

Loblolly pine regeneration and competing vegetation 5 years after implementing uneven-aged silviculture

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The effects of three basal areas (9.2, 13.8, and 18.4 m²/ha), maximum diameters (30.5, 40.6, and 50.8 cm), and site indices (≤ 24.6 , 24.7–27.4, and ≥ 27.5 m at 50 years) on establishment and development of loblolly pine (*Pinus taeda* L.) regeneration and competing vegetation were determined on 81 permanent, 0.20-ha plots in south Arkansas and north Louisiana. Plots were harvested to the designated basal areas, maximum diameters, and a *q*-factor of 1.2 using the single-tree selection method during 1983 (a bumper seed year) and 1985 (a seed year failure); this necessitated including the year of harvest as a fourth variable. Pine regeneration and competing vegetation were evaluated 4 or 5 years after treatment. Models were developed to predict the number and percent stocking of pine seedlings and saplings and the percent coverage of competing vegetation. Fit indices ranged from 0.21 to 0.52 for pine regeneration and from 0.15 to 0.73 for coverage of competing vegetation. Pine regeneration was generally greatest for the 1983 harvest, the largest maximum diameters, and the poorest sites. Coverage for vines, hardwoods, and total vegetation was greatest on the good sites and generally for the lowest basal areas. Coverage of grasses, herbs, and shrubs did not vary significantly among treatments. Results suggest that seed production and competing vegetation influence the initial amounts of loblolly pine regeneration obtained with uneven-aged silviculture using single-tree selection.

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Les effets de trois surfaces terrières (9,2, 13,8 et 18,4 m²/ha), trois diamètres maximaux (30,5, 40,6 et 50,8 cm) et trois indices de qualité de station (inférieur à 24,6, 24,7–27,4 et supérieur à 27,5 m à 50 ans) sur l'établissement et le développement de la régénération du pin à encens (*Pinus taeda* L.) et de la végétation compétitrice ont été déterminés sur 81 parcelles permanentes de 0,2 ha dans le sud de l'Arkansas et le nord de la Louisiane. Les parcelles ont été récoltées en 1983 (excellente année semencière) et en 1985 (très mauvaise année semencière) par un jardinage par pied d'arbre de façon à atteindre les objectifs de surface terrière, de diamètre maximum et une distribution des diamètres en suivant un coefficient de Liocourt de 1,2. Ceci a nécessité l'inclusion de l'année de récolte comme quatrième variable. La régénération du pin et la végétation compétitrice ont été étudiées 4 ou 5 ans après le traitement. Des modèles ont été développés afin de prédire le nombre et le coefficient de distribution des semis et des gaules de pin ainsi que le pourcentage de couverture de la végétation compétitrice. Les indices d'ajustement des courbes allaient de 0,21 à 0,52 pour la régénération de pin et de 0,15 à 0,73 pour la couverture de la végétation compétitrice. La régénération de pin était généralement supérieure avec la récolte de 1983, les diamètres maximaux supérieurs et les moins bonnes stations. La couverture des vignes, des feuillus, et celle de l'ensemble de la végétation était supérieure sur les bonnes stations et généralement pour les plus faibles surfaces terrières. La couverture des graminées, des herbacées et des arbustes ne variait pas significativement selon les traitements. Les résultats suggèrent que la production semencière et la végétation compétitrice influencent la quantité initiale de régénération de pin à encens obtenue en pratiquant un jardinage par pied d'arbre.

[Traduit par la Rédaction]

Introduction

Uneven-aged silviculture has classically been applied to species that can regenerate and develop in partial shade (Marquis 1976). However, uneven-aged silviculture has also been successfully applied to some of the shade-intolerant southern pines, principally loblolly (*Pinus taeda* L.) and shortleaf (*Pinus echinata* Mill.) pines (Williston 1978; Baker 1986; Murphy et al. 1991), and to a limited extent longleaf pine (*Pinus palustris* Mill.) (Farrar and Boyer 1991). This success is mainly due to (i) regulating the structure of the merchantable portion of the stand through periodic harvests and (ii) controlling the species composition of the understory and midcanopy, chiefly with broadcast application of selective herbicides. Such practices yield high rates of merchantable growth and create a favorable environment for the establishment and development of pine regeneration (Reynolds 1959, 1969; Reynolds et al. 1984).

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Knowledge of the regeneration of uneven-aged, loblolly pine stands is largely limited to research conducted at the Crossett Experimental Forest in southern Arkansas (Reynolds et al. 1984). Thus, a long-term regional study was begun in 1983 with the ultimate goal of describing the influence of residual basal area, maximum diameter, and site quality on uneven-aged stand dynamics. The initial silvicultural objective was to secure a new age-class of regeneration in stands with an irregular diameter distribution using single-tree selection as the reproductive cutting method and coupled with hardwood-competition control. Results for pine regeneration and competing vegetation 5 years after implementation are presented here.

Study area

Study sites lie within a 20 000 - km² area located in the West Gulf Coastal Plain of southern Arkansas and northern Louisiana (Fig. 1). Study sites were selected to represent the typical range of loblolly pine productivity within the area, and thus were located

on a wide range of landforms and soils. Landforms include minor flood plains of ephemeral streams, terraces, loessial flats, and gently rolling uplands; elevations range from 46 to 107 m. Soils within the region were derived from unconsolidated sediments of alluvial and loessial origin. Sites with below-average productivity had low moisture holding capacity, restrictions to rooting depth, or low fertility; some representative soils include the Alaga, Cahaba, and Wrightsville series (Typic Quartzsammets, Typic Hapludults, and Typic Glossaqualfs, respectively). Soils with above-average productivity were most common on the lower topographic positions, and some representative soils are the Amy, Arkabutla, and Bude series (Typic Ochraqualts, Aeric Fluvaquents, and Glossaquic Fragiudalfs, respectively).

The study area has a subtropical-humid climate with a mean annual precipitation of 140 cm. Winter is the wettest season and autumn is the driest. Water deficits typically develop during the summer. Temperatures average 8°C during the winter and 27°C during the summer. Both precipitation and temperature decline slightly from south to north within the study area.

Natural vegetation on uplands within the study area is a forest dominated by loblolly and shortleaf pines diversely mixed with southern hardwoods. This composition has historically been maintained by periodic disturbance, both natural and human. In the absence of disturbance, however, succession is clearly toward a hardwood-dominated forest (Switzer et. al 1979; Cain and Yaussy 1984).

Methods

Treatments and field installation

Uneven-aged stand structures can be defined in terms of basal area, maximum diameter, and a quotient (q) that describes the shape of the reverse-J diameter distribution within the stand (Murphy and Farrar 1982; Farrar 1984). Experience has shown that this quotient is the most difficult aspect of uneven-aged stand structure to control. For this reason, three levels of basal area (9.2, 13.8, and 18.4 m²/ha) and three maximum diameters (30.5, 40.6, and 50.8 cm) were tested, while attempting to maintain a uniform q of 1.2 for 2.5-cm diameter classes. Site index was included as a third variable by selecting stands representing three ranges of loblolly pine site index: ≤ 24.6 , 24.7–27.4, and ≥ 27.5 m (base age 50 years). These three factors were replicated three times, yielding a total of 81 plots.

Selected stands had to have at least 70% of their pine basal area in loblolly pine; no evidence of cutting within the last decade; no evidence of catastrophic losses from insects, disease, weather, or fire; and a site index that did not vary by more than 3.0 m across the plot. An attempt was made to locate stands with a balanced, reverse-J diameter distribution and a history of uneven-aged silviculture, but such stands were generally not available. However, selected stands had an irregular diameter distribution that was reflected in multiple product classes (namely, pulpwood and small, medium, and large sawlogs). Although numbers generally declined in successive product classes, the actual age structure of stands was not known. Despite an attempt to select homogeneous stands, an array of different initial stand conditions occurred; such variation is common to any large, regional study. Many stands had a hardwood understory and midstory, but neither this stand component nor the initial levels of pine regeneration were measured. More than one plot was established in most stands. Plots were assigned to a residual basal area and maximum diameter treatment as randomly as possible.

Square, 0.20-ha plots were established and surrounded by 17.8-m buffer strips that were treated identically. Plots and buffer strips were marked to leave loblolly pine trees with priorities in the following order: the designated basal area, the designated maximum diameter, and a q of 1.2 for 2.5-cm diameter classes. All hardwoods with a groundline diameter of 2.5 cm and larger were stem injected with herbicide, before the harvest if possible, but no later than the first growing season after harvest.

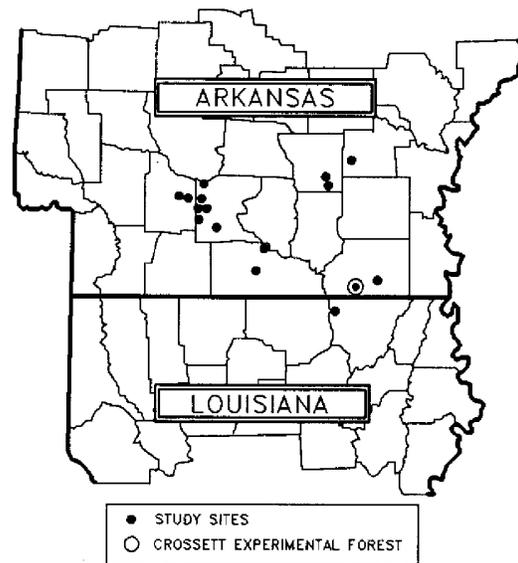


FIG. 1. Location of the study sites and the Crossett Experimental Forest, where data for pine seed production was obtained from other ongoing studies.

Plots were established and harvested over a 3-year period beginning in the fall of 1983. The intention was to establish and harvest about one-third of the plots each year, but the plots established in 1984 were not harvested until the following year because of exceptionally wet weather; they were harvested along with the 1985 plots. Thus, about one-third of the plots were harvested in 1983 and two-thirds in 1985. All harvesting was completed early in the dormant season.

After harvest, the DBH of all residual loblolly pines greater than 8.9 cm was measured to the nearest 0.25 cm by diameter tape in each 0.2-ha plot, and the height and age of 5–10 of the tallest trees were measured. This inventory allowed determining the actual basal area, maximum diameter, and DBH distribution for each 0.20-ha plot. The mean residual size-class distributions are compared with the ideal targets in Fig. 2 for basal area and maximum diameter classes. Differences between the target and actual distributions resulted from (i) tree mortality from logging damage and natural causes, (ii) giving higher priority to achieving the designated basal area than designated maximum diameter, and (iii) the absence of a balanced, reverse-J diameter distribution in the original stand. Residual size classes were consistently deficient in pulpwood-sized trees, but these deficiencies were compensated for by retaining additional sawlog-sized trees, as is typically done in marking uneven-aged stands (Marquis 1976). There was an average of 330 trees/ha that were greater than 8.9 cm in DBH; this was 15% below that for a target stand with a q of 1.2. The average plot after harvest had a basal area of 13.6 m²/ha, a maximum diameter of 41.2 cm, and a site index of 25.2 m at 50 years; this is very close to the mean target across all treatments. The site index determined from the intensive post-harvest inventory was often lower than that determined in the reconnaissance for plot selection; this resulted in fewer stands representing the highest site index class than was originally intended.

Measurements

Loblolly pine regeneration and competing vegetation were evaluated on the plots 4 or 5 years after harvest (5 years for the plots harvested in 1983 and 1985 and 4 years for the plots established in 1984 but harvested in 1985). Evaluations were made in the late summer and early fall. Ten points were systematically located

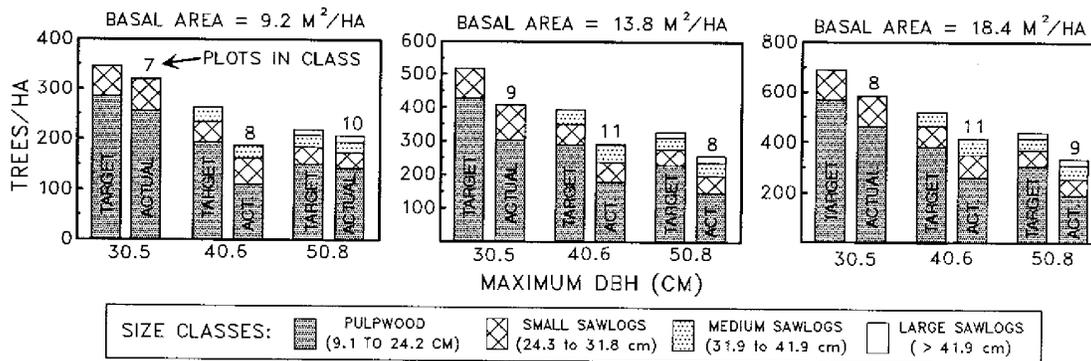


Fig. 2. Target and actual size-class distributions for basal area and maximum diameter classes after implementing uneven-aged silviculture in loblolly pine stands. Basal area (m^2/ha) classes and their ranges are 9.2 (7.3–11.5), 13.8 (11.6–16.0), and 18.2 (16.1–20.2). Maximum diameter classes (cm) and their ranges are 30.5 (29.5–35.6), 40.6 (35.7–45.7), and 50.8 (45.8–55.9).

within each 0.20-ha plot; each point was at least 9.1 m from the 0.20-ha plot boundary and 26.8 m from the outer boundary of the buffer strip. Points were permanently marked for reference in future inventories. Pine seedlings were counted within a circular 4- m^2 subplot centered around each point. The 1989 and 1990 inventories identified the following seedling size classes: 0.15–0.76 m, 0.77–1.37 m, and ≥ 1.38 m in height and ≤ 1.3 cm in DBH. The 1988 inventory did not subdivide the seedling size classes, i.e., ≥ 0.15 m in height and a DBH of ≤ 1.3 cm.

The percentage of horizontal coverage of competing vegetation was ocularly estimated on each 4- m^2 subplot during the 1989 and 1990 inventories by the following vegetative groups: grasses, herbs, vines, shrubs, hardwoods, and total. Evaluations were conducted by different people, but the same people were used each year. The sum of individual groups may exceed total coverage because of overlapping coverage. For each inventory, the species of vine and woody competing vegetation that had the greatest coverage within each 4- m^2 subplot was recorded as the "dominant" species.

During each inventory, DBH of pine saplings (≥ 1.3 to 8.9 cm) was measured (to the nearest 0.25 cm) on a circular 40- m^2 subplot centered around each point. Saplings were subsampled for height.

Data analysis and modeling

Mean values were calculated from the 10 regeneration subplots. Percentage stocking of pine regeneration was determined for each 0.20-ha plot; 4- m^2 subplots were considered stocked if at least one pine seedling was present, and the 40- m^2 subplots were considered stocked if there was at least one pine sapling. Basal area and maximum diameter were determined from the inventory conducted on each plot after harvest. Site index was computed using the function of Farrar (1973) from sample trees whose ring pattern showed a high and consistent rate of growth. A weighted mean seedling height was calculated for the 1989 and 1990 inventories by using the midpoint of each seedling height class as the class height. For the third size class (i.e., ≥ 1.38 m and ≤ 1.3 cm DBH), height for the upper limit was calculated from a height–DBH prediction equation developed from the saplings measured for height (value = 2.6 m).

Although pine seed production is not known for individual plots, seed production in loblolly pine stands in the Crossett Experimental Forest, located at the southeastern corner of the study area, may serve as a relative index for comparing years. Experience has shown that pine seed crops are fairly uniform over large areas in this vicinity. Although these stands had a minor component of shortleaf pine, the seeds of each species were not separated during sampling. Seed production at the Crossett Experimental Forest (Cain 1987, 1988, 1991) over a 5-year period was as follows:

Year	Sound seeds/ha
1983	2 320 000
1984	480 000
1985	5 000
1986	2 040 000
1987	133 000

Thus, plots were harvested during a bumper seed year (1983) and a seed-year failure (1985). Because of this large difference in seed production, the year of harvest was included as an additional treatment variable.

After evaluating several candidate models, the following form for analysis of regeneration and competing vegetation was selected:

$$[1] Y = \exp(b_0 + b_1 H + b_2 B + b_3 D + b_4 S + b_5 P)$$

where Y is the response variable; H is a qualitative variable for the year harvested (0 = 1983; 1 = 1985); B is the measured residual basal area after harvest (m^2/ha); D is the measured maximum diameter (cm) in the residual stand after harvest; S is the mean loblolly pine site index (m at 50 years) from the trees measured for height and age in the plot; P is the length of the observation period (5 years for the 1988 and 1990 inventories and 4 years for the 1989 inventory); and the b_i 's are coefficients to be determined. Response variables were size, number, and stocking of pine seedlings and saplings and coverage of competing vegetation. Equations were fitted by nonlinear least squares regression using the SAS procedure MODEL (SAS Institute Inc. 1988). A reduced model without the H term was used for the equations developed for the mean height of seedlings and the coverage of competing vegetation because these items were evaluated only during the 1989 and 1990 inventories. Variables were dropped from the full model if their coefficient did not significantly differ from zero at a probability of ≤ 0.05 . The importance of individual variables in the models was evaluated by the increase in fit index when adding the specified variable last. Regressions for the mean seedling height and sapling DBH included only those plots with seedlings or saplings present.

The coefficient for P was significantly different from zero only for seedling stocking and total vegetation coverage. These equations were solved for a P of 5 years, and the value was added to the b_0 coefficient to adjust equations to a fixed observation period of 5 years.

For seedling stocking and total coverage of competing vegetation, eq. 1 yielded some predicted values more than 100%. To correct this, the arcsine – square root transformation commonly used in analyzing percentage data was used (Steel and Torrie 1980). For consistency, all response variables expressed in

TABLE 1. Equations and associated statistics for predicting the density and stocking of pine seedlings and saplings, sapling mean DBH, and coverage of competing vegetation

Equation number	Equation*	Fit index [†]	Root MSE [‡]	Mean Y value	Error df
1	$SDL D = \exp(9.91 - 1.29H + 0.122B + 0.0928D - 0.231S)$	0.45	13 500	12 400	76
2	$SDLST = 100\{\sin[\exp(0.0572 - 0.555H + 0.0236D - 0.0350S)]\}^2$	0.52	20.3	58.6	76
3	$SAPD = \exp(6.35 - 1.56H)$	0.21	419	281	79
4	$SAPST = 100\{\sin[\exp(2.68 - 0.707H - 0.113S)]\}^2$	0.47	23.2	29.4	78
5	$DBH = \exp(2.94 + 0.457H - 0.0755S)$	0.32	1.94	3.87	51
6	$VINE = 100\{\sin[\exp(-3.31 - 0.0205B + 0.120S)]\}^2$	0.73	9.46	31.9	49
7	$HDW = 100\{\sin[\exp(-1.79 + 0.0417S)]\}^2$	0.15	8.96	21.4	50
8	$TOTAL = 100\{\sin[\exp(-1.36 - 0.0160B + 0.0673S)]\}^2$	0.56	12.7	75.7	48

NOTE: Response variables that were fit but had no coefficients significantly different from zero were seedling size class and the coverage of grass, herbs, and shrubs.

*SDL D, seedling density (no./ha); SDLST, seedling stocking (%); SAPD, sapling density (no./ha); SAPST, sapling stocking (%); DBH, sapling mean DBH (cm); VINE, vine coverage (%); HDW, hardwood coverage (%); TOTAL, total understory coverage (%); sin, the sine argument in radians; H, harvest year (0 = 1983; 1 = 1985); B, residual basal area (m²/ha); D, maximum diameter (cm); S, site index (m at 50 years).

[†]Fit index = $1 - \Sigma[(Y_i - \bar{Y})^2 / \Sigma(Y_i - \bar{Y})^2]$.

[‡]Mean square error.

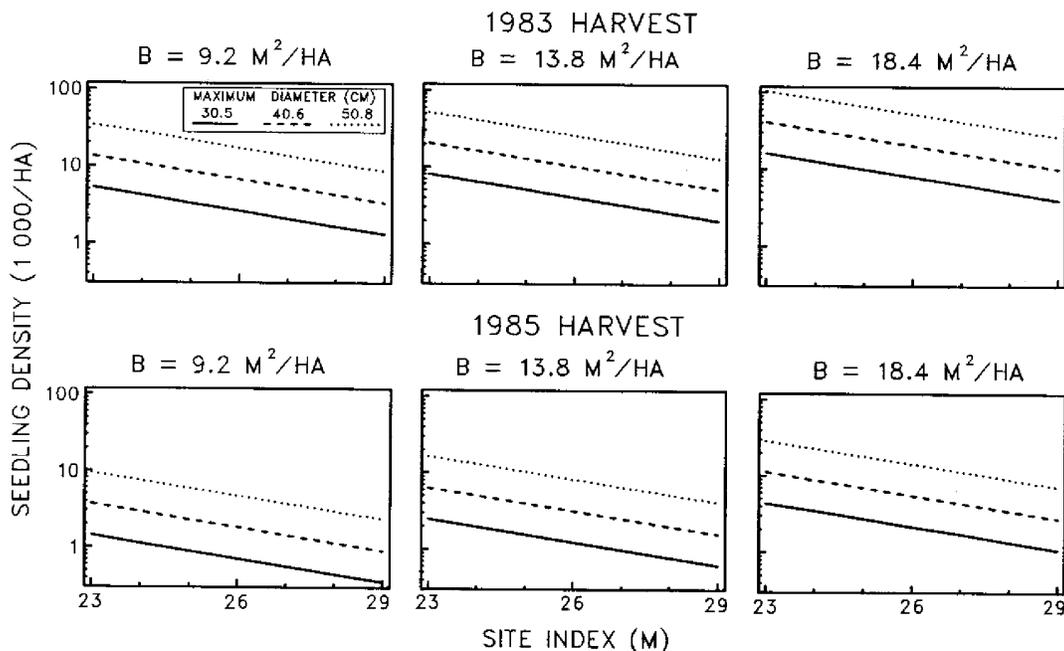


FIG. 3. Predicted number of pine seedlings occurring 5 years after implementing uneven-aged silviculture in loblolly pine stands (B = basal area).

percentages were transformed in this manner when fitting eq. 1. Equations were solved for the class midpoints for treatment variables when presenting trends in illustrations. Because of the complexity of the relationships presented in illustrations, the inclusion of the actual data points was felt to overly clutter the figures. Thus, treatment means are presented separately in the Appendix (Tables A1 and A2) as supporting data.

Results

Pine seedlings

Seedling density 5 years after treatment was highly variable, ranging from 0 to nearly 120 000 seedlings/ha; the independent variables evaluated in this study explained 45% of this variation (Table 1, eq. 1). Coefficients for basal area and maximum diameter were both positive; the coefficient for

site index was negative. Thus, basal area and maximum diameter were positively correlated with seedling numbers, whereas site index was negatively correlated. The importance of the variables was in the following order: year of harvest > maximum diameter > site index > basal area. The greatest mean seedling density predicted was 107 000 seedlings/ha for the 1983 harvest, the poorest site index (22.9 m), the greatest maximum diameter (50.8 cm), and the greatest basal area (18.4 m²/ha) (Fig. 3). The lowest mean seedling density predicted by the equation was 356 seedlings/ha for the 1985 harvest, the best site index (29.0 m), the lowest maximum diameter (30.5 cm), and the lowest basal area (9.2 m²/ha).

The equation for seedling stocking is similar to that for numbers, except that the coefficient for basal area was not

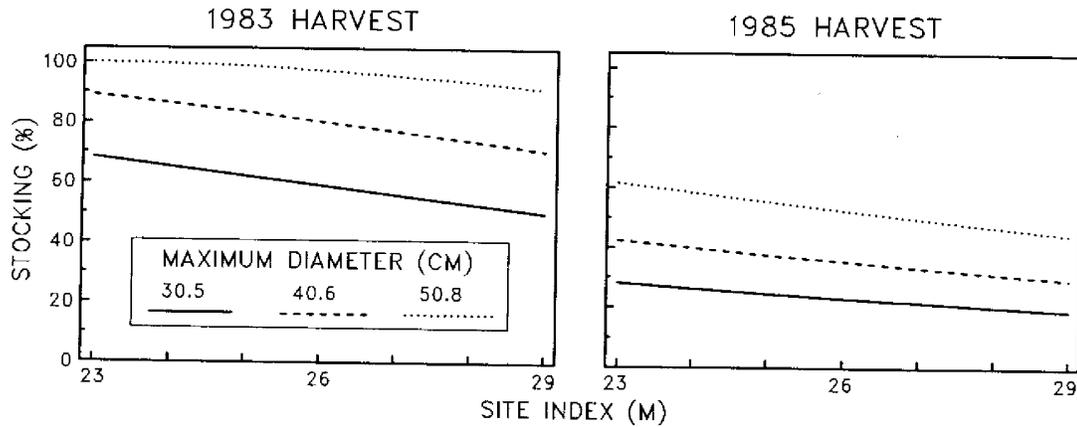


FIG. 4. Predicted stocking of pine seedlings occurring 5 years after implementing uneven-aged silviculture in loblolly pine stands.

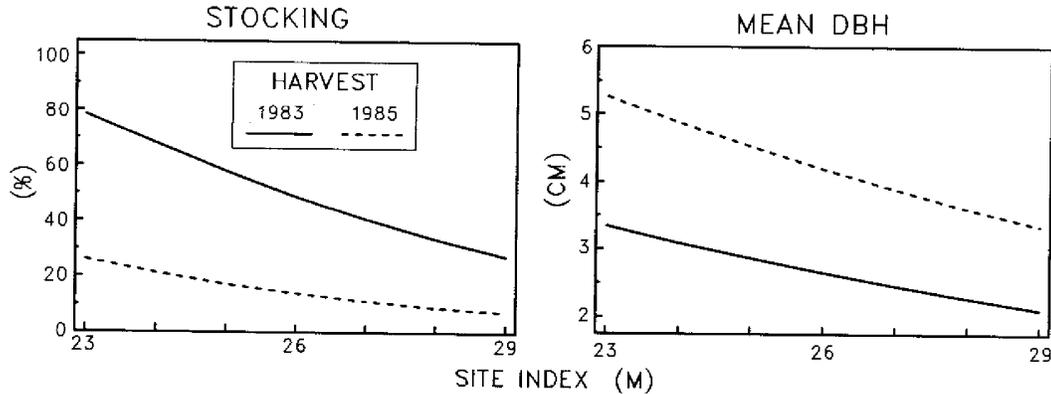


FIG. 5. Predicted stocking and DBH of pine saplings occurring 5 years after implementing uneven-aged silviculture in loblolly pine stands.

significant and thus was dropped from the equation (eq. 2, see Table 1). The treatment variables explained 52% of the variation in seedling stocking. The importance of the treatment variables was in the same order as shown for seedling density. For a specific site index, the seedling stocking for the plots harvested in 1983 was about twice that of the 1985 harvest, and stocking for the 50.8-cm maximum diameter was about twice that of the 30.5-cm maximum diameter (Fig. 4).

Weighted mean height for seedlings did not vary significantly with the treatment variables and averaged 0.58 m. Thus, most seedlings present 5 years after treatment were in the smaller size classes.

Pine saplings

Year of harvest was the only significant variable affecting sapling density; it explained 21% of the variation (eq. 3, see Table 1). Plots harvested in 1983 were predicted to have 570 saplings/ha 5 years after harvest, whereas those harvested in 1985 were predicted to have 120 saplings/ha.

Sapling stocking was affected by both year of harvest and site index, which together explained 47% of the variation (eq. 4, see Table 1); site index was negatively correlated to stocking. Predicted stocking ranged from 80% on poor sites harvested in 1983 to about 10% on good sites harvested in 1985 (Fig. 5). The year of harvest accounted for about a fourfold difference in stocking for a given site index.

Mean DBH of saplings was also affected by both year of harvest and site index (eq. 5, see Table 1). Saplings in plots treated in 1985 had larger mean diameters than those of the 1983 harvest, and mean diameter decreased as site index increased (Fig. 5). The difference between years might reflect a size-density interaction because the 1983 harvest produced four to five times the sapling density than the 1985 harvest. Plots harvested in 1985 may also have more saplings resulting from advance regeneration than plots harvested in 1983.

Competing vegetation

Coverage of grasses, herbs, and shrubs occurring 5 years after harvest did not vary significantly with the treatment variables and averaged 18.6, 5.0, and 9.6%, respectively. In contrast, the coverage of vines, hardwoods, and the total coverage varied significantly with the treatment variables.

Vine coverage 5 years after harvest was negatively correlated with basal area and positively correlated with site index; these variables explained 73% of the variation (eq. 6, see Table 1). Basal area was less important than site index. Vine coverage increased about three times over the range of site indices, from predicted values of 15–20% coverage on the poor sites to 55–70% on the good sites (Fig. 6).

Hardwood coverage was only slightly related to site index, explaining 15% of the variation (eq. 7, see Table 1). Predicted values varied from 18% on the poor sites to 28% on the good

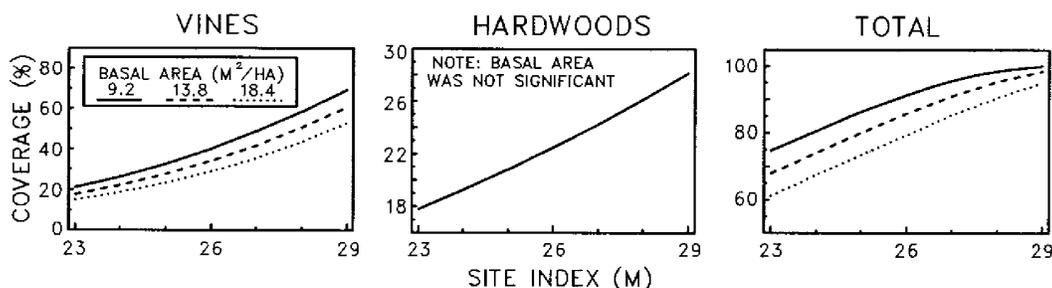


FIG. 6. Predicted coverage of vines, hardwoods, and total vegetation occurring 5 years after implementing uneven-aged silviculture in loblolly pine stands.

sites (Fig. 6). Total coverage was negatively correlated with basal area and positively correlated with site index, explaining 56% of the variation (eq. 8, see Table 1). Site index was the most important treatment variable. Most of the differences in total coverage associated with site index and basal area were in vines and hardwoods. The predicted mean total coverage ranged from 60–75% for the poor sites to 90–100% for the good sites (Fig. 6).

Poor sites had about equal amounts of grasses, hardwoods, and vines (each group averaged 15–20% coverage), while the good sites had a greater coverage of vines (a mean coverage of 55%). Further evidence of the compositional differences among sites is shown by the dominant woody or vine species present on each regeneration subplot (Table 2). Eighteen species or species groups were dominant on 1% or more of the subplots, while another 20 species or species groups were dominant on less than 1% of the subplots. The dominance of some species or species group significantly varied with site index, while others did not. For example, dominance of blackberry (*Rubus* spp.) and greenbrier (*Smilax* spp.) was greatest on plots with high site index, while dominance of persimmon (*Diospyros virginiana* L.) and southern red oak (*Quercus falcata* Michx.) was lowest. Other species, such as sweetgum (*Liquidambar styraciflua* L.) and red maple (*Acer rubrum* L.), were dominant on a similar percentage of subplots across all sites. The three most frequent dominant species on poor sites were grape (*Vitis* spp.), persimmon, and sweetgum, which was in contrast to the blackberry, greenbrier, and grape on good sites. Overall, vines most commonly dominated the good sites, while hardwoods dominated the poor sites.

Discussion

The goal of any reproduction cutting method is to provide an environment that favors the establishment and development of the desired species. The silvicultural goal of this study was to create a new age-class in existing stands by establishing loblolly pine regeneration. This was accomplished by controlling stand basal area and maximum diameter through harvesting and controlling understory and midstory hardwoods with stem-injected herbicides. The variables evaluated in this study (year of harvest, basal area, maximum diameter, and site index) modify the complex set of causal factors that determine the amount, spatial distribution, and growth rates of regeneration. These factors include seed production, seedbed conditions, and environmental conditions such as light, water, and nutrients (Smith 1986). Although none of these causal factors were measured in this study, inferences about these cause-effect relationships

will help to explain results. Such relationships appear to be fairly simple and straightforward in some cases, whereas others involve complex interactions that may change with the development of regeneration. For example, the initial establishment of regeneration may be most strongly affected by levels of seed production and seedbed conditions, while its subsequent development may be more influenced by levels of competition.

Year of harvest

Year of harvest was the most important variable affecting regeneration that was evaluated in this study. Annual loblolly pine seed crops are highly variable, fluctuating from near zero to several million per hectare (Wahlenberg 1960). Because harvesting creates favorable seedbed conditions for loblolly pine by exposing mineral soil and disturbing litter, the seed crop occurring during the year that a stand is harvested will have a pronounced effect on the resulting regeneration (Cain 1991). Plots in this study appear to have been harvested during a bumper seed crop (1983) and a seed crop failure (1985), if the seed production in the Crossett Experimental Forest, located in the southeastern portion of the study area, is representative of the entire study area. Five years after harvest, there were three to four times more seedlings and saplings in the plots harvested during the bumper year than in those harvested during the failure. The 1985 seed crop was so poor that it is probable that most of the regeneration on the plots harvested in 1985 resulted from another bumper seed crop in 1986. However, this seed crop fell on a 1-year-old seedbed, where fresh litter covered the mineral soil exposed by logging and where competing vegetation had a 1-year growth advantage. The resulting environment would likely have been less favorable to pine establishment than it had been the previous year. Trousdell (1954) and Grano (1971) have shown that the opportunity for natural regeneration diminishes with time after harvest and site preparation.

Maximum diameter

Higher seedling density and stocking levels were associated with the higher maximum diameters. Maximum diameter would likely affect levels of seed production because it influences the size-class distribution of the trees in the residual stand. The effect of tree size on seed production has long been known for loblolly pine (Barrett 1940). For example, recommendations for even-aged natural regeneration call for seed trees 29.5 cm in DBH and larger because of their higher potential for seed production (Grano 1957). Thus, few trees in the size classes for good seed production were retained in the plots with the lowest maximum

TABLE 2. Percentage of regeneration subplots dominated by various species of competing vegetation

Species or species group	Site index class*			MSE [†]
	Poor	Medium	Good	
Vines				
Greenbriar (<i>Smilax</i> spp.)	4.4 ^b	12.2 ^{ab}	13.7 ^a	233
Blackberry (<i>Rubus</i> spp.)	2.6 ^b	10.4 ^a	15.2 ^a	201
Grape (<i>Vitis</i> spp.)	7.8 ^{ab}	5.2 ^b	13.7 ^a	218
Japanese honeysuckle (<i>Lonicera japonica</i> Thunb.)	0.0 ^b	9.3 ^a	9.6 ^a	173
Supplejack (<i>Berchemia scandens</i> (Hill) K. Koch)	2.6	0.4	4.1	44
Yellow jessamine (<i>Gelsemium sempervirens</i> L.)	3.3	1.1	1.1	45
Group totals	27.7 ^c	38.9 ^b	57.8 ^a	676
Trees				
Sweetgum (<i>Liquidambar styraciflua</i> L.)	5.9	6.7	7.4	100
Red maple (<i>Acer rubrum</i> L.)	4.8	4.4	3.3	56
Persimmon (<i>Diospyros virginiana</i> L.)	8.2 ^a	0.4 ^b	0.0 ^b	91
Southern red oak (<i>Quercus falcata</i> Michx.)	4.4 ^a	3.0 ^{ab}	1.1 ^b	29
Water oak (<i>Quercus nigra</i> L.)	2.2	2.2	1.8	20
Flowering dogwood (<i>Cornus florida</i> L.)	1.8	2.6	1.5	29
Winged elm (<i>Ulmus alata</i> Michx.)	1.8	2.2	0.7	21
White oak (<i>Quercus alba</i> L.)	1.1	1.1	1.8	15
Eastern hophornbeam (<i>Ostrya virginiana</i> (Mill.) K. Koch)	0.7	1.1	1.5	13
Group totals	38.9 ^a	28.2 ^{ab}	21.8 ^b	465
Shrubs				
American beautyberry (<i>Callicarpa americana</i> L.)	2.6	6.3	4.1	59
Sparkleberry (<i>Vaccinium</i> spp.)	2.6	2.6	0.7	23
Groundsel-tree (<i>Baccharis halimifolia</i> L.)	1.1	1.8	0.7	21
Group totals	19.6 ^a	15.6 ^{ab}	7.8 ^b	213

NOTE: Dominant competing vegetation are the species with the greatest horizontal coverage; shows only those species that averaged 1% and greater. Group totals do not sum to 100% because some subplots did not have a dominant species.

*Row means followed by different letters are significantly different by Duncan's multiple range test ($P = 0.05$).

[†]Mean square error.

diameter in this study; trees 29.5 cm in DBH and larger averaged 13, 48, and 61% of the total basal area for the 30.5-, 40.6-, and 50.8-cm maximum diameters, respectively.

Maximum diameter may also affect the amount and type of shade produced by the overstory because taller trees are retained in stands with the higher maximum diameters. Height of the canopy in even-aged stands has been shown to affect the rate of height growth of loblolly pine seedlings; a high canopy resulted in less suppression than a low canopy because of differences in high versus low shade (Brender and Barber 1956). The effects of different types of shade are well known in forest ecosystems (Oliver and Larson 1990).

Basal area

Basal area was positively correlated with the density of pine seedlings. This relationship may reflect the effects of overstory density on seed production and the suppression of competing vegetation. For example, Grano (1970) found greatest seed production at basal areas of 13.8–16.1 m²/ha in loblolly pine stands with a long history of uneven-aged silviculture. The moderate shade tolerance displayed by loblolly pine seedlings may also help explain this result. Seedlings can become established and survive in shade for several years before dying (Wahlenberg 1960). This results

because seedlings become less shade tolerant as they develop (Bormann 1956). This early shade tolerance makes loblolly pine especially adaptable to uneven-aged silviculture.

The positive effect of basal area on the initial establishment of pine seedlings is not expected to continue during their subsequent development. The conventional wisdom in the uneven-aged silviculture of loblolly pine is that basal areas over 17.2 m²/ha will prevent the successful development of submerchantable trees into the merchantable-size classes (Reynolds 1959). Of course, the 5-year results of this study are too early to confirm this threshold, but subsequent inventories will hopefully provide a more definitive pattern of understory stand dynamics.

Basal area was negatively correlated with the coverage of competing vegetation, and this simply reflects the levels of overstory competition. Tappe et al. (1993), for example, found a negative relationship between light intensity at 1.4 m in height and the basal area in natural, even-aged loblolly pine stands. Competing vegetation was apparently more responsive than pine seedlings to the lower levels of competition resulting from low basal areas. This may reflect the fact that many species of competing vegetation were already established in the understory and were able to respond rapidly after harvesting.

Site index

Site index was negatively correlated with seedling density, seedling stocking, and sapling stocking, and it was positively correlated with the coverage of competing vegetation. The effects of site index reflect the availability of limited resources, especially water and nutrients. Competing vegetation was apparently able to respond more quickly than pine regeneration and usurp the resource-rich environment created by harvesting and hardwood control, particularly on the better sites. Similar response of understory vegetation has been described for various reproduction cutting methods and overstory conditions (e.g., Blair and Brunett 1976; Nixon et al. 1981; Stransky et al. 1986; Cain 1991). The positive relationship between site quality and the intensity of competing vegetation is well known throughout the range of loblolly pine (Coile 1950; Brender and Davis 1959; Schuster 1967; Reed and Noble 1986). The higher levels of competing vegetation on the better sites apparently suppressed the establishment of pine seedlings and their subsequent development.

Implications

Results of this study show that the initial establishment of loblolly pine seedlings is best under fairly dense canopies with large diameter trees in the overstory. However, the overstories retaining 18.4 m²/ha of basal area are not expected to provide a suitable environment for the subsequent development of regeneration, but this will have to be confirmed by future inventories of the study. Loblolly pine requires abundant light for rapid growth, and regeneration grows best under full sunlight (Wahlenberg 1960). Because of its intolerance to shade after early establishment, the growth of regeneration will be somewhat suppressed under any regeneration method that retains an overstory (Chapman 1945; Wahlenberg 1948; Jackson 1959; Ferguson 1963; Murphy and Shelton 1991). Thus, uneven-aged silviculture for loblolly pine must compromise between retaining adequate overstory stocking for acceptable merchantable growth and reducing the overstory to provide acceptable environmental conditions for regeneration. A long-term goal of this study is to determine these acceptable thresholds in uneven-aged loblolly pine stands.

Initial results of this study suggest that uneven-aged pine stands will be far easier to create and sustain on the poorer sites because of less competing vegetation and the ease of securing natural regeneration. The high levels of competing vegetation observed in this study, especially on the better sites and lower basal areas, stress the importance of periodic competition control in uneven-aged loblolly pine stands. Young stands of loblolly pine will often overcome intensive competing vegetation by sustaining high rates of height growth (Chapman 1942). However, the overstory maintained in uneven-aged silviculture suppresses height growth, and this intensifies the need for periodic release of pine regeneration from competing vegetation in uneven-aged stands. Without some type of species control, applying uneven-aged silviculture to shade-intolerant loblolly pine is expected to cause a shift in species composition to its more shade-tolerant competitors. This change in composition frequently limits the successful application of uneven-aged silviculture to intolerant species (Trimble 1965; Franklin 1976; Crow and Metzger 1987).

Results of this study show that the timing of a good seed crop with harvest and control of competing vegetation is

the most important factor in securing abundant loblolly pine regeneration. However, the sparse regeneration present in some of the plots harvested in 1985 is of little immediate concern, because the short cutting cycles and frequent competition control used in uneven-aged loblolly pine stands allow many opportunities to secure acceptable regeneration. In addition, the residual stand maintained in uneven-aged silviculture moderates the short-term impacts of regeneration problems.

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- Baker, J.B. 1986. The Crossett Farm Forestry Forties after forty-one years of management. *South. J. Appl. For.* **10**: 233–236.
- Barrett, L.I. 1940. Requirements for restocking cutover loblolly and shortleaf pine stands. *South. Lumberman*, **161**(2033): 200–202.
- Blair, R.M., and Brunett, L.E. 1976. Phytosociological changes after harvest in a southern pine ecosystem. *Ecology*, **57**: 18–32.
- Bormann, F.H. 1956. Ecological implications of changes in the photosynthetic response of *Pinus taeda* seedlings during ontogeny. *Ecology*, **37**: 70–75.
- Brender, E.V., and Barber, J.C. 1956. Influence of loblolly pine overwood on advance reproduction. U.S. For. Serv. South. For. Exp. Stn. Stn. Pap. 62.
- Brender, E.V., and Davis, L.S. 1959. Influence of topography on the future composition of lower Piedmont forests. *J. For.* **57**: 33–34.
- Cain, M.D. 1987. Site-preparation techniques for establishing natural pine regeneration on small forest properties. *South. J. Appl. For.* **11**: 41–45.
- Cain, M.D. 1988. Hardwood control before harvest improves natural pine regeneration. U.S. For. Serv. South. For. Exp. Stn. Res. Pap. SO-249.
- Cain, M.D. 1991. Importance of seedyear, seedbed, and overstory for establishment of natural loblolly and shortleaf pine regeneration in southern Arkansas. U.S. For. Serv. South. For. Exp. Stn. Res. Pap. SO-268.
- Cain, M.D., and Yaussy, D.A. 1984. Can hardwoods be eradicated from pine sites? *South. J. Appl. For.* **8**: 7–12.
- Chapman, H.H. 1942. Management of loblolly pine in the pine-hardwood regions in Arkansas and Louisiana west of the Mississippi River. *Yale Univ. Sch. For. Bull.* **49**.
- Chapman, H.H. 1945. The effect of overhead shade on the survival of loblolly pine seedlings. *Ecology*, **26**: 274–282.
- Coile, T.S. 1950. Effect of soil on the development of hardwood understories in pine stands of the Piedmont Plateau. *Soil Sci. Soc. Am. Proc.* **14**: 350–352.
- Crow, T.R., and Metzger, F.T. 1987. Regeneration under selection cutting. *In* *Managing Northern Hardwoods: Proceedings of a Silvicultural Symposium*, 23–25 June 1986, Syracuse, N.Y. Edited by R.D. Nyland. State University of New York, Syracuse. pp. 81–94.
- Farrar, R.M., Jr. 1973. Southern pine site index equations. *J. For.* **71**: 696–697.
- Farrar, R.M., Jr. 1984. Density control—natural stands. *In* *Proceedings of the Symposium on the Loblolly Pine Ecosystem (West Region)*, 20–22 Mar. 1984, Jackson, Miss. Edited by B.L. Karr, J.B. Baker, and T. Monaghan. Mississippi Cooperative Extension Service, Mississippi State, Miss. pp. 129–154.
- Farrar, R.M., Jr., and Boyer, W.D. 1991. Managing longleaf pine under the selection system—promises and problems. *In* *Proceedings of the Sixth Biennial Southern Silvicultural Research*

- Conference, 30 Oct. – 1 Nov. 1990, Memphis, Tenn. *Edited by* S.S. Coleman and D.G. Neary. U.S. For. Serv. Southeast. For. Exp. Stn. Gen. Tech. Rep. SE-70. pp. 357–368.
- Ferguson, E.R. 1963. Overstory density key to pine seedling survival and growth in east Texas. *J. For.* **61**: 597–598.
- Franklin, J.F. 1976. Effects of uneven-aged management on species composition. *In Uneven-aged silviculture and management in the United States*. U.S. For. Serv. Wash. Off. Gen. Tech. Rep. WO-24. pp. 169–175.
- Grano, C.X. 1957. Indices to potential cone production of loblolly pine. *J. For.* **55**: 890–891.
- Grano, C.X. 1970. Seed yields in loblolly-shortleaf pine selection stands. U.S. For. Serv. South. For. Exp. Stn. Res. Note SO-109.
- Grano, C.X. 1971. Conditioning loessial soils for natural loblolly and shortleaf pine seeding. U.S. For. Serv. South. For. Exp. Stn. Res. Note SO-116.
- Jackson, L.W.R. 1959. Relation of pine forest overstory opening diameter to growth of pine reproduction. *Ecology*, **40**: 478–480.
- Marquis, D.A. 1976. Application of uneven-aged silviculture on public and private lands. *In Uneven-Aged Silviculture and Management in the United States*, 15–17 July 1975, Morgantown, W.V., and 19–21 Oct. 1976, Redding, Calif. U.S. For. Serv. Wash. Off. Gen. Tech. Rep. WO-24. pp. 25–63.
- Murphy, P.A., and Farrar, R.M., Jr. 1982. Calculation of theoretical uneven-aged stand structures with the exponential distribution. *For. Sci.* **28**: 105–109.
- Murphy, P.A., and Shelton, M.G. 1991. Stand development five years after cutting to different diameter limits in loblolly-shortleaf pine stands. *In Proceedings of the Sixth Biennial Southern Silvicultural Research Conference*, 30 Oct. – 1 Nov. 1990, Memphis, Tenn. *Edited by* S.S. Coleman and D.G. Neary. U.S. For. Serv. Southeast. For. Exp. Stn. Gen. Tech. Rep. SE-70. pp. 384–393.
- Murphy, P.A., Baker, J.B., and Lawson, E.R. 1991. Selection management of shortleaf pine in the Ouachita Mountains. *South. J. Appl. For.* **15**: 61–67.
- Nixon, E.S., Willett, R.L., Butts, M.L., and Burandt, C.L., Jr. 1981. Early seral development following partial clearcutting in east Texas. *Texas J. Sci.* **33**: 25–32.
- Oliver, C.D., and Larson, B.C. 1990. *Forest stand dynamics*. McGraw-Hill, New York.
- Reed, D.P., and Noble, R.E. 1986. Understory biomass production in central Louisiana. *Proc. La. Acad. Sci.* **49**: 15–22.
- Reynolds, R.R. 1959. Eighteen years of selection management on the Crossett Experimental Forest. *Tech. Bull. U.S. Dep. Agric.* No. 1206.
- Reynolds, R.R. 1969. Twenty-nine years of selection management on the Crossett Experimental Forest. U.S. For. Serv. South. For. Exp. Stn. Res. Pap. SO-40.
- Reynolds, R.R., Baker, J.B., and Ku, T.T. 1984. Four decades of selection management on the Crossett Farm Forestry Forties. *Arkansas Agric. Exp. Stn. Bull.* 872.
- SAS Institute Inc. 1988. *SAS/ETS user's guide*, version 6. 1st ed. SAS Institute Inc., Cary, N.C.
- Schuster J.L. 1967. The relation of understory vegetation to cutting treatments and habitat factors in an east Texas pine-hardwood type. *Southwest. Nat.* **12**: 339–364.
- Smith, D.M. 1986. *The practice of silviculture*. 8th ed. John Wiley & Sons, New York.
- Steel, R.G.D., and Torrie, J.H. 1980. *Principles and procedures of statistics: a biometrical approach*. 2nd ed. McGraw-Hill, New York.
- Stransky, J.J., Huntley, J.C., and Risner, W. 1986. Net community production dynamics in the herb-shrub stratum of a loblolly pine – hardwood forest: effects of clearcutting and site preparation. U.S. For. Serv. South. For. Exp. Stn. Gen. Tech. Rep. SO-61.
- Switzer, G.L., Shelton, M.G., and Nelson, L.E. 1979. Successional development of the forest floor and soil surface on upland sites of the East Gulf Coastal Plain. *Ecology*, **60**: 1162–1171.
- Tappe, P.A., Shelton, M.G., and Wigley, T.B. 1993. Overstory-understory relationships in natural loblolly pine – hardwood stands: implications for wildlife habitat. *In Proceedings of the Seventh Biennial Southern Silvicultural Research Conference*, 1992, 17–19 Nov. 1993, Mobile, Ala. *Edited by* J.C. Brissette. U.S. For. Serv. South. For. Exp. Stn. Gen. Tech. Rep. SO-93. pp. 613–619.
- Trimble, G.R., Jr. 1965. Species composition changes under individual tree selection cutting in cove hardwoods. U.S. For. Serv. Northeast. For. Exp. Stn. Res. Note NE-30.
- Trousdell, K.B. 1954. Favorable seedbed conditions for loblolly pine disappear 3 years after logging. *J. For.* **52**: 174–176.
- Wahlenberg, W.G. 1948. Effect of forest shade and openings on loblolly pine seedlings. *J. For.* **46**: 832–834.
- Wahlenberg, W.G. 1960. *Loblolly pine*. School of Forestry, Duke University, Durham, N.C.
- Williston, H.L. 1978. Uneven-aged management in the loblolly-shortleaf pine type. *South. J. Appl. For.* **2**(3): 78–82.

Appendix

TABLE A1. Means for the density and stocking of pine regeneration in the plots treated in 1983

Treatment class*			No. of plots	Seedlings		Saplings	
Site index (m)	Basal area (m ² /ha)	Max. DBH (cm)		Density (1000/ha)	Stocking (%)	Density (no./ha)	Stocking (%)
Class means							
22.9	9.2	30.5	3	10.5	73	576	67
22.9	9.2	40.6	2	29.1	100	370	50
22.9	9.2	50.8	1	62.2	90	25	10
22.9	13.8	30.5	0	—	—	—	—
22.9	13.8	40.6	3	13.5	80	601	67
22.9	13.8	50.8	1	20.7	90	839	60
22.9	18.4	30.5	0	—	—	—	—
22.9	18.4	40.6	1	14.3	60	1186	90
22.9	18.4	50.8	1	118.1	90	494	80
26.0	9.2	30.5	0	—	—	—	—
26.0	9.2	40.6	2	35.2	85	1321	75
26.0	9.2	50.8	1	7.9	90	741	90
26.0	13.8	30.5	3	9.6	67	659	43
26.0	13.8	40.6	1	63.7	100	346	50
26.0	13.8	50.8	1	20.3	90	49	20
26.0	18.4	30.5	1	12.6	50	173	40
26.0	18.4	40.6	1	23.2	100	25	10
26.0	18.4	50.8	2	15.9	85	630	65
29.0	9.2	30.5	0	—	—	—	—
29.0	9.2	40.6	0	—	—	—	—
29.0	9.2	50.8	0	—	—	—	—
29.0	13.8	30.5	0	—	—	—	—
29.0	13.8	40.6	1	9.6	90	1334	100
29.0	13.8	50.8	0	—	—	—	—
29.0	18.4	30.5	1	1.0	20	198	30
29.0	18.4	40.6	3	8.2	70	329	40
29.0	18.4	50.8	0	—	—	—	—
Treatment means							
22.9	—	—	12	28.8	82	568	62
26.0	—	—	12	21.6	81	601	52
29.0	—	—	5	7.1	64	504	50
—	9.2	—	9	25.6	86	653	61
—	13.8	—	10	18.4	81	635	56
—	18.4	—	10	22.6	70	432	50
—	—	30.5	8	9.2	61	509	50
—	—	40.6	14	21.8	84	647	59
—	—	50.8	7	37.3	89	487	56
Overall mean							
—	—	—	29	22.1	79	571	56

*Site index (m) classes and their ranges are 22.9 (17.1–24.6), 26.0 (24.7–27.4), and 29.0 (27.5–29.6). Basal area (m²/ha) classes and their ranges are 9.2 (7.3–11.5), 13.8 (11.6–16.0), and 18.2 (16.1–20.2). Maximum diameter (cm) classes and their ranges are 30.5 (29.5–35.6), 40.6 (35.7–45.7), and 50.8 (45.8–55.9).

TABLE A2. Means for the density and stocking of pine regeneration and coverage of competing vegetation in plots treated in 1985

Treatment class*				Seedlings		Saplings		Competing vegetation		
Site index (m)	Basal area (m ² /ha)	Max. DBH (cm)	No. of plots	Density (1000/ha)	Stocking (%)	Density (no./ha)	Stocking (%)	Vines (%)	Hardwoods (%)	Total (%)
Class means										
22.9	9.2	30.5	2	4.2	40	50	10	26	28	75
22.9	9.2	40.6	1	2.7	40	25	10	14	30	67
22.9	9.2	50.8	3	2.6	50	856	57	27	15	60
22.9	13.8	30.5	3	0.7	17	66	23	17	19	81
22.9	13.8	40.6	2	11.0	85	1025	50	15	17	50
22.9	13.8	50.8	2	20.0	75	161	40	11	12	72
22.9	18.4	30.5	3	4.3	37	124	40	14	9	60
22.9	18.4	40.6	3	13.6	47	25	10	20	32	72
22.9	18.4	50.8	2	29.0	90	124	35	5	16	46
26.0	9.2	30.5	2	1.1	30	25	10	41	24	89
26.0	9.2	40.6	2	4.1	50	0	0	38	17	81
26.0	9.2	50.8	5	4.4	56	10	4	43	20	85
26.0	13.8	30.5	3	1.0	27	8	3	35	28	79
26.0	13.8	40.6	2	2.2	40	12	5	43	24	85
26.0	13.8	50.8	3	5.6	43	0	0	50	18	90
26.0	18.4	30.5	3	7.2	43	4.9	13	14	14	44
26.0	18.4	40.6	2	0.1	5	0	0	35	20	75
26.0	18.4	50.8	1	1.2	50	0	0	62	31	88
29.0	9.2	30.5	0	—	—	—	—	—	—	—
29.0	9.2	40.6	1	6.9	60	0	0	55	16	88
29.0	9.2	50.8	0	—	—	—	—	—	—	—
29.0	13.8	30.5	0	—	—	—	—	—	—	—
29.0	13.8	40.6	2	12.2	60	0	0	43	32	94
29.0	13.8	50.8	1	4.7	60	0	0	58	28	95
29.0	18.4	30.5	0	—	—	—	—	—	—	—
29.0	18.4	40.6	1	15.8	50	0	0	57	36	92
29.0	18.4	50.8	3	13.1	63	0	0	50	30	94
Treatment means										
22.9	—	—	21	9.3	51	283	32	17	19	65
26.0	—	—	23	3.4	40	13	4	39	21	79
29.0	—	—	8	11.4	60	0	0	51	29	93
—	9.2	—	16	3.6	48	174	15	36	20	78
—	13.8	—	18	6.5	47	145	15	33	22	80
—	18.4	—	18	10.5	48	47	14	27	22	68
—	—	30.5	16	3.1	32	56	18	24	20	70
—	—	40.6	16	7.8	48	136	9	33	25	77
—	—	50.8	20	9.5	60	159	17	37	20	79
Overall mean										
—	—	—	52	7.0	48	120	15	32	21	76

*Site index (m) classes and their ranges are 22.9 (17.1–24.6), 26.0 (24.7–27.4), and 29.0 (27.5–29.6). Basal area (m²/ha) classes and their ranges are 9.2 (7.3–11.5), 13.8 (11.6–16.0), and 18.2 (16.1–20.2). Maximum diameter (cm) classes and their ranges are 30.5 (29.5–35.6), 40.6 (35.7–45.7), and 50.8 (45.8–55.9).