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Age structure and possible origins of old *Pinus taeda* stands in a floodplain forest[1]

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PEDERSON, N. A. (School of Forestry, Auburn University, AL 36849), R. H. JONES (Department of Biology, Virginia Tech, Blacksburg, VA 24061), AND R. R. SHARITZ (Savannah River Ecology Laboratory, Aiken, SC 19802 and Department of Botany, University of Georgia, Athens GA 30602). J. Torrey Bot. Soc. 124:111–123. 1997.—Stand structure and ages were measured in six old stands of *Pinus taeda* L. (loblolly pine) and one younger stand within Congaree Swamp National Monument, South Carolina. Dominant overstory species included loblolly pine, shade intolerant hardwoods and tolerant hardwoods. All overstory species except pine also occurred in the sapling layer. Five of the six old stands had two or more pine age classes. All but one individual pine was less than 200 years old. According to estimates of future survival, current loblolly pine seedling densities in recently hurricane-disturbed and clearcut areas are inadequate to reproduce tree densities measured in extant old stands. Spatial distributions of mature trees suggest that pines have established in gaps as large as 0.3 ha and as small as a single overstory tree. No evidence of fire (scars on existing trees or charcoal in the upper 10 cm of soil) was found in any old stand. From these results, we speculate that the old loblolly pine stands in Congaree Swamp resulted from small-scale agricultural activities, although wind storms, fires, or combinations of these may have played contributing roles. Because of its apparent ability to regenerate in gaps, loblolly pine will probably remain in Congaree Swamp for several centuries as small clumps and scattered individuals.

Key words: loblolly pine, Congaree Swamp National Monument, *Pinus taeda*, Hurricane Hugo, forest succession, disturbance, regeneration.

Establishment of pine forests in North America occurs mainly through large-scale disturbances such as catastrophic fire (Heinselman 1973; Romme 1982), agriculture (Quarterman and Keever 1962) and large blowdowns (Foster 1988). Less severe disturbances, such as surface fires, perpetuate pine dominance following establishment (Garren 1943). In the absence of fire, pines are often succeeded by hardwoods (Quarterman and Keever 1962).

Loblolly pine (*Pinus taeda* L.) is currently the most abundant pine in the southeastern United States (USDA 1988). Its dominance in the landscape has been facilitated by consistent and abundant annual seed crops, wide dispersal of seeds, large areas of abandoned agricultural land, and massive tree planting efforts (Quarterman and Keever 1962; USDA 1988; Honkala et al. 1990a). Many naturally established loblolly pine forests are even-aged with characteristically low species diversity and high pine density (Quarterman and Keever 1962).

Before the advent of large-scale agriculture and logging, loblolly pine may have existed primarily as scattered individuals and small groups (Mohr 1896; Ashe 1915), especially in floodplains where fire is infrequent. However, it remains unclear how loblolly pine was able to coexist with more shade tolerant hardwood species in floodplains. Jones et al. (1981) postulated that infrequent catastrophes—events such as fire, windstorms, or abandonment of agricultural activities—accounted for the presence of loblolly

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pine in an old floodplain forest in South Carolina.

Extensive acreage of old loblolly pine forest exists in Congaree Swamp National Monument, a relatively new national park located in central South Carolina. These stands offer an opportunity to study loblolly pine forest dynamics under conditions that may be similar to those prior to European settlement. The size and age of the pines are unusual in today's landscape (Burns and Honkala 1990a, 1990b; May 1990; Helm et al. 1991; Jones 1997). Some occur as scattered individuals or small clusters as described for pre-European settlement forests. However, many occur within dense stands with relatively even sizes. This has led to the hypothesis that the stands are even-aged (Swails et al. 1957; Stalter 1971) and possibly initiated after large-scale disturbances such as fire, clearing for agriculture (e.g., from very early or pre-European cultures), or windstorms (Swails et al. 1957).

The primary objectives of this project were to determine age structure of old loblolly pine forests at Congaree Swamp, and to uncover the event(s) that might have led to their establishment and continued development. Our null hypothesis was that the stands were even-aged. We tested this by determining stand age structure in one young, and six old stands. We also measured loblolly pine seedling densities in a hurricane blowdown and a clearcut to determine if these disturbances are capable of stimulating large-scale pine reproduction.

Methods. STUDY AREA. Congaree Swamp National Monument is located along the Congaree River in the upper Coastal Plain of central South Carolina. Established by the federal government in 1976, the Monument contains one of the greatest concentrations of large trees in the eastern United States (Gaddy 1978; Jones 1997). Much of the park's 5,000 ha of floodplain forest shows little or no evidence that human disturbance has occurred during the past century, making this area one of the last old-growth bottomland hardwood forests in the southeastern U.S. (Gaddy 1977).

A variety of geomorphic features occur within the Monument including deep water sloughs, oxbow lakes, ephemeral and permanent streams, levees, broad flats, and bluffs. Forest vegetation is complex, including over 90 species of trees and twenty-seven plant community types (Smathers 1980). Most of the loblolly pines occur in the northern half of the Monument in a 1 km band adjacent to the floodplain-upland ecotone.

STAND SELECTION. Prior to this study, Hurricane Hugo moved through the Monument in September 1989 destroying up to 50% of the loblolly pine/mixed hardwood forest (Putz and Sharitz 1991). In order to reconstruct undisturbed loblolly pine stand characteristics, a precondition for study site selection was the presence of standing, live trees in relatively undisturbed patches. Seven stands with levels of hurricane damage ranging from light (essentially none) to moderate (25% of canopy trees down or dead) were chosen for study. They differed in vegetation type (Smathers 1980), topography, and apparent age. One stand was clearly not an old forest but was included anyway as a possible model of loblolly pine stand development at Congaree Swamp. It had evidence of past agricultural and timber harvesting activities including a drainage ditch and scattered stumps. Stands ranged from one to several hectares in size and were concentrated in the northwest portion of the Monument (Fig. 1).

Within each of the selected old stands, six 0.053 ha, circular plots were used to estimate pre-hurricane species composition and structure. Plots were centered around an upper canopy loblolly pine within patches of relatively undisturbed trees. In the younger stand, seven plots of the same size were randomly selected from two randomly placed, parallel transects.

In all stands, species and diameter at breast height (DBH; measured at 1.3 m) of trees (stems $\geq$10 cm DBH) and saplings (stems $\geq$2.5 cm and $<$10 cm DBH) within plots were recorded. Total area sampled for trees and saplings was 0.32 ha per stand (except 0.37 ha in the younger stand).

All loblolly pines within each stand (but only those within the plots in the young stand) were tagged, checked for fire scars and mapped. In each stand, the upper 10 cm of soil was excavated at three or more 1 m^2 sites to look for evidence of past fires (i.e., charcoal).

STAND AGE STRUCTURE. Age of each stand was determined by coring one-quarter of the tagged pines (71 of 213 pines in all seven stands) with a 71 cm increment borer. Two cores were extracted from each tree as low on the trunk as possible, usually at 0.5 meters above ground. Cores were taken at least 90° apart to increase the chances of locating missing or partial annual growth rings.

Cores were mounted in the field, air dried and

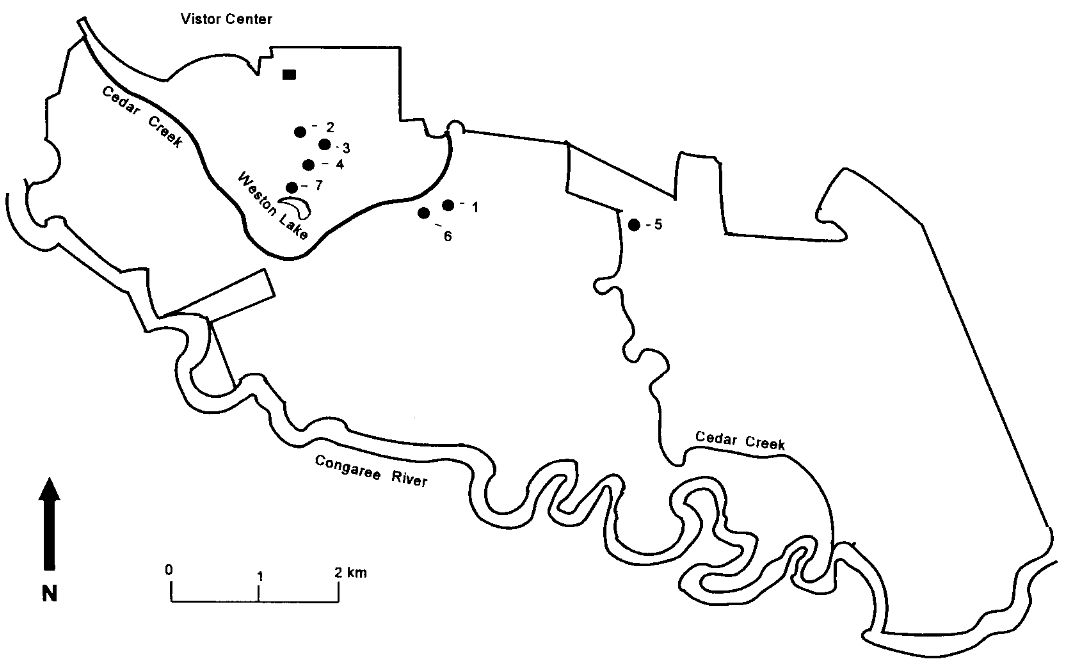

Fig. 1. Distribution of sampled loblolly pine stands in Congaree Swamp National Monument.

sanded, and rings were counted. For cores that missed the pith, age was estimated by the method described by Arno and Sneck (1977).

Accuracy of the Arno and Sneck age estimation technique was assessed by simulating the estimation technique on cores that hit the pith or were close enough (≤2.0 cm) to provide essentially 100% accuracy in age estimation at cored height. Differences between estimated and true ages were then averaged to compute a mean correction factor and a 95% confidence interval estimate of the correction factor for cores that missed the pith by various distances. Fractions of a year were conservatively interpreted as another whole year. The final age estimate for an individual tree was determined by the ring count of the core with the most rings present, plus the estimated additional rings needed to reach the pith according to the Arno and Sneck method, plus or minus the correction factor. A 95% confidence interval estimate of age was then constructed using a 95% confidence interval estimate of the correction factor centered on the final age estimate (Pederson 1994).

To determine the number of distinct age classes within a stand, all trees were arrayed from youngest to oldest on an x-axis with ages plotted on the y-axis. Discrete age classes were identified wherever error bars for age did not overlap (Pederson, 1994).

To determine if historical patterns of blowdown may have been correlated with loblolly pine establishment, all trees aged in this study were combined into cohorts of 10-year age classes using two time frames: decades ending in the number 0 (1871–1880, 1881–1890, etc.) and number 5 (1876–1885, 1886–1895, etc.). Numbers of trees established per decade were correlated with numbers of hurricane tracks per decade recorded for areas in South Carolina near Congaree Swamp (Ramsay 1809; Simms 1840; Tannehill 1952; Kovacik and Winberry 1987).

SEEDLING DENSITIES AND DISTURBANCE. Loblolly pine seedling densities were estimated within a hurricane blowdown (Hurricane Hugo 1989) located approximately 100 m south of stand two (Fig. 1). Loblolly pine seedlings were counted within twenty-five 50 m^2 seedling regeneration plots (total sample area of 0.125 ha) randomly located along five east-west random transects.

A similar survey was carried out in an area where all sawtimber-sized trees (DBH ≥ 30 cm) were removed in 1972. This previously logged area is located approximately 2.5 km west of stand #2 (Fig. 1). Loblolly pine saplings were tallied in twenty-five 50 m^2 plots randomly placed on six east-west random transects.

Data from both seedling surveys and published mortality rates were used to estimate how many pines might exist in these disturbed stands at various times in the future. Two annual rates were chosen to give upper and lower levels of loblolly pine mortality. An annual rate of 0.4%, derived from a loblolly pine plantation (Somers et. al. 1980), was used as the lower level and a value of 3.3% taken from a study of naturally regenerated, mixed species Piedmont forests (Peet and Christensen 1987), was the higher level. The extrapolated densities were then compared to densities in current old stands to determine whether the recent disturbances could result in old forests similar to those that exist today.

Results. STRUCTURE OF OLD STANDS. Shade intolerant and tolerant species occurred in each stand (Table 1). The four with greatest mean importance values (relative density plus relative basal area) were: loblolly pine, sweetgum (*Liquidambar styraciflua* L.), American hornbeam (*Carpinus caroliniana* Walt.), and American holly (*Ilex opaca* Ait.). All species found in the tree layer were also found in the sapling layer except for loblolly pine and cherrybark oak (*Ouercus pagoda* Raf.). Pine density was 234/ha in the young stand and ranged between 28 and 66/ha in the six old stands.

Within and among stands, loblolly pines had considerable variation in DBH. Size distributions were strongly uni-modal in four stands (Fig. 2) suggesting even-aged structure. Weak or strong multi-modal distributions were observed in the remaining three stands (Fig. 3).

Using the pith estimation technique, we were able to age over 90% of the sampled loblolly pines to within plus or minus seven years of true age. Age estimates ranged between 33 and 227 years with about half of the trees between 125 and 150 years old (Fig. 4).

Although diameter can sometimes be used to predict age in loblolly pine, such was not the case in this study. Within each stand, diameter was a poor indicator of tree age (regression r^2 values generally less than 0.20). When all seven stands were combined, a quadratic regression provided a significant fit ($P < 0.05$), but explained variance was still relatively low ($r^2 = 0.65$). Extrapolation of age from diameter in these old loblolly pine stands would be very imprecise.

The seven stands exhibited a variety of age structures. Stand #1 was clearly even-aged. The remaining stands included two-age and uneven-age structures (Pederson 1994). The youngest stand (#3) showed a distinct spatial separation of age classes within the area sampled; most trees in the northeast part were less than 55 years old while most in the southwest were older than 60 (Fig. 5). Three older trees (>70 years), probably relic fence-row pines, were also found. Stand #2 had an age pattern similar to stand #3 (Pederson 1994) with younger stems distinctly separated from older ones. In stands #4 and #5, small even-aged patches occurred adjacent to older trees (Fig. 5). Here, the younger age class existed within an older remnant stand. In contrast, stands #6 and #7 had highly mixed distributions of ages. Neighboring loblolly pines differed in age by up to 30 years at stand #7, and by a little less than 20 years at stand 6 (Fig. 6).

SEEDLING DENSITIES AND DISTURBANCE. Pine regeneration was found in both the hurricane blowdown and logged areas. Most stems (seedlings) in the blowdown area and all stems (saplings) in the logged area were found on sites where the soil surface was disturbed.

Regeneration density in both areas was inadequate to produce old stands similar in density to those remaining in Congaree Swamp today. Loblolly seedling density in the blowdown area was 157/ha, but only 35/ha were in full sun conditions where there is a chance for growth into future upper canopy positions (i.e., seedlings not overtopped by other vegetation). Densities in the logged area were 14/ha with 11/ha not overtopped. Using a 3.3% mortality rate, the projected number of non-overtopped loblolly per hectare surviving 180 years into the future was below densities found in the extant stands and very few, if any, trees will exist beyond age 100 (Table 2). When the lower mortality rate of 0.4% was used, more pines were predicted to live past age 100, but densities would still be low relative to upper canopy pines in existing stands (Table 2). When new stands were projected forward and the old stands were projected backward to an intermediate age of 60 using the conservative 0.4% mortality rate, neither of the new stands had loblolly pine densities within the range of the older stands (Table 3).

Fire and past frequencies of hurricanes were not correlated with stand initiation or maintenance in the stands studied. Charcoal was found in the soil of only one stand - the young forest (stand #3). No fire scars were found on any of the pines in any stand. No relationship between hurricanes and the establishment of loblolly pine

Table 1. Importance values (IV = relative density + relative basal area) for trees (stems ≥ 10 cm DBH) and saplings (stems ≥ 2.5 cm and < 10 cm DBH) in seven loblolly pine dominated stands at Congaree Swamp, South Carolina. Top IV is trees, bottom is saplings.

	Stand						
Species	3	4	2	5	7	6	1
Pinus taeda	128.9	64.7	56.9	66.0	60.4	86.7	68.7
	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Liquidambar styraciflua	39.1	15.9	22.8	31.2	35.9	31.5	28.6
	66.8	8.2	5.7	11.5	0.0	0.0	13.2
Carpinus caroliniana	1.8	44.1	25.8	27.6	22.0	19.5	10.4
	10.8	121.8	55.6	45.3	46.8	74.4	30.0
Ilex opaca	3.7	2.8	19.6	32.8	7.9	21.4	15.3
	29.0	50.0	53.8	87.0	22.6	46.4	19.9
Quercus laurifolia	1.0	19.5	5.5	8.7	20.2	2.1	0.0
	5.2	0.0	14.4	4.6	8.2	0.0	5.4
Quercus michauxii	0.0	2.3	0.0	2.7	1.2	5.3	4.0
	0.7	5.4	8.1	6.1	29.5	2.5	3.0
Ulmus alata	0.6	1.5	0.0	3.4	2.7	8.7	8.3
	3.9	0.0	1.4	1.5	9.5	5.0	3.7
Quercus nigra	2.3	1.7	0.0	1.8	—	1.0	3.8
	2.3	0.0	2.4	0.0	—	4.0	5.3
Acer rubrum	6.7	3.0	12.0	0.0	4.4	—	6.3
	54.0	0.0	23.9	1.3	0.0	—	1.5
Nyssa sylvatica var. *biflora*	2.6	3.7	45.2	17.3	13.1	1.3	—
	8.2	0.0	2.4	2.8	0.0	0.0	—
Cornus florida	1.7	—	—	—	—	—	—
	4.5	—	—	—	—	—	—
Fagus grandifolia	0.0	—	—	—	—	—	—
	4.2	—	—	—	—	—	—
Prunus serotina	0.0	—	—	—	—	—	—
	0.4	—	—	—	—	—	—
Quercus pagoda	5.5	—	—	—	—	—	—
	0.0	—	—	—	—	—	—
Quercus phellos	6.2	40.8	1.2	—	—	—	—
	1.8	0.0	0.8	—	—	—	—
Rhododendron sp.	0.0	—	0.0	—	—	—	—
	4.2	—	0.7	—	—	—	—
Cornus stricta	—	—	0.0	—	—	—	—
	—	—	1.4	—	—	—	—
Liriodendron tulipifera	—	—	3.3	—	—	—	—
	—	—	12.6	—	—	—	—
Persea borbonia	—	—	0.0	—	—	—	—
	—	—	2.2	—	—	—	—
Ilex verticillata	0.0	—	—	0.0	—	—	—
	0.3	—	—	13.1	—	—	—
Ulmus americana	—	0.0	6.2	3.7	13.1	7.4	21.2
	—	8.9	3.2	6.4	6.0	2.4	7.4
Carya ovata	—	—	0.0	1.6	—	0.0	0.0
	—	—	2.6	3.8	—	2.6	3.0
Ilex decidua	0.0	—	—	0.0	1.2	0.0	2.5
	3.5	—	—	2.8	23.3	10.4	54.1
Fraxinus pennslyvanica	—	0.0	0.8	—	8.1	1.9	7.0
	—	5.6	7.2	—	0.0	2.6	3.1
Quercus lyrata	—	—	0.8	1.2	—	—	6.1
	—	—	1.5	1.5	—	—	0.0
Carya cordiformis	—	—	—	1.0	—	2.1	0.0
	—	—	—	0.0	—	4.8	4.6
Fraxinus caroliniana	—	—	—	—	0.0	—	—
	—	—	—	—	2.9	—	—
Morus rubra	—	—	—	0.9	1.2	1.4	2.0
	—	—	—	9.4	3.0	0.0	6.3
Celtis laevigata	—	—	—	0.0	8.6	9.6	14.4
	—	—	—	2.9	48.2	41.0	36.0
Crataegus sp.	—	—	—	—	—	0.0	1.3
	—	—	—	—	—	3.9	3.5

Note: we excluded *Asimina triloba* from this table in order to more accurately characterize pre-hurricane Hugo conditions; *A. triloba* was rare before the hurricane but formed dense thickets in some plots afterward.

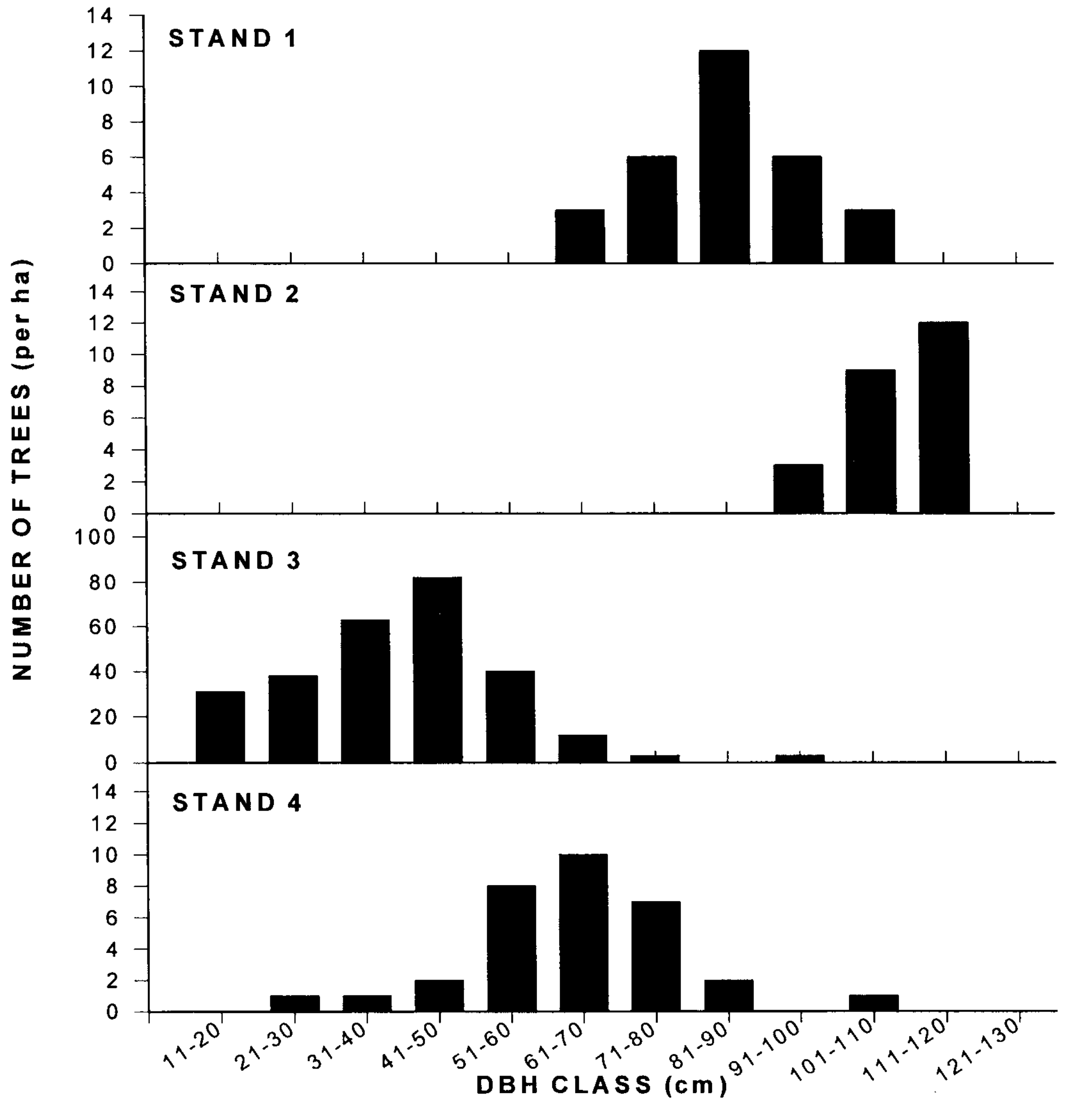

Fig. 2. Loblolly pine stands in Congaree Swamp National Monument with uni-modal diameter distributions.

was evident (Fig. 7). Correlation coefficients for numbers of hurricanes versus numbers of trees per decade were not significant ($P > 0.05$) in either of the two time frames tested (r values of 0.23 and −0.47 for decades ending with a year of 0 and 5, respectively).

Discussion. STRUCTURE OF OLD STANDS. We reject our hypothesis that loblolly pine stands at Congaree Swamp are even-aged and conclude that most are at least two-aged. In five of the six old stands, two to five distinct age classes were found. A mix of ages was also reported for the old pine forest at Boiling Springs Natural Area, South Carolina (Jones et al. 1981). Five pines cored at that site were between 85 and 105 years old and some that were not cored were estimated at closer to 200 years of age.

If size instead of age data were used to test the hypothesis of even-aged structure, a less clear conclusion may have resulted due to the presence of nearly uni-model diameter distributions in some stands (i.e., stands #1 through #4). The poor correlation between size and age, especially within stands, was somewhat surprising for a shade intolerant species, considering the results of Lorimer (1985).

All stands were dominated by two shade-in-

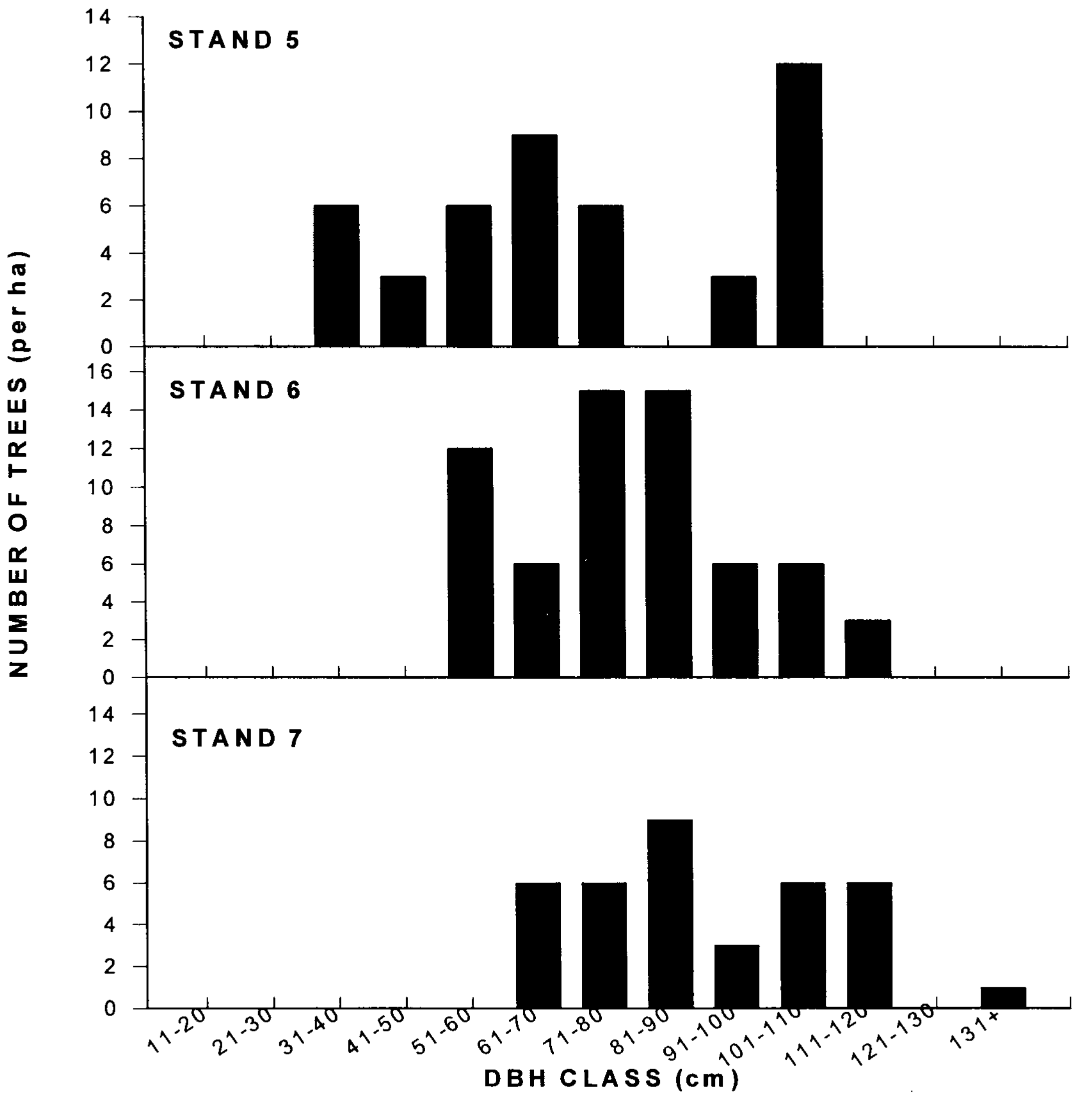

Fig. 3. Loblolly pine stands in Congaree Swamp National Monument with multi-modal diameter distributions.

tolerant species, loblolly pine and sweetgum; however, each stand included species covering the shade tolerance spectrum from intolerant to very tolerant (Table 1; Burns and Honkala 1990a, 1990b). Jones et al. (1981) found the same at Boiling Springs, except that yellow-poplar (*Liriodendron tulipifera* L.) was the dominant hardwood species rather than sweetgum. Predominance of shade intolerant species in old floodplain forests is a widespread phenomenon (Robertson et al. 1978; Streng et al. 1989; Putz and Sharitz 1991) that may reflect a prevalence of intense, large-scale disturbances. However, small-scale canopy disturbances (e.g., single tree gaps) plus flooding may lead to the same pattern (Robertson et al. 1978; Hall 1993) because floods can periodically set succession back in the seedling and sapling layers (Streng et al. 1989).

Stand Initiation. Our data and field observations suggest that a major disturbance probably initiated some or all of the old loblolly pine stands at Congaree Swamp. However, we can not differentiate between three major disturbance types: large blowdowns, fire, or agricultural activities.

Blowdowns may be the least important direct cause of stand initiation. We base this contention on two lines of evidence. First, current pine

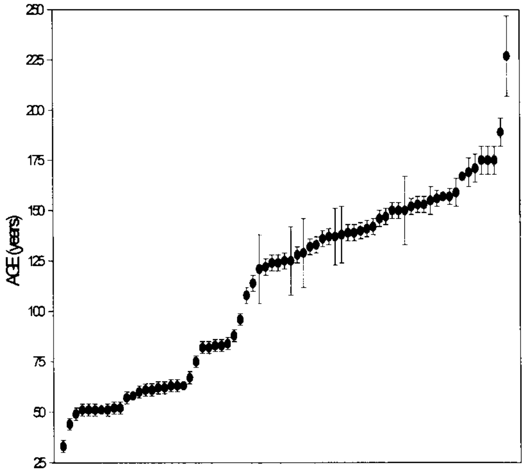

Fig. 4. Age distribution of all loblolly pines sampled in Congaree Swamp with trees arranged from youngest to oldest. Error bars represent 95% confidence intervals. Lack of error bars represents a core that hit the pith.

seedling densities in both the hurricane disturbed and logged (i.e., simulated blowdown) sites are clearly too low to recreate extant old stands. This was true even if we used a mortality estimate of 0.4% per year which is probably much too low for a highly competitive environment such as Congaree Swamp (Allen 1961; Somers et al. 1980; Peet and Christensen 1987). However, there is no guarantee that these regeneration episodes are representative of all such events. For example, seedling densities in the recently disturbed areas may be unusually low due to flood-induced mortality. Significant summer floods were noted at Congaree Swamp in summer 1991 and spring 1993, the second and fourth growing seasons after Hurricane Hugo. Floods that overtop tree seedlings during the growing season result in high rates of seedling mortality (Jones et al. 1989). The second line of evidence that suggests that blowdowns have been unimportant is the lack of correlation between past hurricane frequencies and initiation of age classes. However, interpretation of this result may be confounded by variation in hurricane intensity. One powerful storm may initiate stands whereas several weak ones may have no effect on pine regeneration. Since our hurricane data do not include information on storm severity, we can not eliminate hurricanes as a possible cause of stand initiation. On the other hand, Hurricane Hugo was a major storm that resulted in nearly 100% loss of the overstory in some of the pine stands at Congaree Swamp. The fact that this storm resulted in establishment of only a few scattered seedlings supports the contention that hurricanes may be unimportant for major regeneration events, although they may be important for gap formation and establishment of small patches of pines. There is also the possibility that some blowdowns, in conjunction with drought conditions and a source of ignition, result in fires that expose mineral soil and thereby stimulate pine regeneration.

We cannot eliminate fire as an important stand-initiating disturbance for loblolly pine at Congaree Swamp. The lack of fire scars on existing trees does not preclude a major fire prior to stand establishment. Moreover, the lack of charcoal in the old stands could result from export out of the system or burial under imported alluvium. Also, fire can be spatially patchy resulting in a mixture of age classes (Heinselman 1973) similar to those seen in current stands. A study to examine lake sediments and deep soil horizons may help determine whether fires were associated with loblolly establishment in Congaree Swamp.

We believe that agriculture was an important factor in stand initiation at Congaree Swamp. Although we have no direct proof of this contention, there is a strong possibility that large areas in the swamp were at one time cultivated or grazed. In the 1700s, European settlers cleared small patches of land for indigo and corn along the Congaree River levees (Hulick et al. 1981). Early settlers commonly used the upper floodplain of river systems in South Carolina for cattle grazing and corn (South Carolina Dept. of Agri. 1883; Savage 1973). The abolition of slavery, the common occurrence of floods in August, the threat of September hurricanes, and competition from more efficient farming in Louisiana caused a decline and abandonment of South Carolina floodplain farms in the 1800s (Savage 1973), a time frame that corresponds with the large number of 125–150 year-old pines in current old stands.

Some of the current stands, and even-aged patches within them, could be the result of subsistence type farming, or "girdle farming." Farmers as late as the early 1900s in parts of the southeastern U.S. would girdle and farm around large trees instead of clearing large tracts of land (Harper 1943). Savage (1973) noted that rice, corn, and grains were once planted in stump-filled fields within river floodplains in South Carolina. Small-scale agriculture was also practiced by pre-European cultures which raises the

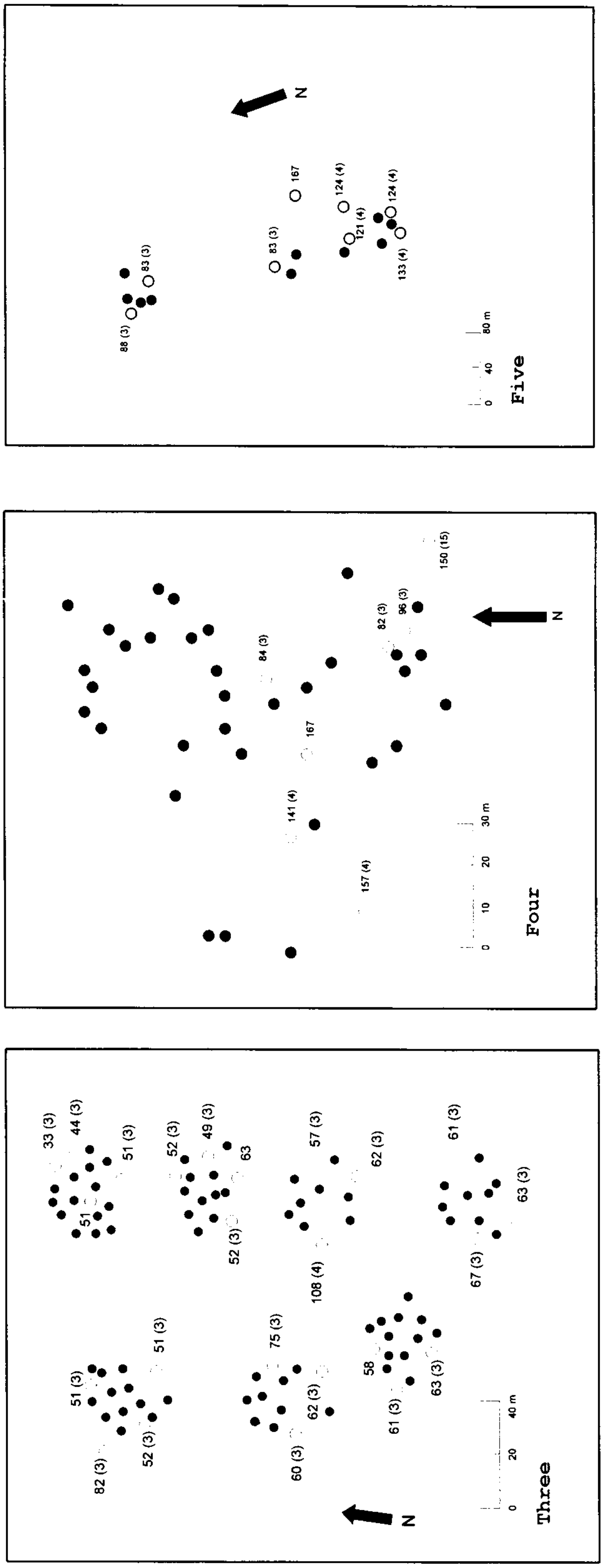

Fig. 5. Spatial distribution of loblolly pines in stands #3, #4, and #5. Hollow dots represent aged individuals; numbers are age in years with ½ of 95% confidence interval in parentheses.

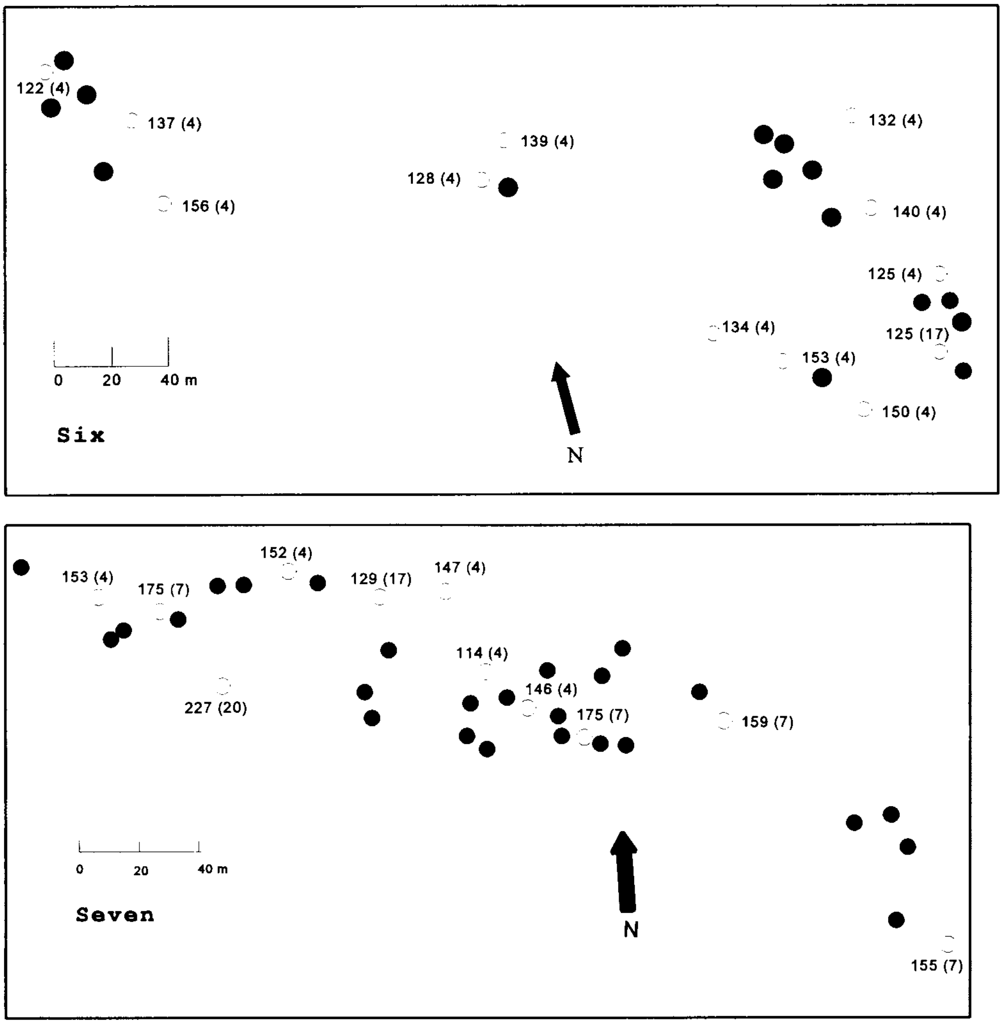

Fig. 6. Spatial distribution of loblolly pines in stands #6 and #7. Hollow dots represent aged individuals; numbers are age in years with ½ of 95% confidence interval in parentheses.

Table 2. Density (stems/ha) of surviving loblolly pines up to 180 years after 1992, assuming current seedlings have mortality rates of 3.3% and 0.4% per year.

Years from 1992	3.3% Mortality: Blowdown Total	3.3% Mortality: Blowdown In full sun	3.3% Mortality: Logged area Total	3.3% Mortality: Logged area In full sun	0.4% Mortality: Blowdown Total	0.4% Mortality: Blowdown In full sun	0.4% Mortality: Logged area Total	0.4% Mortality: Logged area In full sun
0	157	35	14	11	157	35	14	11
10	113	25	10	8	150	34	13	11
20	82	18	7	6	145	32	13	10
60	22	4	2	2	123	27	11	9
100	6	1	1	—	105	23	9	7
120	3	1	—	—	97	22	9	7
140	2	—	—	—	90	20	8	6
160	1	—	—	—	83	18	7	6
180	—	—	—	—	76	17	7	5

Table 3. Estimated loblolly pine densities for mature and newly regenerated stands adjusted to age 60 based on a presumed mortality of 0.4% per yr.

Area	Density individuals/ha
Regenerating forests	
Logged	9
Hurricane blowdown	27
Older stands	
#1	48
#2	44
#3	243
#4	74
#5	71
#6	90
#7	56

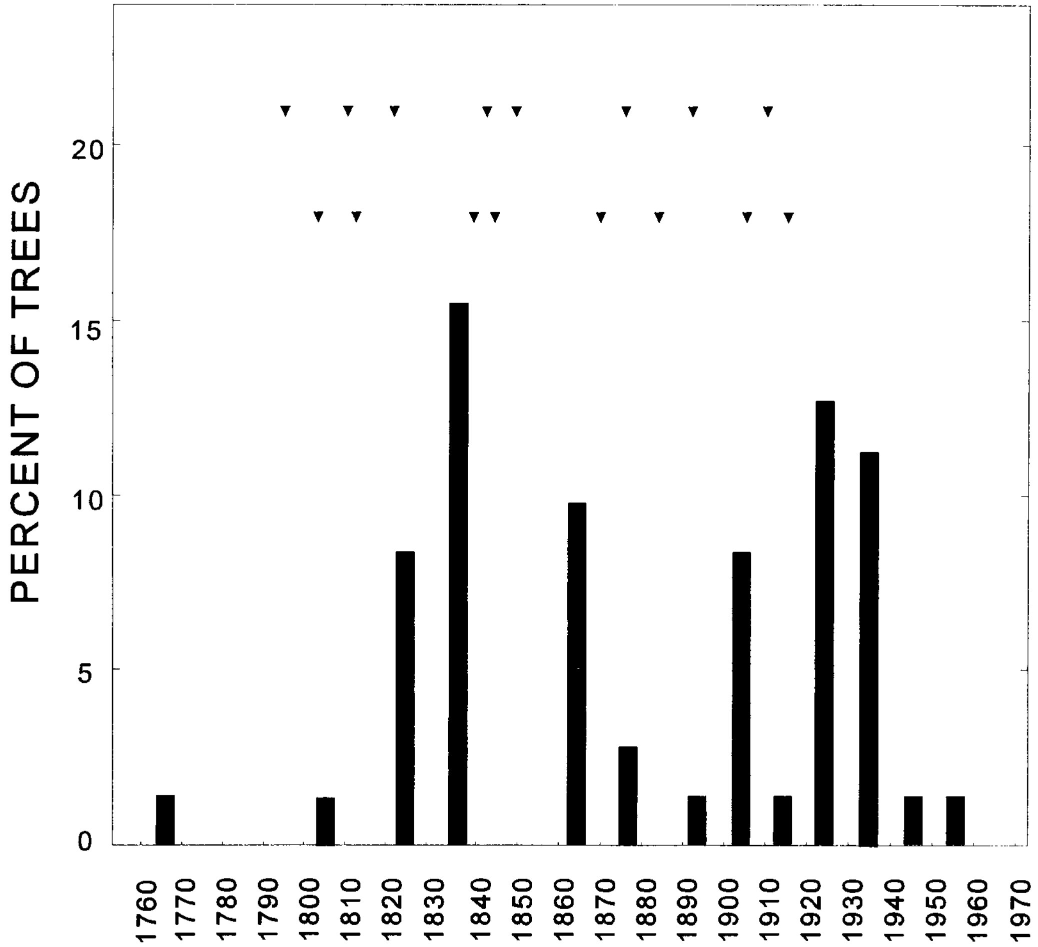

Fig. 7. Decadel establishment dates for loblolly pine in Congaree Swamp (bars) and historical hurricane dates in South Carolina (triangles).

possibility that loblolly pine has been regenerating in small patches for thousands of years at Congaree Swamp and elsewhere.

Two additional points support the contention that current old stands established in old agricultural fields. First, croplands provide two conditions that stimulate dense loblolly pine establishment: exposed mineral soil (Burns and Honkala 1990a) and absence of competition from hardwood rootstocks. Second, the youngest stand measured (stand 3) was clearly an old-field site, and had sufficient pine densities to produce densities seen in extant old stands.

GAP DYNAMICS AND LONG-TERM OUTLOOK. After initial establishment, additional recruitment events have occurred in most of the loblolly pine stands at Congaree Swamp. The younger age classes occurred as clusters of various sizes or as isolated trees (Figs. 5, 6). The presence of multiple age classes may reflect a lengthy period of initial stand establishment. Succession of old fields from an herb-dominated to a loblolly pine-dominated stage can take decades (Golley et al. 1994). Pine invasion of old fields may be slowed by limited seed dispersal, seed or seedling herbivory, or flooding of lower microsites. Flooding may have been the key in stand 3 where two large groups of loblolly pine regenerated over a 20 year time period.

An alternative hypothesis is that different age groups of advanced seedling regeneration became established, but all were released at the same time. Loblolly pine can persist in intermittent shade for up to two decades if hardwood competition is weak and drought doesn't occur (Chapman 1945). However, establishment of slow-growing loblolly pine seedling populations at Congaree is highly unlikely because hardwood competition is intense and droughts are relatively common in central South Carolina (Stahle and Cleaveland 1992). Jones et al. (1981) observed no loblolly pine regeneration in the understory at Boiling Springs Natural Area. They described relatively high mortality rates of old loblolly pines, but most that had perished within the preceding 25 years had died standing, with a tendency to break up gradually. Windthrown trees may be required to create the bare soil conditions that would allow pine regeneration.

In two of the oldest stands (#6 and #7), small gaps, perhaps the size of a single overstory tree, have been filled by younger loblolly pines. This is best seen in stand #7 where a 114-year-old tree was found within 20 meters of 146-year-old tree, which in turn was within 30 meters of a 175-year-old tree (Fig. 6). The gap sizes implied by these data are unusually small for the regeneration of a shade-intolerant species such as loblolly pine, and are also small relative to gap sizes needed to stimulate canopy replacement in other southeastern forests (Harcombe and Marks 1978). If single tree or small gap replacement does occur at Congaree Swamp, populations of loblolly pine may be sustainable for an extended period of time. If no more large-scale stand establishment events occur, today's extensive old pine stands will eventually be replaced by scattered individuals and small clusters of pines, a pattern that may reflect pre-European settlement conditions.

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