Overstory mortality and canopy disturbances in longleaf pine ecosystems

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Abstract: We studied longleaf pine (*Pinus palustris* Mill.) ecosystems to determine causes and rates of overstory mortality, size of canopy disturbances, and the effects of disturbance on canopy structure. Further, we used redundancy analysis to relate variation in characteristics of mortality across a landscape to site and stand variables. We analyzed mortality that occurred from 1990 to 1994 in 70 second-growth plots that spanned a range of site conditions and stand structures, and in five large disturbances that occurred outside the random sample of plots. Half of pine mortality over 5 years in the 70 plots was from unknown causes. Lightning was the primary identifiable cause of mortality, followed by suppression and wind. Lightning mortality was most frequent on xeric sites, while windthrow was common on wet–mesic sites. Suppression mortality was frequent on wet–mesic sites and in higher density stands. Five-year mortality rates averaged 2.3 trees/ha, or 1.9% of original density. Most mortality consisted of single trees. Large disturbances (mostly from lightning) of 15–30 trees were rare, occurring once per 1000 ha in 5 years. Variation in amount of mortality and size of disturbance were unrelated to soil or stand structural characteristics. Low mortality rates from small-scale disturbances result in slow canopy turnover. These results indicate that large openings sufficient for natural regeneration of longleaf pine develop slowly in the absence of hurricanes. Silvicultural options for longleaf pine can be designed to mimic the canopy structure that results from natural canopy disturbances, which leave many live trees standing. Such options may be desirable if a goal of silviculture is to increase structural complexity in stands managed for timber.

Résumé : Les auteurs ont étudié des écosystèmes du pin à longues feuilles (*Pinus palustris* Mill.) en vue d'établir les causes et les taux de mortalité dans l'étage supérieur, la dimension des perturbations du couvert, ainsi que les effets des perturbations sur la structure du couvert. De plus, ils ont utilisé les analyses de redondance afin de relier les variations dans les caractéristiques de la mortalité à l'échelle du paysage aux caractéristiques de la station et du peuplement. La mortalité survenue entre 1990 et 1994 a été étudiée dans 70 parcelles de forêt de seconde venue qui couvraient une gamme de conditions de station et de peuplement et dans cinq grandes perturbations survenues à l'extérieur de l'échantillon aléatoire de parcelles. La cause de la moitié de la mortalité survenue au cours des cinq années dans les 70 parcelles n'a pu être déterminée. La foudre, suivie par la suppression et le vent ont été les principales causes identifiables de mortalité. La mortalité par la foudre était plus fréquente sur les stations xériques, alors que le chablis était plus commun sur les stations humides–mésiques. La mortalité par suppression était fréquente sur les stations humides–mésiques ainsi que dans les peuplements les plus denses. Le taux quinquennal de mortalité était en moyenne de 2,3 arbres/ha, soit 1,9% de la densité originale. La majeure partie de la mortalité était constituée d'arbres individuels. Les perturbations importantes (principalement attribuables à la foudre) affectant de 15 à 30 arbres étaient rares, ne survenant qu'une fois par 1000 ha en 5 ans. La variation de la mortalité et de la taille des perturbations n'était pas reliée aux caractéristiques du sol ou à la structure du peuplement. De faibles taux de mortalité dus à des perturbations à petite échelle conduisent à un remplacement lent du couvert. Ces résultats indiquent que de grandes ouvertures suffisantes pour la régénération naturelle du pin à longues feuilles se développent lentement en l'absence d'ouragans. Des stratégies sylvicoles peuvent être conçues pour le pin à longues feuilles afin d'amiter la structure du couvert qui résulte des perturbations naturelles, qui laissent plusieurs arbres vivants sur pied. De telles stratégies peuvent s'avérer désirables si la sylviculture vise à augmenter la complexité structurale des peuplements aménagés pour la production de matière ligneuse.

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Introduction

The importance of tree mortality in forest ecosystems has been well documented (Franklin et al. 1987; Peet and Christensen 1987). Mortality alters population age and size structures (Oliver and Larson 1990); creates habitat for plants, animals, and microbes (Beatty 1984; Franklin et al. 1981; Peterson et al. 1990; Swanson and Franklin

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1992); and liberates plant resources in the growing space vacated by dead trees (Denslow 1980; Canham and Marks 1985; Parsons et al. 1994). Coarse woody debris formed by mortality functions as a sink or source of resources, including water, nutrients, and energy (Franklin et al. 1981; Harmon et al. 1986).

Despite its importance, tree mortality is a poorly understood process in most forest types. Specific information is needed on rates and causes of death, within-stand patterns of mortality, effects of mortality on stand structure, and variation in characteristics of mortality across landscapes (Franklin et al. 1987). Such information will facilitate understanding linkages between stand structure and ecosystem function and can prove valuable for developing silvicultural options to meet objectives of ecosystems management (Vogl 1974; Harris 1984; Covington and Moore 1992). For example, the stand structures that result from natural overstory mortality may serve as structural targets in silvicultural systems designed to sustain both populations of commercial tree species and ecosystem processes comparable to those of natural forests (Seymour and Hunter 1992; McComb et al. 1993).

We examined overstory mortality and canopy disturbances in a southeastern United States longleaf pine (*Pinus palustris* Mill.) forest. Detailed studies of natural disturbance regimes and tree mortality do not exist for longleaf pine ecosystems, hindering development of a conceptual understanding of stand structural dynamics. Our objectives were to (*i*) quantify causes and rates of longleaf pine mortality; (*ii*) characterize sizes of overstory mortality events and the effect of mortality on canopy structure; and (*iii*) examine variation in characteristics of mortality across a landscape, as related to soil, physiographic, and stand structural conditions.

Study area

We conducted our study at the Joseph W. Jones Ecological Research Center located in southwestern Georgia, U.S.A., in the lower Gulf Coastal Plain. The 11 300 ha property contains approximately 7500 ha of ecosystems dominated by longleaf pine. Prior to 1989 the Jones Center was managed primarily as an eastern bobwhite quail (*Colinus virginianus*) hunting plantation. Longleaf pine site types in the study area range from xeric sandhills to seasonally wet flatwoods. Slash pine (*Pinus elliottii* Engelm.) often is dominant or codominant at the wetter end of this gradient (Ware et al. 1993).

Most of the forest in the study area is second growth, originating following old-field abandonment or clearcutting between 1900 and 1920 (B. Palik, unpublished data). Scattered longleaf pines exceeding 180 years in age are found in some areas. The study area contains some younger even-aged stands that initiated following clearcutting between 1950 and 1960. Naturally regenerated stands less than 30 years old are absent.

Past stand management in the study area included periodic harvesting of large pines and salvage logging of nearly all dead pines. These practices are common on many Coastal Plain hunting plantations, but were discontinued in our study area during 1989, providing a unique opportunity to quantify mortality and its effects on stand structure from a known starting date.

Prescribed surface fires have been used in the study area for at least the past 50 years to reduce hardwood encroachment and maintain quail habitat. Most fires are set between February and May, at 2- to 3-year intervals. In contrast, pre-European fire regimes of the longleaf pine region probably were dominated by growing-season fires (May–July) occurring every 2–10 years, depending on particular site conditions (Christensen 1981, 1988; Robbins and Myers 1992; Ware et al. 1993).

Over the last several decades, frequent dormant season fires have limited establishment of new regeneration in much of the study area. Additionally, past high-grade logging removed mostly large pines. Consequently, some areas have low overstory densities and open canopies. However, since these practices are common throughout the Coastal Plain, overstory densities and canopy coverage in the study area are representative of much of the second-growth longleaf pine in the region and, further, are not atypical of the few old-growth stands that have been studied (Schwarz 1907; Chapman 1909, 1923; Penfound and Watkins 1937).

Methods

Plot selection

The study area was subdivided into five large blocks of 2000–3000 ha each to facilitate dispersion of sample plots across the landscape. We selected a total of 70 plots by traversing the blocks along several parallel east–west transects. In each block, an initial transect was located by choosing a random starting point along a north–south road. Transects were at least 500 m apart. Plot locations were selected by pacing random distances between 150 and 1000 m along the east–west transects. Point locations along the transects were used as corners for plot delineation (see below). Plot locations met the following criteria: (*i*) minimum of 2 ha in size; (*ii*) dominated by longleaf pine or slash pine with longleaf pine; and (*iii*) located on a homogeneous physiographic feature.

Plots occurred within sites ranging from wet–mesic to xeric, as indicated by soil maps for the study area (United States Department of Agriculture 1986) and field observations. We discarded plots falling within xeric sandhill ecosystems because of low longleaf pine density (≤50 stems/ha), since low densities greatly reduced the probability of recording any recent mortality. Sandhill sites made up approximately 5% of total forest area. Additionally, we discarded several locations on wet–mesic sites bordering nonalluvial wetlands, because of difficulty in locating large plots (see next paragraph) within the same physiographic feature around the wetlands.

At each location, we established a square 1.32-ha plot (115 × 115 m) using the randomly located sample point as the northwest corner. If necessary, the corner location was shifted up to 100 m to minimize inclusion of heterogeneous site conditions. Additionally, we tried to minimize inclusion of human-caused soil disturbances, such as fire breaks or wildlife food plots. In some areas, however, small soil disturbances (<0.10 ha in size) could not be avoided, so we subtracted the area of the disturbance from the total plot area of 1.32 ha. Actual plot areas ranged from 0.96 to 1.32 ha. Plot corners were permanently monumented and georeferenced using a global positioning system.

Site characterization

We assessed physiographic feature, or landform, for each plot. Landform classes included high flats (above a perched water table for most of the year) and low flats (influenced by a perched water table for part of the year). Within each plot, the following soil characteristics were evaluated to a depth of 3.35 m using a bucket auger: (*i*) depth to mottling; (*ii*) thickness of a sandy epipedon (i.e., thickness of sand or loamy sand horizons beginning immediately below an A horizon and above a Bt horizon); (*iii*) depth to a clay pan; (*iv*) depth to bedrock; and (*v*) total thickness of sandy loam or finer textured soil materials as determined through field assessment. We collected a single auger sample from a central location for plots on highly homogeneous landforms. In most plots, we collected multiple auger samples from different locations and averaged the measurements. Soil samples were removed at 50- and 100-cm depths for laboratory particle size analysis. Air-dried samples were passed through a 2-mm mesh sieve to remove coarse fragments (2–75 mm; a small percentage of total soil weight in all samples). Silt + clay (<0.05 mm) and sand content of samples were determined by wet sieving after dispersion in a Calgon solution. Sand size fractions, including very coarse + coarse sand (0.5–2.0 mm), medium sand (0.25–0.5 mm), and fine + very fine sand (0.05–0.25 mm), were separated through dry sieving.

Tree sampling

We divided each plot into nine 1470-m^2 subplots (38.33 × 38.33 m) and identified all live stems ≥2.5 cm DBH to species and measured them for DBH. Two canopy longleaf pines (or slash pines in some plots) were selected in each subplot for detailed size measurements, including total height (using a clinometer) and stem diameter at groundline in two perpendicular directions (measured with tree calipers). For this study, a canopy individual was defined as any stem ≥2.5 cm DBH having a crown that received direct sunlight from above. Total and exposed crown radii (that portion receiving direct sunlight from above based on visual assessment) were measured for each tree along the north, south, east, and west crown axes by stretching a tape from the bole to the widest portion of the crown. Increment cores were extracted at a height of 0.3–1.0 m from this same subset of pines.

We determined the agricultural history of each plot by noting the presence or absence of wire grass (either *Aristida stricta* Michx. or *Aristida beyrichiana* Trin. & Rupr.) ground cover. These species are indicators of undisturbed soil conditions in longleaf pine forests of the region (Lynch et al. 1986) and typically are not present on previously tilled soils.

Mortality sampling

During June–August 1994, we recorded, mapped, and tagged the total numbers of dead longleaf pines and slash pines, both standing and down, with reconstructed diameters (in 1989) ≥10 cm. Pines <10 cm DBH were limited in number in the study area (see Results) and were not sampled for mortality. Sound increment cores could not be extracted from dead trees because of rapid sapwood decomposition, so we could not cross-date annual increments with those from live trees to determine year of tree death. However, the majority of dead trees in this study died after 1989, when the long-standing practice of salvage logging was discontinued. Dead pines predating the moratorium on deadwood removal were distinguishable by their advanced decay condition relative to pines that had died after 1989.

Table 1. Causes of pine mortality.

Cause	Description
Lightning	Lightning scar was visible on the tree.
Suppression	Dead tree that was clearly overtopped while living.
Windthrow	Downed tree that had an upturned root plate.
Wind snap	Downed tree with a snapped or twisted bole.
Root rot	Fallen tree with rot below the root collar; lacking solid structural roots at the root plate; not overtopped (suppressed) prior to death.
Fire	Tree having excessively charred bole or crown.
Crushing	Hit by another tree.
Unknown	Having none of the above characteristics.

We measured DBH directly on snags and downed trees having sound upper boles. Additionally, we took two perpendicular measurements at the base of each snag or remnant stump using tree calipers and averaged them to determine diameter at groundline. Base diameters were used in a regression model to predict DBH of decomposed trees. Cause of death was determined in the field by assigning dead pines to one of eight mortality classes based on visual criteria (Table 1). Categories included lightning, suppression, windthrow, wind snap, fire, root rot, crushing (i.e., being hit by another tree), or death from unknown causes. Our classes reflect primary mortality agents only, i.e., agents that cause death or initiate decline, and are not meant to identify interactions between a particular agent and secondary agents that hasten death.

We did not attribute any mortality directly to insect infestation, although most dead pines had evidence of bark beetle activity. Black turpentine beetles (*Dendroctonus terebrans* Oliver) and *Ips* beetles (*Ips grandicollis* Eichh., *Ips calligraphus* Germ., *Ips aoulsus* Eichh.) are the primary bark beetles infesting longleaf pine (Lee and Smith 1955; Thatcher 1960; Rohlfs and Hyche 1981), particularly those struck by lightning (Anderson and Anderson 1968; Coster and Searcy 1981). These nonaggressive beetles (sensu Rudinsky 1962) infest trees weakened or killed by some other disturbance (Hetrick 1949; Lee and Smith 1955; Smith 1957), rarely causing death directly. Longleaf pine is highly resistant to the southern pine beetle (*Dendroctonus* *frontalis* Zimm.), compared with other southern pines (Hedden and Lorio 1985; Belanger et al. 1993).

We also quantified mortality in five large patch disturbances that occurred since 1989, but were located outside of the random sample. None of the disturbances contained any live or dead slash pine. These disturbances involved at least 15 longleaf pines that had died within a short period of time. We used the distance between live crowns of trees bordering the patch, along the long and short axes, to estimate the area of an ellipse representing the size of the disturbance. Mortality characteristics recorded in each disturbance included (*i*) the number of dead pines; (*ii*) the original DBH of dead pines having sound boles; (*iii*) the groundline diameters of dead pines (as described previously); and (*iv*) the number and DBH of live longleaf pines remaining within the disturbance patch. Causes and dates of the disturbances were determined through conversations with land managers who observed the patches shortly after they formed.

Data analysis

We determined the age distributions of canopy pines in each of the 70 plots by examining increment cores from the intensively measured pines (18–27 aged pines per plot). The cores were cross-dated (following Yamaguchi 1991) and measured for number and width of annual rings using an image analysis system. The number of missing rings on cores that missed the pith was estimated with a center-locating technique (Arno and Sneck 1977). The age sample did not include overtopped trees. These represented, on average, only 15% of the population of pines ≥2.5 cm DBH. Thus, our age sample should be generally representative of the larger population.

We estimated original overstory pine density (DBH ≥ 10 cm) and basal area (5 years before sampling) for each plot by adding density and basal area of mortality to live density and basal area, followed by subtraction of pine ingrowth into the overstory that occurred during the 5-year period. Our estimate of ingrowth for canopy pines is based on radial growth rates for the aged trees (all of which were canopy individuals). Cumulative radial increment over the 5 years before sampling did not exceed 2.5 cm in any of these trees (mean = 0.95 cm), so only pines <15 cm DBH at the time of sampling could have grown into the overstory (≥10 cm DBH) during the previous 5 years. In fact, 71% of aged canopy pines in the 10–12.5 cm DBH class had grown into this size class during the previous 5 years, so this percentage was subtracted from the density estimate of each plot to account for ingrowth. None of the aged canopy pines in the 12.5–15 cm DBH class had grown from the understory during the previous 5 years. Using growth rates from another study (R. Mitchell and B. Palik, unpublished data), we estimated that mean cumulative increment over 5 years for suppressed trees (those not receiving direct sunlight from above) was 0.19 cm, or 20% of canopy trees. Based on this growth rate, only 19% of suppressed pines in the 10–12.5 cm DBH class would have grown into the overstory during the 5 years prior to sampling, so we subtracted this percentage from the density estimate of each plot to account for canopy ingrowth of suppressed trees. Basal area ingrowth was estimated by multiplying density ingrowth by the mean basal area of pines in the 10–12.5 cm DBH class (0.01 m^2).

We related live pine groundline diameter (cm) to DBH (cm) using a linear regression model:

$$[1]\quad \log(\text{DBH}) = 0.78259 + 0.02149(\text{groundline diam.}) - 0.00012(\text{groundline diam.})^2$$

The model predicts original DBH of 40 dead pines that had upper boles too decomposed for accurate DBH measurement. Equation 1 was developed using 504 longleaf pines and had a coefficient of determination of 0.95 and standard error of the estimate of 0.04. No strong violations of distributional assumptions were apparent when standardized residuals were plotted against independent and predicted values.

We estimated exposed crown area (i.e., the projected area of a crown receiving direct sunlight from above) of the intensively sampled canopy pines by summing the area of the four quarter ellipses formed by sequential combinations of exposed crown radii, i.e., north and east, east and south, etc. Projected exposed crown area (m^2) was related to DBH (cm) through linear regression using the following equation:

$$[2]\quad \log(\text{exposed crown area} + 1) = -0.78124 + 1.59136(\log \text{DBH})$$

Equation 2 was based on a sample size of 1311 trees and had a coefficient of determination of 0.89 and a standard error of the estimate of 0.15. No violations of distributional assumptions were apparent when standardized residuals were plotted against independent and predicted values. For each plot, cumulative canopy coverage of overstory pines was calculated by summing exposed crown area, as estimated through regression, of all pines ≥2.5 cm DBH. Additionally, we used eq. 2 to estimate exposed crown area of longleaf pines removed through mortality in the 70 sample plots and in the five large disturbance patches, as well as the crown area of live pines remaining within the large disturbance patches. Our goal in these analyses was to estimate percent plot area in gaps and the rate of gap area increase with canopy disturbance. Cumulative exposed crown area is a better estimate of projected canopy coverage than is total crown area because it does not inflate the estimate by double counting the overlapping crowns of adjacent trees.

Redundancy analysis (RDA) (Davies and Tso 1982) was used to explore relationships between characteristics of mortality and features of sites and stands that may influence amount and causes of tree death. Two sets of mortality variables were used: (*i*) primary causes of mortality (Table 1) and (*ii*) variables reflecting amount of mortality within plots including density and basal area of dead pines, density of mortality events (one or more trees dying concurrently in a group), number of trees in the largest mortality event, and percentage of subplots with mortality. RDA is a form of constrained linear ordination, or direct gradient analysis, that is similar in principle to canonical correlation analysis, but does not require sample sizes that greatly exceed the combined number of dependent and independent variables (Ter Braak and Prentice 1988). Site variables

Table 2. Summary statistics for site factors used in redundancy analysis (n = 70 plots).

Variable	Mean	SD	Range
Depth to mottling (m)[a]	1.83	0.89	0.50–3.40[b]
Thickness of surface sand (m)[a]	0.87	0.54	0.05–2.70
Total thickness (m) of clay textures (sandy loam or finer)[a]	2.32	0.64	0.50–3.30
Depth to bedrock (m)[a]	3.33	0.26	1.85–3.40
Depth to clay pan (m)[a]	2.69	0.74	0.75–3.40
Silt + clay at 50 cm (%)	28.7	14.2	9.0–90.9
Very coarse + coarse sand at 50 cm (%)	11.6	5.3	0.7–26.3
Medium sand at 50 cm (%)	22.2	7.4	2.0–51.3
Fine + very fine sand at 50 cm (%)	37.3	9.4	0.5–51.2
Silt + clay at 100 cm (%)	31.3	14.1	8.6–83.8
Very coarse + coarse sand at 100 cm (%)	13.3	7.4	0.3–43.5
Medium sand at 100 cm (%)	20.3	6.5	0.0–37.2
Fine + very fine sand at 100 cm (%)	34.9	9.8	8.4–56.4
Topographic position:	High flat	51 plots	
	Low flat	19 plots	

[a] Within 3.35 m.

[b] Assumed depth if >3.35 m.

Table 3. Summary statistics for stand structural characteristics used in redundancy analysis (n = 70 plots).

Variable	Mean	SD	Range
Original pine overstory[a] density (no./ha)[b]	127	63	56–349
Relative density of longleaf pine	91.2	25.8	0–100
Mean DBH (cm) of overstory pines	32.9	4.9	22.4–41.5
Coefficient of variation (%) of mean DBH	33.3	7.3	20.4–58.0
Mean age of overstory pines	61.6	9.9	40–84
Coefficient of variation (%) of mean age	33.2	18.3	5.8–68.8
Cut pine stumps/ha	49	21	22–114
Ground cover condition:	Wire grass	49 plots	
	Old field	21 plots	

[a] DBH ≥10 cm.

[b] Estimated density of living longleaf pine and slash pine 5 years prior to sampling.

used in RDA included the soil and landform variables described under Site characterization (Table 2). Stand variables are summarized in Table 3. These analyses were exploratory in nature and designed to formulate hypotheses rather than test them. Redundancy analyses were run on correlation matrices, and ordination diagrams were constructed using correlation biplot scaling. Mortality variables were square-root transformed prior to analysis. RDA was run using CANOCO software (Ter Braak 1988).

Results

Forest composition and structure

Longleaf pine dominated the overstories of the sample plots, accounting for 83% of total basal area and 85% of total density (Table 4). Slash pine was only a minor component of the study area as a whole (Table 4), but dominated the overstory in a few plots. Loblolly pine (*Pinus taeda* L.) and shortleaf pine (*Pinus echinata* Mill.) were minor components of both the study area and individual plots (Table 4). Hardwoods, mostly oaks (*Quercus* spp.), were a minor component of the overstories, but were common in the understories of some plots (Table 4). Pine advance regeneration (DBH <10 cm) was uncommon in many of the plots.

Only a few of the stands were narrowly even aged, which made characterization of age structure difficult. Mean (SD) age of sampled pines within stands was 62 (10) years and varied from 40 to 84 years among stands. Within stands, the age range of sampled trees averaged 76 (39) years and varied from 13 to 176 years among stands. The oldest and youngest canopy pines were 4 and 187 years, respectively.

Causes of pine mortality

A total of 195 longleaf pines and 8 slash pines ≥10 cm DBH died over the 5-year period of record (1990–1994). Trees died on 61 of the 70 sample plots. Lightning strikes (22% of total mortality), competitive suppression (21%), and windthrow (4%) were the most common identifiable causes of pine mortality. Mortality from root rot (2%), fire (1%), crushing (1%), and wind snap (1%) were all rare in the study area.

The cause of mortality for nearly 50% of the dead pines was not determined. Many of these trees were standing at the time of sampling, but were already missing much of their bark and had substantial sapwood decomposition, which would have obscured or removed a lightning scar if one had been present. Some unknown dead pines consisted of a short snag and a downed bole. These trees may have been wind snapped, but had decomposed to the point that no physical evidence of this (e.g., twisted or snapped boles) was apparent.

Relationships of mortality to pine diameter distributions

Diameter distributions of pines dying from common causes of mortality, relative to the diameter distribution of the original pine overstory (Fig. 1), give some insight into the effects of mortality on stand structure and, possibly, the cause of unknown mortality. Wind mortality (windthrow + wind snap) occurred most frequently in the 25–50 cm diameter range. Lightning killed trees across nearly the entire diameter distribution, but was concentrated in larger diameter classes (30–45 cm). Lightning and wind both thinned stands from above by removing large trees. The

Table 4. Tree species composition of the study area (means of 70 stands (SD)).

	Overstory ($DBH \geq 10$ cm)		Understory ($2.5 \leq DBH < 10$ cm)
Species	Basal area (m^2/ha)	Stems/ha	Stems/ha
Longleaf pine	10.1 (4.5)	120.0 (70.0)	32.0 (46.0)
Slash pine	0.8 (2.9)	7.0 (27.0)	0.5 (3.0)
Loblolly pine	0.02 (0.1)	0.2 (0.9)	0.03 (0.3)
Shortleaf pine	0.01 (0.1)	0.3 (2.0)	0.13 (0.7)
Oak spp.[a]	1.2 (0.7)	14.7 (15.0)	28.6 (46.0)
Miscellaneous hardwoods[b]	0.0 (0.0)	0.0 (0.0)	18.0 (40.0)
Total	12.1 (5.1)	142.0 (86.0)	79.0 (50.0)

[a] Includes *Quercus falcata* Michaux, *Quercus geminata* Small, *Quercus hemisphaerica* Bartram ex Willd., *Quercus incana* Bartram, *Quercus laevis* Walter, *Quercus laurifolia* Michaux, *Quercus margaretta* Ashe, *Quercus nigra* L., *Quercus stellata* Wangenh., *Quercus virginiana* Miller.

[b] Includes *Acer rubrum* L., *Carya tomentosa* (Poiret) Nutt., *Celtis laevigata* Willd., *Cornus florida* L., *Crataegus* spp., *Diospyros virginiana* L., *Liquidambar styraciflua* L., *Myrica cerifera* L., *Nyssa sylvatica* Marshall var. *sylvatica*, *Prunus angustifolia* Marsh., *Prunus serotina* Ehrh., *Sassafras albidum* (Nutt.) Nees, *Vaccinium arboreum* Marshall.

diameter distribution for trees dying from unknown causes (Fig. 1) was similar to that for lightning. The two distributions did not differ significantly (Kolmogorov–Smirnov two-sample test, $P > 0.10$), suggesting that some of the unknown trees may have died from lightning injury. Suppression mortality was concentrated in smaller diameter classes (Fig. 1), thinning stands from below.

Rates and within-plot distribution of pine mortality

Rates of pine mortality varied from 0 to 12 trees/ha among plots over 5 years (Fig. 2). Percent mortality (of original overstory density) over the same time period varied from 0 to 8.2%. Mean (SD) number of dead pines and mean percent mortality were 2.3 (2.0) pines/ha and 1.9 (1.5)%, respectively. Pine basal area removed through mortality over 5 years varied from 0 to 1.0 m^2/ha among plots (Fig. 2), while mortality as a percentage of original basal area ranged from 0 to 9.5%. Mean (SD) basal area of dead pines was 0.19 (0.18) m^2/ha, or 1.8 (1.7)% of original basal area.

The percentage of subplots (nine per plot) containing mortality (as a measure of distribution of mortality within a plot) varied from 0 to 78.0% among plots, while the mean (SD) percentage of subplots containing mortality was 24.0 (17.6)%. The number of discrete mortality events (i.e., one or more pines dying concurrently in a group) occurring over 5 years ranged from 0 to 9/ha among plots, while the mean (SD) number of mortality events over 5 years was 1.9 (1.7)/ha. Sizes of individual mortality events within plots ranged from 1 to 5 trees, with a mean (SD) event size of 1.4 (1.1) trees.

Effects of mortality on canopy structure

Mean (SD) cumulative exposed crown area of live canopy pines (≥2.5 cm DBH) was 49 (14)% of total projected ground surface area. Among plots, cumulative exposed crown area varied from 25 to 90% of total ground surface area. Eighty percent of the plots had cumulative exposed crown area projections of 60% or less. In all plots, at least 99% of exposed crown area was in pines >10 cm DBH, because of both the rarity of smaller trees and the narrow columnar crown form of sapling longleaf pine.

Cumulative exposed crown area (of trees ≥10 cm DBH) removed through mortality over 5 years ranged from 0 to 451 m^2/ha (0–4.5% of plot area) among plots. Mean (SD) exposed crown area removed through mortality over 5 years was 0.84 (0.78)% of plot area (assuming no ingrowth of trees <10 cm DBH). This value excludes the crown area of trees dying from suppression, since their crowns were not exposed. An average of two mortality events per hectare occurred over the 5-year period. Thus, the mean rate of canopy opening from individual disturbances was approximately 0.42% of total ground surface area over 5 years.

Variation in characteristics of mortality

The first two axes of the redundancy analysis between the number of pines dying from common causes of mortality and site factors (from Table 2) accounted for 34.0% of total variation (Table 5). The third and fourth axes (not interpreted below) accounted for only 4.7% of additional variation. Mortality from unknown causes was not included in this analysis, nor was mortality from wind snap, fire, and crushing, since these disturbances were rare in this study. The RDA biplot of axes 1 and 2 (Fig. 3) reflects several relationships between causes of mortality and site factors. The biplot is interpreted as follows: The RDA axes are related to one or more of the continuous site variables (from Table 2); the strength of relationship is proportional to vector length and its orientation relative to the axis (Fig. 3, dashed lines). The longer the vector, the greater weight that variable has in the analysis. The smaller the vector angle with the axis, the closer the relationship between that variable and the axis. For clarity, only site variables with strong relationships to the axes are shown on the biplot. The vectors for causes of mortality (Fig. 3, solid lines) have a similar interpretation. The longer the vector and the smaller the angle between a mortality characteristic and a site variable, the closer the relationship between the two variables. Additionally, centroid locations for nominal variables (the two classes of landforms; Fig. 3, open triangles) reflect associations between causes of mortality and classes of the variable.

On RDA axis 1, root rot was somewhat associated with deeper depths to mottling, while windthrow and suppression mortality were more frequent in low-flat topographic positions that had a shallower depth to mottling. Similarly, on RDA axis 2, mortality from lightning was positively correlated with amount of coarse sand at 100 cm and deeper depth to a clay pan and negatively correlated with amount of silt + clay at 100 cm (Fig. 3). The correlation coefficients between causes of mortality and site variables on the first and second axes were 0.71 and 0.68, respectively, indicating strong relationships between the two sets of variables.

The redundancy analysis of site factors with amount of mortality accounted for only 14.6% of total variation among plots (Table 5). Mortality–site correlation coefficients were low for all axes (Table 5), indicating no strong relationships between the measured site factors and these mortality variables (no graph is presented for this analysis).

Redundancy analysis between causes of mortality and stand factors (from Table 3) accounted for 35.3% of total variation among plots with respect to these mortality variables (Table 6). Twenty-seven percent of total variation was accounted for by the first axis alone. The axis 1 correlation between causes of mortality and stand variables was 0.76. Axis 1 was positively correlated with original overstory density and negatively correlated with mean diameter of live pines (Fig. 4A). Suppression mortality in a plot was closely associated with RDA 1 (Fig. 4A), suggesting a self-thinning relationship. Density of cut stumps in a plot (as a measure of past high grading and salvage logging) was an important stand variable on RDA axis 2, but no mortality characteristics were associated with this axis (Fig. 4A).

Redundancy analysis between amount of mortality and stand factors accounted for 22.3% of total variation among plots. The first axis alone accounted for 20% of total variation (Table 6). The mortality–stand correlation coefficient was not particularly high for axis 1 (0.49). However, the stand variables related to axis 1, original overstory density and mean pine diameter, were the same as those in the previous analysis (Fig. 4B). Amount of mortality (density of dead pines, subplots with mortality, density of mortality events) increased with increasing original overstory density and decreasing mean pine diameter (Fig. 4B), indicating that some variation in amount of mortality among plots was associated with natural thinning.

Characteristics of large disturbance patches

Approximate sizes of the five large disturbance patches ranged from 1000 to 2000 m^2 and involved 15–33 longleaf pines per disturbance (Table 7). The total cumulative exposed crown area of longleaf pines removed through mortality ranged from about 550 to 1300 m^2 (Table 7) and involved 53–85% of patch area. Four of the disturbances were caused by multiple lightning strikes (lightning scars visible on some individuals). These disturbances dated to 1990 (one patch) and 1991 (three patches). The fifth disturbance was dated to spring 1992, when a hot prescribed surface fire caused excessive crown scorch and mortality. The disturbances did not always kill all longleaf pines within a patch. Four of the patches contained live longleaf pines (mean = three live pines ≥10 cm DBH per patch), with associated live crown areas of 103–396 m^2 (Table 7). Three additional

Fig. 1. Diameter (DBH) distributions of original pines (live) and pines dying from different mortality agents over the 5-year period 1989–1994. Trees from all plots are combined in each distribution.

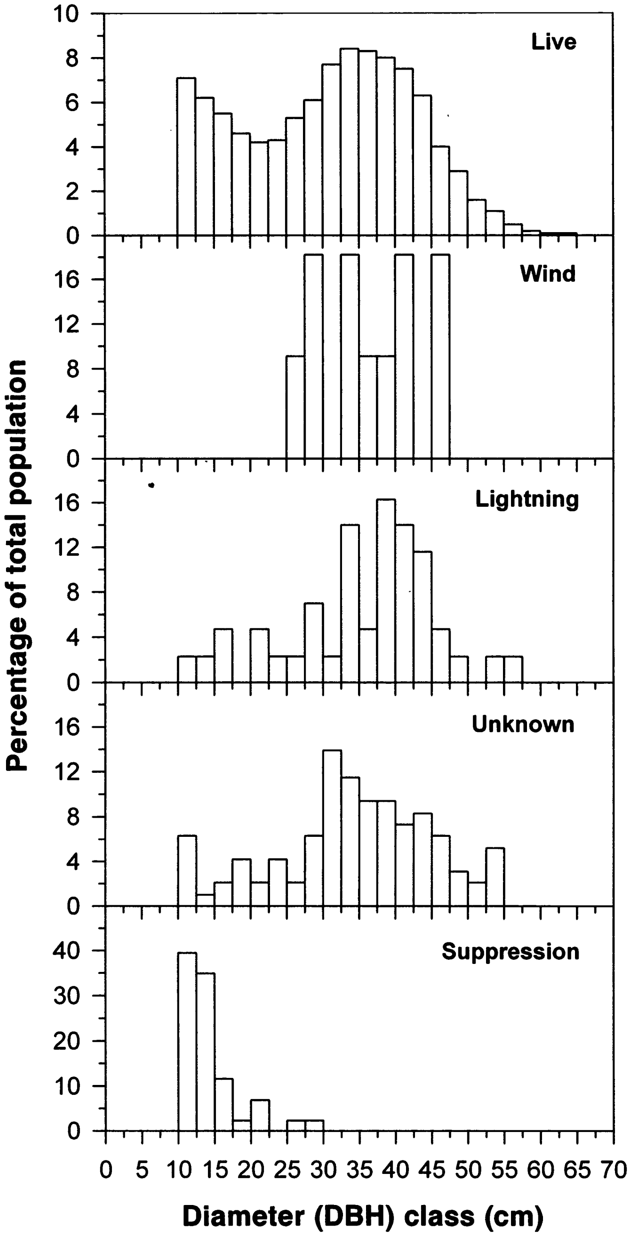
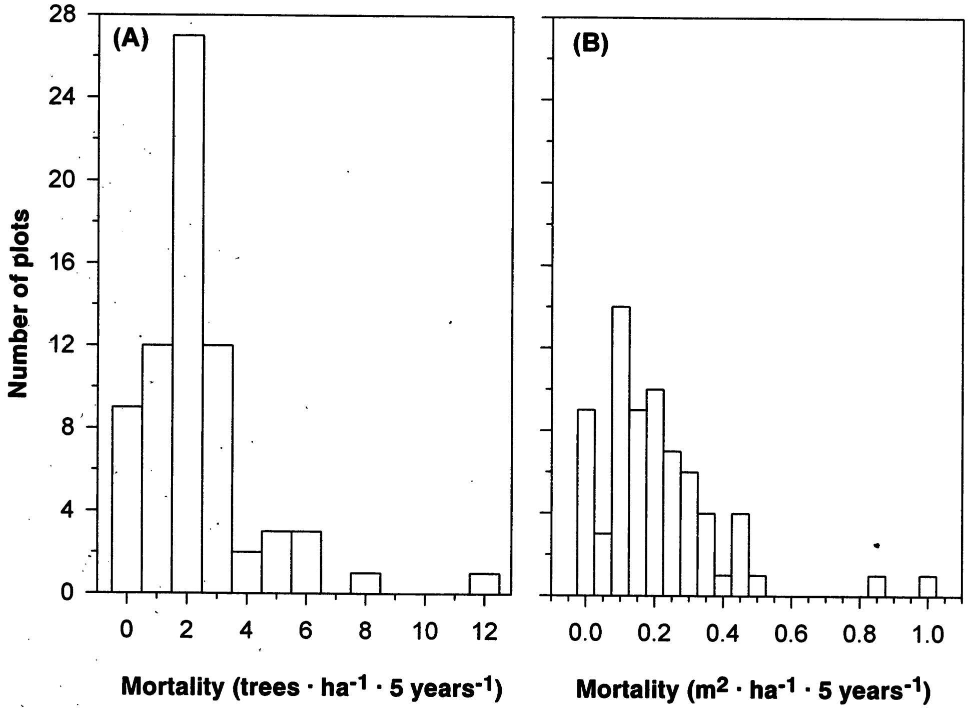


Fig. 2. Distribution of longleaf pine mortality among plots. (A) Density mortality per unit area. (B) Basal area loss per unit area.



large patch disturbances of similar size and age to those sampled were located within the 7500-ha portion of the study area dominated by longleaf pine. Based on a total of eight patches, the frequency of occurrence for this scale of disturbance was 1.1 per 1000 ha over 5 years.

Discussion

Causes of pine mortality

The importance of lightning mortality in this study is consistent with the high frequency of lightning storms in the southeastern United States (Komarek 1968; Maier et al. 1979) and supports results from other studies in longleaf pine ecosystems (Platt et al. 1988; Boyer 1993). In fact, we believe that most mortality from unidentified causes in our study resulted from lightning as well, and thus the frequency of this disturbance was probably greater than what we quantified directly. The group lightning mortality that we observed also is consistent with a similar report for an old-growth longleaf pine stand (Platt and Rathbun 1995). Additionally, our results provide quantitative support for largely anecdotal evidence that lightning strikes are most frequent on large trees (Chapman 1923; Wahlenberg 1946; Platt and Rathbun 1995) and thereby thin stands from above. Also, our results suggest that lightning mortality may be more frequent on drier sites, as indicated by positive relationships between lightning kill and coarser-textured surface soils and depth to a clay pan. Perhaps lightning-struck pines are more likely to die on drier sites because they experience greater moisture stress. However, we have no data that suggest that pines on mesic sites have an increased probability of recovery from lightning.

Suppression mortality was an important cause of death for pines <20 cm DBH and was most frequent in higher density stands. Higher density stands were not necessarily younger (i.e., stand density and age were not correlated). Rather, thinning mortality often occurred within dense groups of longleaf pines that were interspersed within a more open matrix of larger trees (personal observations), a stand structure that is characteristic of some old-growth longleaf pine forests (Platt et al. 1988). Suppression mortality was most frequent in low flats and on sites with finer textured surface soils, perhaps because these sites had high productivity and may have supported a greater number of denser patches of longleaf pines.

Windthrow and wind snap accounted for 5.5% of total mortality over the 5-year study period and occurred in 11% of the sample plots. These results contrast sharply with those from other studies of longleaf pine ecosystems, which report much higher percentages of mortality from wind (31–43%) over similar lengths of time (Chapman 1923; Platt et al. 1988). In the studies by Chapman (1923) and Platt et al. (1988), and in ours, no major windstorms occurred during the periods of record. Windthrow was most frequent on sites in low topographic positions with a shallow depth to mottling, indicative of a near surface water table. Rooting depth and soil firmness are reduced on wetter sites, increasing probability of windthrow (Derr and Enghardt 1957; Brewer and Merritt 1978; Foster 1988).

Strong windstorms do cause significant tree mortality in Coastal Plain forests (Derr and Enghardt 1957; Doren et al. 1993), substantially altering stand structure and composition (Glitzenstein and Harcombe 1988; Putz and Sharitz 1991; Platt and Rathbun 1995). In November 1985,

Table 5. Summary statistics for two redundancy analyses of mortality characteristics with site factors.

	Causes of mortality[a] and site factors				Amount of mortality[b] and site factors			
	RDA 1	RDA 2	RDA 3	RDA 4	RDA 1	RDA 2	RDA 3	RDA 4
Eigenvalue	0.192	0.146	0.032	0.017	0.110	0.022	0.011	0.002
Mortality–site correlation	0.707	0.683	0.395	0.419	0.363	0.461	0.516	0.392
Cumulative variation of mortality characteristics (%)	19.2	33.8	37.1	38.7	11.0	13.3	14.4	14.6
Cumulative variation of mortality–site relation (%)	49.6	87.3	95.7	100.0	75.2	90.5	98.3	99.7

[a] Includes mortality from lightning, windthrow, suppression, and root rot.

[b] Includes density of dead pines (no./ha), basal area of dead pines (m^2/ha), density of discrete mortality events (no./ha), largest mortality event in a plot (no. of trees), and percentage of subplots containing mortality.

for instance, Hurricane Kate killed 137 longleaf pines on a 42-ha plot in an old-growth stand (Platt and Rathbun 1995). The storm was indirectly responsible for an additional 95 tree deaths. With return intervals of 50 years or less in the lower Coastal Plain, hurricanes are likely to be a significant source of longleaf pine mortality over longer time periods. Early reports of even-aged old-growth longleaf pine forests (Chapman 1909, 1923; Schwarz 1907; Forbes 1921, 1930; Penfound and Watkins 1937; Wahlenberg 1946) suggest that severe windstorms may initiate whole stands in some parts of the Coastal Plain.

Mortality from root rot was not common in the study area, which is consistent with reports that longleaf pine is less susceptible to some root rots, (e.g., *Heterobasidion annosum*) than are loblolly and slash pines (Hodges 1974). We caution, however, that the actual agent causing root rot was not identified, nor can we say with confidence that another, unidentified, mortality agent was not involved. Apparent root rot occurred on sites with increased depth to mottling, suggesting that this type of mortality is more common on drier soils.

The low incidence of mortality from fire in our study is consistent with other reports (Chapman 1923; Boyer 1987). Stand-replacement crown fires are not characteristic of longleaf pine ecosystems because of low horizontal continuity of crown fuels. Observations in Coastal Plain forests suggest that pines greater than 10 cm DBH are not easily killed by low- to mid-intensity surface fires (Wade and Johansen 1986; Boyer 1990; Rebertus et al. 1995). Probability of mortality increases with stem charring and extensive crown scorch or crown consumption (Ferguson 1955; Mann and Gunter 1960; Storey and Merkel 1960; Wade and Ward 1975; Waldrop and Van Lear 1984; Wade 1985), and in fact, high-intensity fire with crown scorch was the cause of mortality in one of the large disturbances in this study. The hot fires necessary for significant longleaf pine mortality may be more common during the growing season (Ferguson 1955; Wade and Johansen 1986; Boyer 1987), suggesting that mortality of large pines from surface fire may have been more frequent in presettlement forests.

In our study, past harvesting practices, including cutting large trees and salvage logging, may have influenced the frequency of different types of mortality over the 5-year period. Lightning strikes or windthrow may have been reduced because of fewer tall trees, and suppression mortality may have been less because of reduced overtopping. The increase in numbers of dead trees in the forest, with cessation of salvage logging, is not likely to result in bark beetle infestations of live trees in the future because of the nonaggressive behavior of *Ips* and black turpentine beetles (Hetrick 1949; Lee and Smith 1955; Smith 1957).

Fig. 3. Redundancy analysis biplot of mortality characteristics (causes of mortality; solid vectors) and site factors (dashed vectors; open triangles). RDA axis 1 is related to depth to mottling and topographic position (low fat), while RDA axis 2 is related to percentage of coarse sand at 50 and 100 cm, silt + clay at 100 cm, and, to a lesser degree, depth to a clay pan. Site variables not strongly related to the RDA axes are not shown. Causes of mortality are correlated to the site variables that they most closely parallel.

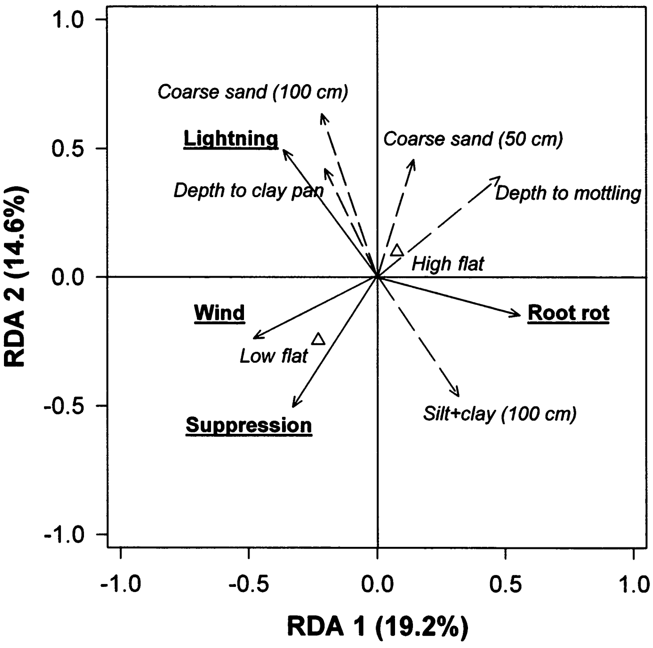


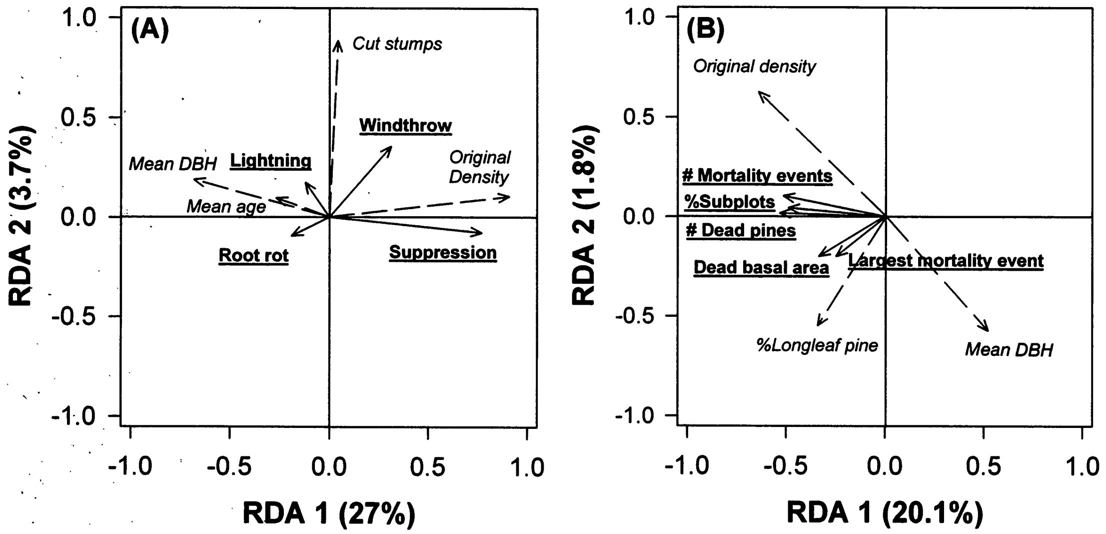
Table 6. Summary statistics for two redundancy analyses of mortality characteristics with stand variables.

	Causes of mortality[a] and stand variables				Amount of mortality[b] and stand variables			
	RDA 1	RDA 2	RDA 3	RDA 4	RDA 1	RDA 2	RDA 3	RDA 4
Eigenvalue	0.270	0.037	0.034	0.011	0.201	0.017	0.004	0.001
Mortality–stand correlation	0.755	0.421	0.442	0.284	0.491	0.409	0.299	0.307
Cumulative variation of mortality characteristics (%)	27.0	30.7	34.1	35.3	20.1	21.9	22.2	22.3
Cumulative variation of mortality–stand relation (%)	76.5	87.0	96.8	100.0	90.2	97.9	99.7	100.0

[a] Includes mortality from lightning, windthrow, suppression, and root rot.

[b] Includes density of dead pines (no./ha), basal area of dead pines (m^2/ha), density of discrete mortality events (no./ha), largest mortality event in a plot (no. of trees), and percentage of subplots containing mortality.

Fig. 4. Redundancy analysis biplots of mortality characteristics (solid vectors) and stand variables (dashed vectors). (A) Includes causes of mortality. (B) Includes amount of mortality. In both biplots, RDA axis 1 is related to original pine density and mean pine DBH. RDA axis 2 is related to number of cut stumps in Fig. 4A and percent longleaf pine in the overstory in Fig. 4B. Mortality characteristics are correlated with the stand variables that they most closely parallel.



Mortality rates

Longleaf pine mortality, as a percentage of original overstory density, was low compared with other published estimates for this forest type. Annual mortality of overstory longleaf pines in shelterwood stands across the southeastern United States averaged 0.9% (Boyer 1979), compared with an annual rate of 0.4% for trees ≥10 cm DBH in this study. Our estimate of percent mortality may be affected to some degree by failure to account directly for ingrowth of trees into the overstory (≥10 cm DBH). Even on an area basis, however, annualized mortality in our study was low, averaging 0.5 trees/ha (0.3 trees/ha for trees ≥20 cm DBH), compared with 1.0 tree/ha in the shelterwood stands (Boyer 1979).

Mortality rates varied among plots, yet this variation was largely unexplained by site factors. A small percentage of variation was related to initial stand density and mean diameter of overstory pines. The direction of the correlations reflected suppression mortality from natural thinning. The remaining unexplained variation in rates of mortality among plots, after accounting for suppression, may reflect the random occurrence of some forms of canopy disturbances in the study landscape.

Effects of mortality on canopy structure

Horizontal canopy structure of longleaf pine ecosystems often is open and patchy, reflecting a legacy of surface fires that limit recruitment of regeneration (Robbins and Myers 1992). Our study is one of the few that has actually quantified this structure. Occupation of soil volume by longleaf pine root systems may be similarly low and patchy, although this has not been investigated adequately. Despite this open matrix, exploitive resource competition may be an important mechanism controlling survival and growth of longleaf pine regeneration (Davis 1955; Smith

Table 7. Characteristics of large longleaf pine disturbance patches.

			Dead pines				Live pines remaining		
Patch	Cause	Size (m^2)	No.[a]	No./ha	Crown area (m^2)	% patch area	No.	Crown area (m^2)	% patch area
1	Lightning	1265	22	174	1073	85	4	159	12
2	Lightning	2051	24	117	1184	58	7	396	19
3	Lightning	1054	18	171	558	53	2	115	11
4	Fire	1529	33	216	1303	85	3	103	7
5	Lightning	1071	15	140	614	57	0	0	0
	Mean	1394	22	164	947	68	3	155	10
	SD	414	7	38	339	16	3	147	7

[a] DBH ≥10 cm.

1955; Boyer 1963, 1993; Grace and Platt 1995), although this has yet to be demonstrated experimentally. Variation in fire intensity also is important for regeneration, particularly survival (Platt et al. 1988), and is essential for reducing competition from hardwood and herbaceous species, which also capitalize on canopy openings (Myers 1990; Platt and Rathbun 1995; Rebertus et al. 1995). The stand structures of some mature and old-growth longleaf pine forests, which are characterized by uneven-aged mosaics of even-aged patches of trees (Schwarz 1907; Chapman 1909; Platt et al. 1988), reflect the influence of competition between adult longleaf pines and regeneration.

Competitive influences of mature pines on regeneration may extend up to 20 m from large trees (Walker and Davis 1956; Farrar and Boyer 1990; Grace and Platt 1995), suggesting that all growing space in small openings (e.g., <0.10 ha) would be influenced by overstory competition and only the center of large openings (e.g., 1.0 ha) would be free of competition (Farrar and Boyer 1990). Mean regeneration patch size in one old-growth stand was estimated to be about 700 m^2 (Platt and Rathbun 1995). The size of actual stand openings in which regeneration develops is likely to be larger than 700 m^2 (e.g., 1000–1200 m^2), because of the extended competitive influence of large overstory trees.

Platt and Rathbun (1995) suggest that large canopy openings required for longleaf pine regeneration develop rapidly from infrequent hurricanes. In contrast, more frequent low-intensity disturbances, such as lightning and individual windthrow, form large openings slowly over time, perhaps requiring two to three centuries. The slow rate of crown removal from small-scale disturbances in our study (0.84% of plot area over 5 years) and the low mortality rate of large trees (1.9%) support their latter contention. Based on our mean stem mortality rate, canopy turnover would take an average of 263 years. Similarly, turnover as estimated from our rate of crown removal would take 292 years (assumes a mean canopy coverage of 49%).

In addition to hurricanes and small-scale disturbances, group lightning strikes also form large openings. In our study, patch disturbances removed 550–1300 m^2 of exposed crown area to form openings of 1000–2000 m^2. The limited data we have on this type of disturbance suggest that it is infrequent, occurring only once per 1000 ha in 5 years. Further, these disturbances may not occur randomly across the landscape, since the patches themselves had higher than average longleaf pine densities before disturbance (164/ha), compared with mean density of the 70 plots (120/ha).

Implications for silviculture of longleaf pine

Our study demonstrates the importance of small-scale mortality events as a component of canopy disturbance regimes in longleaf pine ecosystems. Small-scale disturbances compliment better studied large-scale disturbances from hurricanes (Derr and Enghardt 1957; Putz and Sharitz 1991; Platt and Rathbun 1995) and midsized patch disturbances (e.g., 15–30 trees) from group lightning strikes. Understanding the complete canopy disturbance regime of longleaf pine ecosystems and the influence of these disturbances on stand structure has implications for the development of silvicultural options for this forest type. One goal of silviculture may be to increase structural similarities between natural stands and those managed for timber. Spatial and temporal patterns of harvesting that are based on natural canopy disturbances can be used to achieve this goal (Seymour and Hunter 1992; McComb et al. 1993). In longleaf pine ecosystems, natural canopy disturbances could be mimicked in a variety of ways, including individual tree selection, used to expand existing gaps, and large patch cuts that create new openings. In all cases, some mature canopy structure should be maintained across time, since natural canopy disturbances leave many large live trees standing. Some live trees and mature canopy structure should be maintained even within larger silvicultural openings themselves, if they are to mimic the structural legacies (sensu Swanson and Franklin 1992; Franklin 1993) of large patch disturbances, such as those examined in this study.

Maintenance of structural complexity across time has not been a goal of many timber-oriented silvicultural systems for longleaf pine, which include clear-cutting with planting and shelterwood regeneration systems (Croker and Boyer 1975; Boyer 1993). Selection systems for longleaf pine, which maintain mature overstory structure across cutting cycles, are used occasionally in the Southeast (e.g., Farrar and Boyer 1990; L. Neal, Tallahassee, Florida, personal communication; D. Handley, Florence, South Carolina, personal communication), but even these systems have not been corroborated with a quantified conceptual understanding of overstory mortality and canopy disturbance regimes. Continued observations in our study area will allow us to better understand longer term trends in canopy dynamics and will help in developing silvicultural options for longleaf pine ecosystems that are based on natural disturbance regimes.

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