustris*. In the lowlands, however, *Q. velutina* was not abundant. Although *Q. laevis* was not abundant in the uplands, very large numbers of small stems were present in the lowlands (Figure 1c); as a result, the importance value of *Q. laevis* was larger than that for *P. palustris* in the lowlands. In addition, the importance of *Carya* sp. and other woody species was greater in the uplands than lowlands; this resulted from more stems of all sizes in the uplands than the lowlands (Figure 1d).

Ages and diameters of *P. palustris* on the Boyd Tract were significantly correlated ($r^2 = 0.48$; $p < 0.01$). Log-log transformation of the data improved the fit to the data ($r^2 = 0.58$; $p < 0.01$). Accordingly, ages of individual pines on the Boyd Tract were estimated using the following equation:

$$\mathrm{A} = 10^{[(\log \mathrm{D} - 0.46)/0.52]}, \quad (1)$$

where A is age in yr and D is dbh in cm (Figure 2).

The frequency distributions of ages of *P. palustris* predicted for the two site types using equation (1) are presented in Figure 3. On both site types there were trees in all 20 yr age classes up to >300 years; no obvious long-term gaps were present in the age-class distributions. Sizable numbers of trees (∼50 and ∼25% of the uplands and lowlands, respectively) were >200 years, and there were a few trees predicted to be more than 400 years. There were some differences between uplands and lowlands. Largest number of trees were predicted for the 80–100 and 100–120 yr class in the uplands, but in the 0–20, 20–40, 40–60, and 60–80 yr classes in the lowlands (Figure 3).

Wade Tract

The basal area, density, and importance values for *P. palustris* and the more prominent hardwoods in the Wade Tract are presented in Table 2. *Pinus palustris* comprised the vast majority (>95%) of the basal area and more than 75% of the stems. As a result, about 87% of the total importance value was represented by *P. palustris* on the Wade Tract. Four species of oaks, *Q. incana*, *Q. laevis*, *Q. margaretta*, and *Q. marylandica*, together comprised 12% of the total importance value. The other 16 woody species with stems ≥2 cm dbh comprised 1% of the total importance value (Table 2).

Discussion

Stand composition and structure

The composition and structure of the woody plant communities in the two preserves display impressive differences. The basal area and density of woody plants in the Wade Tract are about one-fourth and one-fifth those in the Boyd Tract. For *P. palustris* alone, the basal area in the Wade Tract was one half that in the Boyd Tract, although densities of pines tended to be similar. As a result, the aspect of the Wade Tract is more a pine savanna with scattered oaks, whereas the aspect of the Boyd Tract is more a pine-oak woodland or forest.

We can identify two likely casual forces that might produce these differences: hurricanes and fires. Hurricanes are much more frequent along the Gulf coastal plain than along the Atlantic coastline (Simpson et al. 1971). Low-intensity hurricanes have occurred in the region of the Wade Tract on average every couple of decades over the past century (Platt & Schwartz 1990, Batista & Platt 1997). Although these hurricanes cause low rates of damage and mortality in the old-growth pine stands, they probably maintain lower basal areas than in areas with lower hurricane frequencies because large, slow-growing trees are the most susceptible to wind damage (Platt & Rathbun 1993). As a result, open patches occur within stands (see Noel et al. 1998).

Fires, especially those in the growing season and those of higher intensity, are more likely to affect

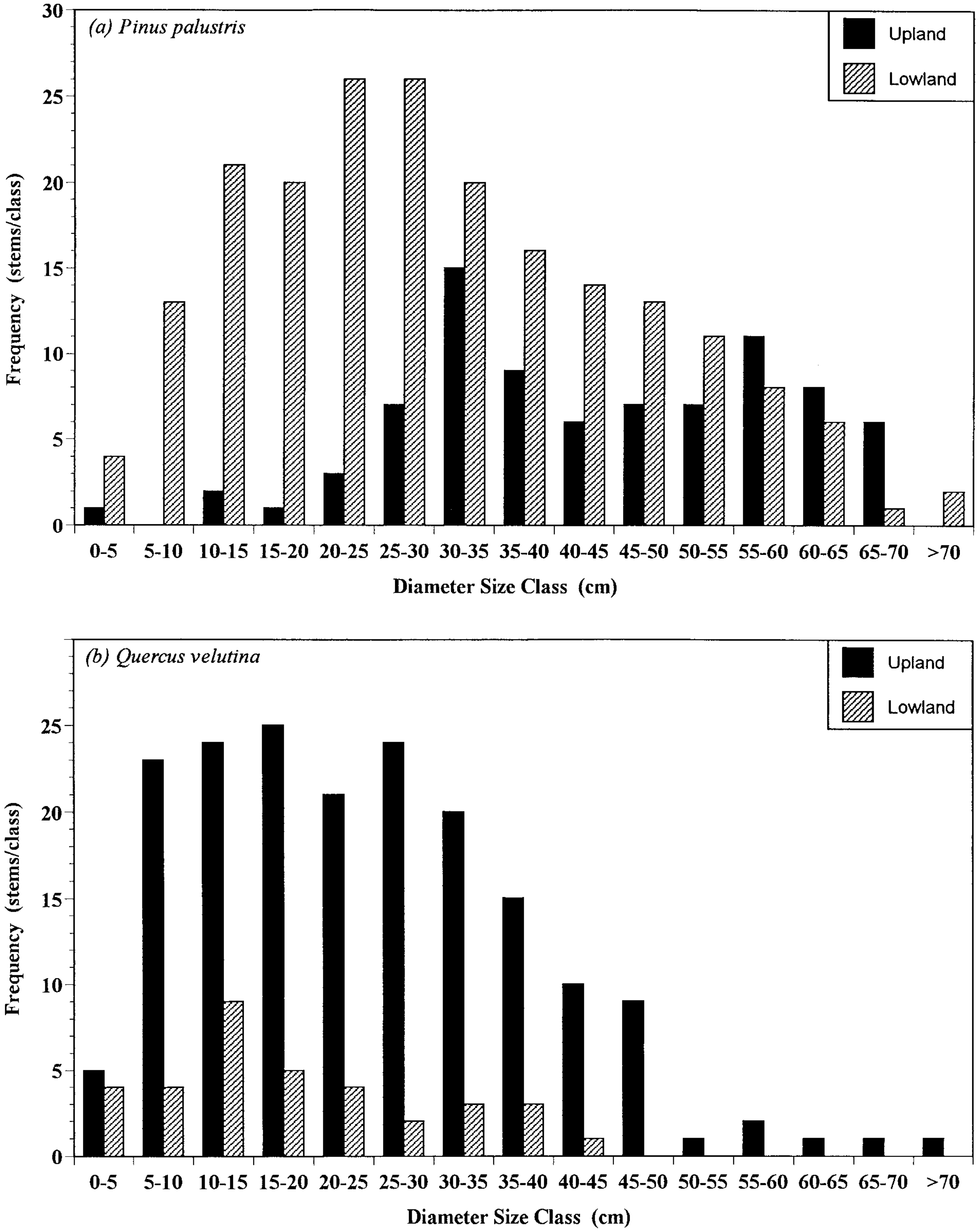
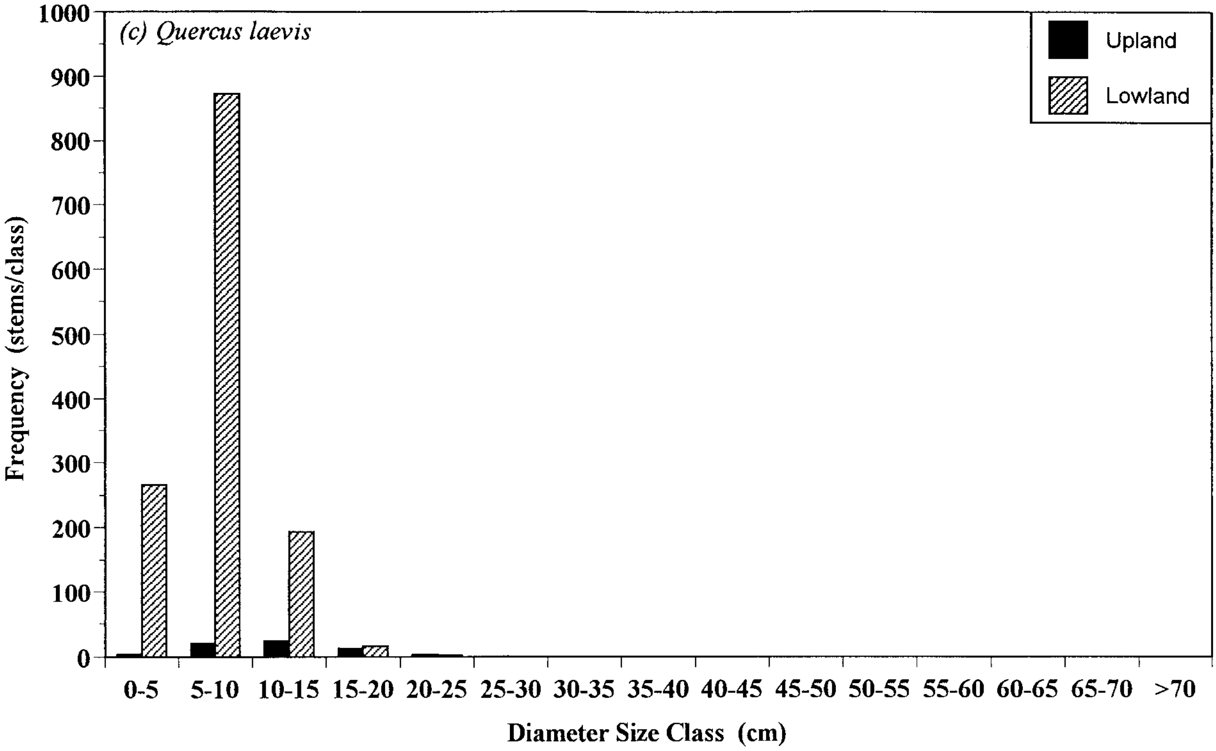


Figure 1. Diameter size-class frequency distributions for dominant tree species on upland and lowland sites of the Boyd Tract. (a) *Pinus palustris*; (b) *Quercus velutina*; (c) *Q. laevis*; (d) *Carya* spp. Note ordinate scale differences.



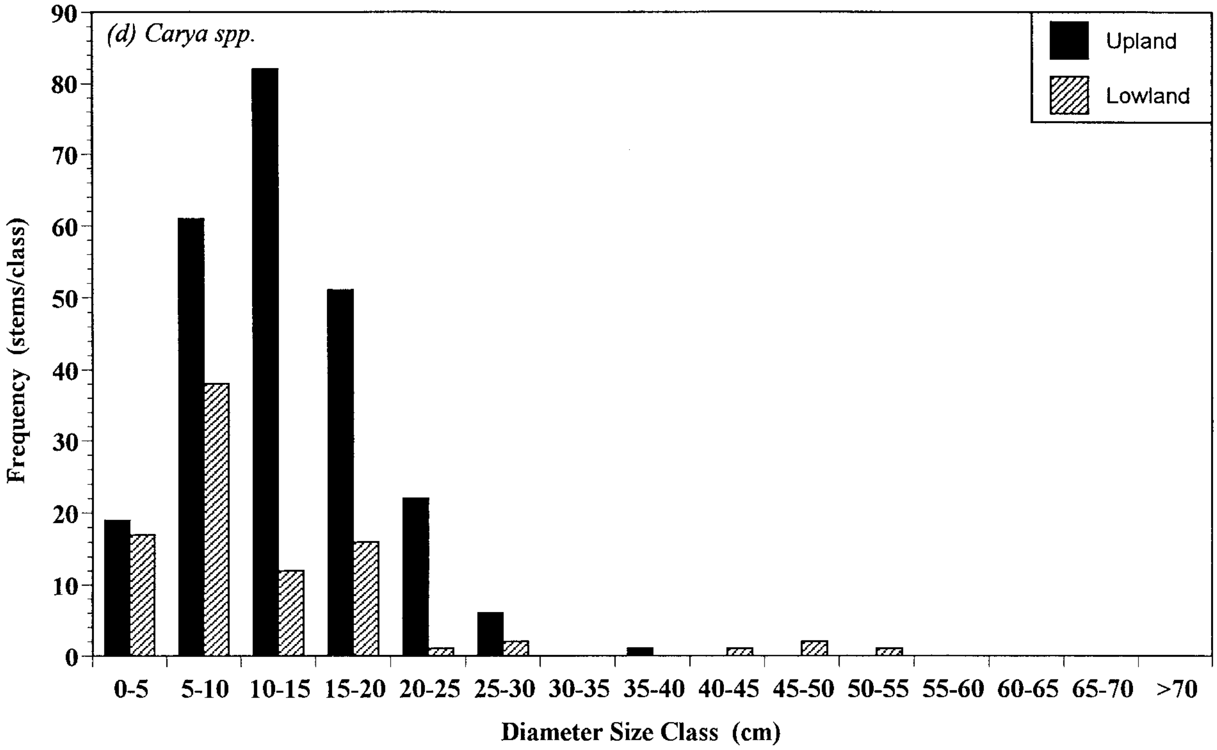


Figure 1. Continued.

Table 2. Importance values (IV) for dominant species of the Boyd Tract as a whole ('Mean') and for upland and lowland sites separately. IV for each species is based on sum of relative basal area (BA) and relative density (D) (relative values not shown). Also shown are data from the Wade Tract.

Species	Boyd Tract									Wade Tract		
	Upland			Lowland			Mean					
	BA m^2 ha^{-1}	D stems ha^{-1}	IV	BA m^2 ha^{-1}	D stems ha^{-1}	IV	BA m^2 ha^{-1}	D stems ha^{-1}	IV	BA m^2 ha^{-1}	D stems ha^{-1}	IV
Pinus palustris	15.9	74	26	18.5	168	37	17.2	121	31	8.5	139	87
Quercus laevis	0.8	53	4	6.6	1124	46	3.7	588	29	0.1	12	3
Q. velutina	11.4	151	23	1.2	29	3	6.3	90	13	–	–	–
Q. incana	–	–	–	–	–	–	–	–	–	<0.1	16	5
Q. margaretta	0.2	22	2	0.3	8	1	0.3	14	1	0.1	8	2
Q. marylandica	1.2	64	5	0.3	22	1	0.8	43	3	<0.1	3	1
Carya spp.	3.8	200	16	1.6	74	5	2.5	137	9	<0.1	1	1
Other	3.2	381	24	1.0	176	7	2.2	280	14	<0.1	2	1
Total	36.5	945	100	29.5	1601	100	33.0	1273	100	8.8	181	100

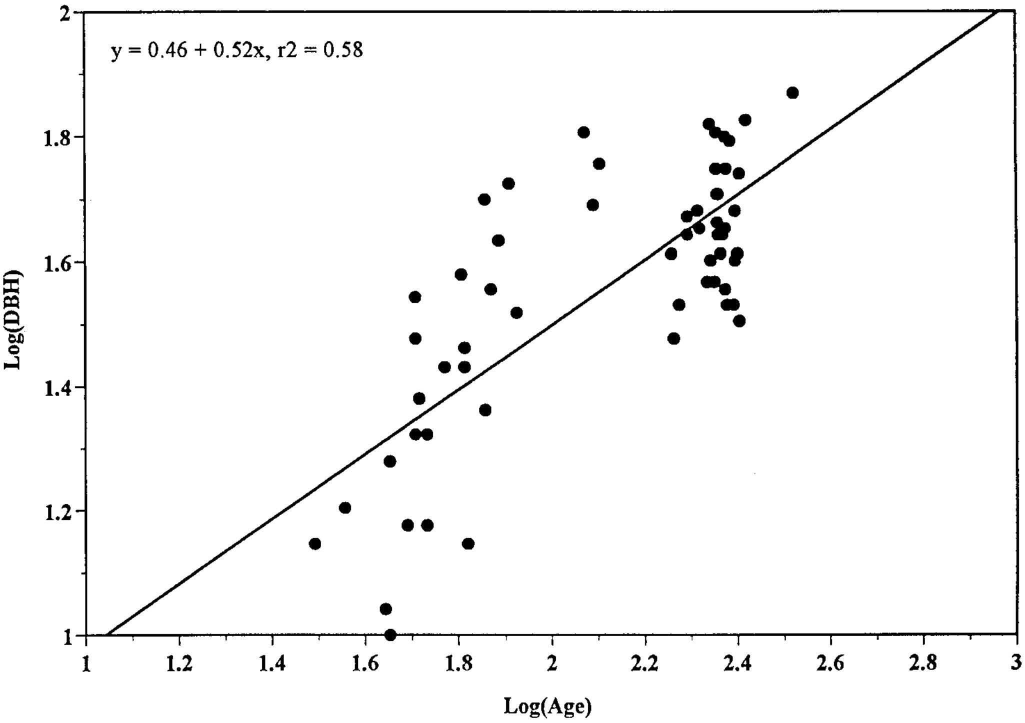


Figure 2. Diameter versus age for 60 longleaf pine stems on upland and lowland sites of the Boyd Tract. Line given is a least-squares regression of $\log_{10}$-transformed diameter on $\log_{10}$-transformed age, and is significant at $P < 0.001$.

oaks than pines. Glitzenstein et al. (1995) documented that frequent fires result in low mortality of pines of all sizes, but in high mortality of scrub oaks. Fires that had the greatest effects on oaks were those (1) occurring early in the growing season and (2) producing higher-than-average temperatures. Thus, the differences in importance values of oaks in the two old-growth tracts are most likely the consequence of very frequent fires (especially during the growing season) on the Wade Tract and complete fire suppression in the Boyd Tract over the past 80 years.

There also were differences in stand structure and species composition between site types on the Boyd Tract, consistent with results of Gilliam et al. (1993). Lowland stands were dominated by sparse, large *P. palustris* and numerous, small *Q. laevis*, resembling vegetation of other sandhills areas of North Carolina. Indeed, Wells (1928) listed these two species as sole woody dominants in what he called 'xeric coarse sand ridge and interridge communities.' High densities of small *Q. laevis* were a result of this species' small stature as a scrub oak and its tendency for clonal growth (Rebertus et al. 1989, 1993). Upland stands were mixtures of *P. palustris*, *Q. velutina* Lam. (black oak), and *Carya* spp. (hickories). Other than the presence of *P. palustris*, these stands more closely resembled oak-hickory forests of the adjacent piedmont region of North Carolina (Oosting 1942). Oaks and hickories made up nearly 50% of the basal area of the upland stands of the Boyd Tract. This accounted for 85% of the non-*P. palustris* basal area, a proportion similar to results reported by Christensen (1977), who found oaks and hickories to be 87% of the basal area of a $>$140 yr old stand in the Durham (North Carolina) Division of the Duke Forest. Although the non-*P. palustris* basal area of the Wade Tract was also largely oaks and hickories, it must be noted that non-*P. palustris* basal area at the Wade Tract was also very low overall (i.e., <1 m^2 ha^{-1}, compared to >10 m^2 ha^{-1} for the Boyd Tract).

The large number of longleaf stems that were approximately 300 yr or greater is consistent with the old-growth status of this site (see Oliver & Larson 1996 for other criteria). Greater than 10% of all longleaf stems of the lowland and nearly 40% of all longleaf stems of the upland were in this age class. These findings (1) further substantiate unpublished records at Weymouth Woods Sandhills Nature Preserve indicating that this stand did not become established within the past three centuries and (2) confirm that major damage to the stand during this time has been minimal (Gilliam et al. 1993). Because this area was not settled until between 1740 and 1750 (Clay et al. 1975), this is essentially a remnant of the virgin forest of the region.

Effects of fire and subsequent fire exclusion at the Boyd Tract

Age-class frequencies of *P. palustris* diverge between upland and lowland sites at the 80-100 yr age class, where numbers of pine stems decline sharply for younger age classes in the upland, while increasing and remaining high in the lowland (Figure 3). This 80–100-yr peak corresponds very closely with a major fire that occurred on the Boyd Tract and surrounding areas in 1909. Although there are no published accounts of this event in the ecological literature, newspaper stories reported that the fire was especially intense and spread extensively throughout the region surrounding the Boyd Tract (Huttenhauer 1980). This event strongly suggests that the high frequency in the 80–100 yr class represents recruitment of *P. palustris* following fire.

These differences further suggest that there have been large differences in recruitment of trees into the upland and lowland stands during the past century, attenuating rapidly through time in the upland and remaining high for $\sim$60 yr in lowland sites. Therefore, recruitment rates of *P. palustris* may be highly site-dependent in the short-term under conditions of fire exclusion.

Currently, *P. palustris* regeneration is suppressed in both site types, as indicated by low densities of *P. palustris* juveniles, which ranged from 50–70 seedlings ha^{-1} and were not significantly different between site types (Figure 4). Plots established in a nearby longleaf stand which had been burned biennially for more than 15 year had nearly 100-fold higher densities (Figure 4), further demonstrating that *P. palustris* regeneration increases in the presence of fire and declines under conditions of fire exclusion.

Mechanisms for such stimulation of reproductive success in *P. palustris* in response to fire are reasonably well-understood and are of both a physical and chemical nature. Some earlier studies emphasized the importance of fire in removing litter (Chapman 1936) and competing vegetation (Pessin 1938). Other studies have suggested the importance of fire in increasing soil organic matter in surface horizons (Heyward 1937) and improving fertility of nutrient-poor Coastal Plain soils (Christensen 1987, 1993; Gilliam & Christensen 1986). Phosphorus may be especially important in

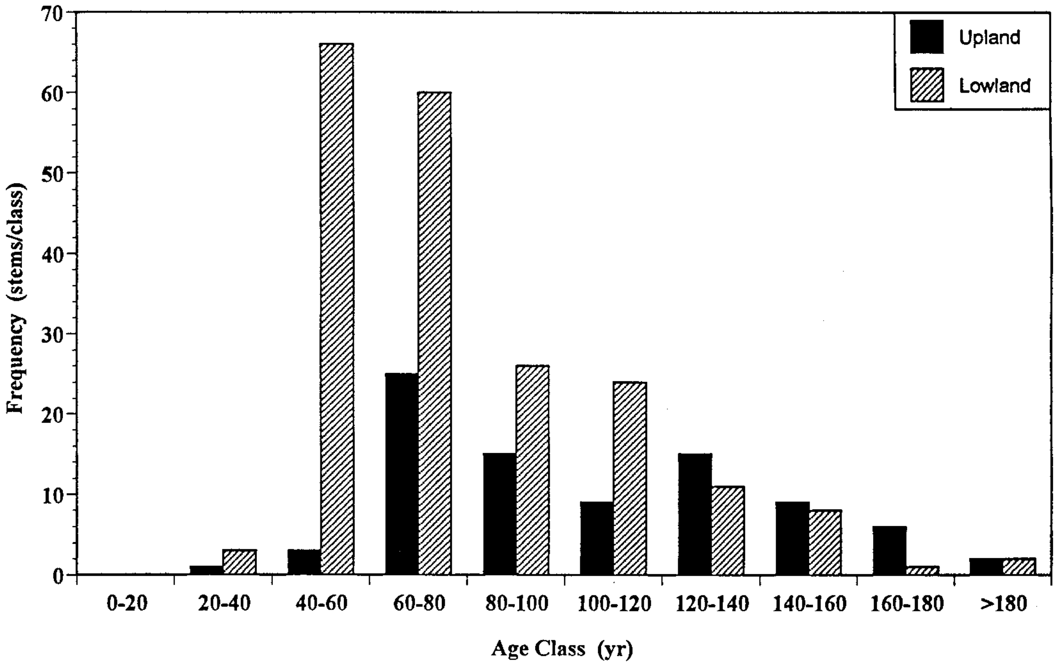


Figure 3. Age-class frequency distributions of *P. palustris* on upland and lowland sites of the Boyd Tract.

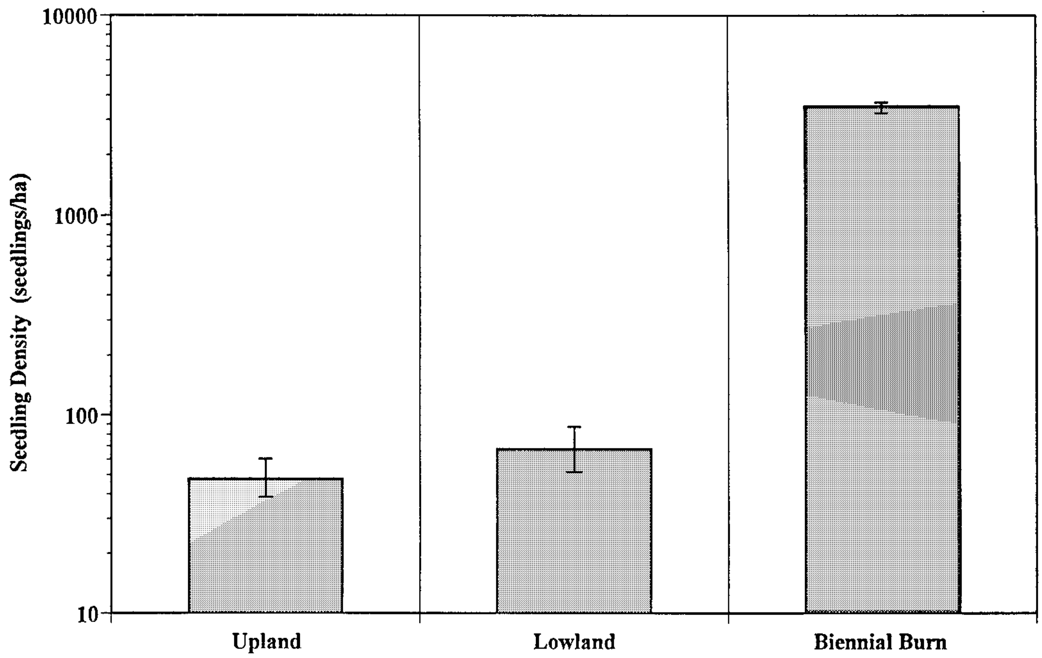


Figure 4. Seedling density of *P. palustris* on upland and lowland sites of the Boyd Tract. 'Biennial Burn' is a nearby *P. palustris* site burned biennially for >15 yr. Note logarithmic scale on ordinate.

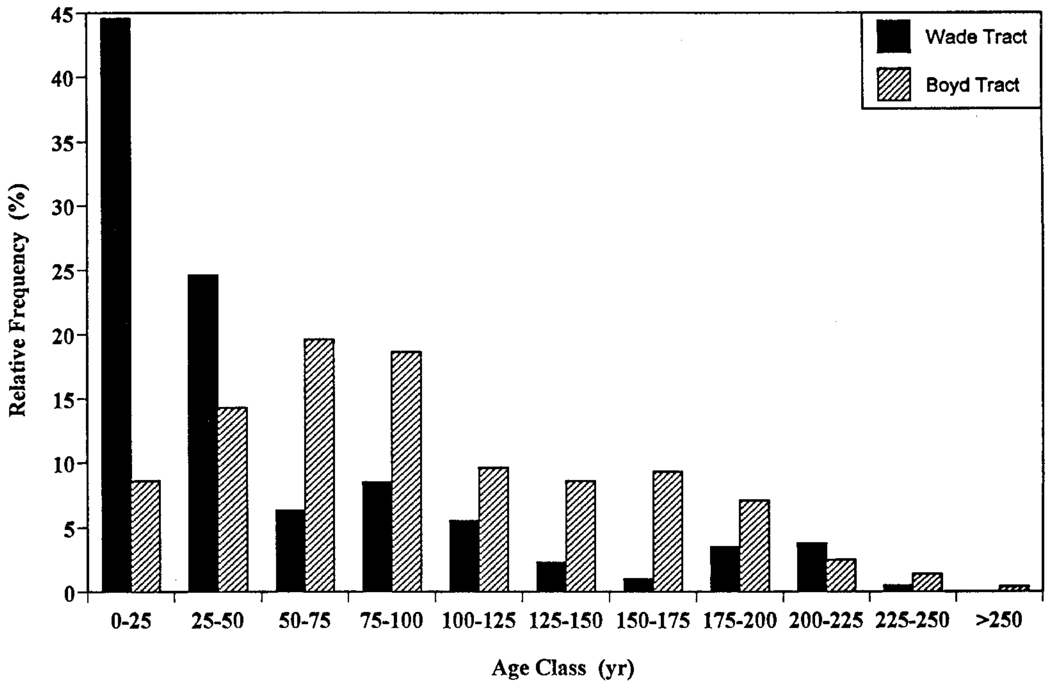


Figure 5. Relative age-class frequency distributions of *P. palustris* on Boyd Tract and Wade Tract in southern Georgia. Data for Wade Tract taken from Platt et al. (1988).

this context, as it is often growth-limiting in southeastern pine ecosystems (Shoulders & Tiarks 1980; Gilliam 1988) and typically increases in availability in response to fire in Coastal Plain soils (McKee 1982; Gilliam 1988; Christensen 1993).

Site-related differences in age-class distributions of *P. palustris* at the Boyd Tract support, in part, conclusions of Glitzenstein, et al. (1995) based on data from sandhills and flatwoods stands in the St. Marks National Wildlife Refuge, Florida. They found that, although population dynamics of *P. palustris* responded neither to fire frequency nor fire season, they did vary greatly with respect to habitat type (sandhills versus flatwoods). These habitat types differed primarily in moisture regime (from xeric sandhills to mesic flatwoods) in ways analogous to the lowland (xeric) and upland (mesic) areas of the Boyd Tract. Glitzenstein, et al. (1995) concluded that, whereas *P. palustris* populations were density regulated in the sandhills, they were declining independently of intraspecific competition in the flatwoods.

Further evidence of suppressed *P. palustris* regeneration under fire exclusion at the Boyd Tract can be seen by comparing data in this study with those of the Wade Tract in southern Georgia. The Wade Tract is 80 ha of old-growth *P. palustris* that has experienced fire since presettlement times. For direct comparison, data for the Wade Tract (Platt et al. 1988) and from the Boyd Tract were grouped into 25-yr age classes and converted to relative frequencies (Figure 5). The effects of fire exclusion were evident for both site types at the Boyd Tract, particularly for the 0–25 yr age class in the upland (Figure 5). Nearly 45% of all longleaf stems were in this class at the Wade Tract, whereas this number was less than 20% and less than 5% for lowland and upland sites, respectively, at the Boyd Tract. Thus, a negative exponential frequency distribution pattern, characteristic of successful regeneration (Barbour et al. 1999), was largely evident under the frequent fire regime of the Wade Tract and was notably absent from the unburned Boyd Tract.

Noel et al. (1998) demonstrated quantitatively that, under frequent burning regimes, the structure of old-growth longleaf stands is characterized by dense patches of small trees that are interspersed with sparse, large trees and sizeable areas of open space. These structural characteristics can be found at the Wade Tract, but are absent from the Boyd Tract. Fire suppression has allowed hardwoods, particularly oaks, to fill in the otherwise open spaces between longleaf stems at the Boyd Tract – turkey oak in the lowland, black oak in the upland – further limiting opportunities for establishment of *P. palustris* seedlings.

In conclusion, there were substantial differences in tree species composition and stand structure between site types of the Boyd Tract, with the lowland being typical of true Sandhills and the upland more closely resembling oak-hickory forests of the adjacent North Carolina Piedmont region. These differences appeared to be related to soil texture and presumably soil moisture and/or fertility (Gilliam et al. 1993). Age-class distributions of *P. palustris* show 1) evidence of an extensive fire at the Boyd Tract just over 80 years ago, and 2) high post-burn longleaf recruitment for approximately 60 yr in xeric lowland and rapidly attenuated recruitment in mesic upland sites. Finally, long-term fire exclusion at this site has altered stand structure and composition by decreasing *P. palustris* regeneration. Although the response was initially site-dependent in the short-term, the general long-term pattern appeared to be largely independent of site type.

Finally, it is clear that anthropogenic factors such as land use and urban development have contributed markedly to the decline of the *P. palustris* ecosystem throughout the southeastern United States (Frost 1993). In addition, results of our study confirm conclusions of Noel, et al. (1998) that fire is important both in maintaining successful regeneration of *P. palustris* and in maintaining structure of longleaf stands, and that fire suppression greatly alters stand structure. This open structure is not only characteristic of *P. palustris* ecosystems, but also contributes to the sustainability in this declining, but ecologically significant, ecosystem type.

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