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Effects of Seed Production, Seedbed Condition, and Overstory Basal Area on the Establishment of Shortleaf Pine Seedlings in the Ouachita Mountains

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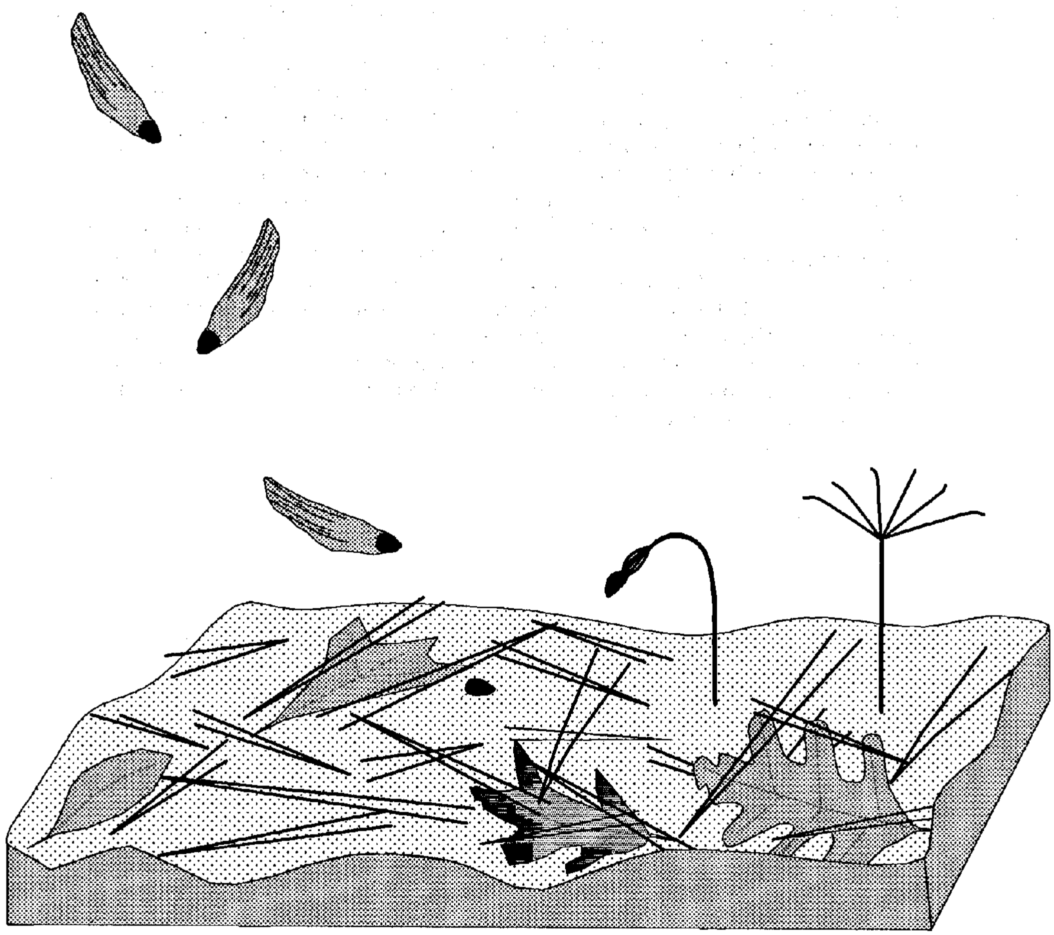

SUMMARY

First-year seedling establishment was determined across an array of seedbed conditions and overstory basal areas in stands of shortleaf pine (*Pinus echinata* Mill.) and hardwoods following the initial harvest implementing uneven-aged silviculture. Seedbed treatments were mineral soil, partial litter, undisturbed litter, and enhanced litter, and overstory treatments consisted of three hardwood basal areas (0, 15, and 30 ft^2/acre) retained with 60 ft^2/acre of pine. The seedbed treatments were established over a 3-year period, which permitted evaluation of the seedlings resulting from a seed-crop failure, a below average seed crop, and an above-average seed crop. Seedling density was positively related to the level of seed production and negatively related to litter depth and overstory basal area. However, some seedlings became established even in the deepest litter, indicating that the barrier presented by litter is not complete. Results indicate the importance of regulating overstory basal area in the application of uneven-aged silviculture in stands featuring shortleaf pine. When total overstory basal area was within the guidelines for uneven-aged stands (45 to 75 ft^2/acre), seedbeds of mineral soil and partial and undisturbed litter resulted in ample regeneration even with seed crops that were slightly below regional averages. Composition of the overstory basal area apparently did not strongly affect initial seedling establishment. However, results of this study apply only to initial seedling establishment in areas having sparse ground vegetation and should not be extended to longer time periods or other conditions.

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INTRODUCTION

Natural regeneration is a viable alternative for establishing shortleaf pine (*Pinus echinata* Mill.) stands in the Ouachita Mountains (Baker 1992, Lawson 1986), and it may be the best technique for landowners who have limited capital (Willett and Baker 1991) and who desire the favorable visual properties of partial cutting techniques (Stignani 1986). Successful natural regeneration of shortleaf pine depends on obtaining acceptable levels of seeds and limited resources—such as light, water, and nutrients—and having suitable seedbed conditions. Each of these factors is under a different degree of silvicultural control. For example, seedbed conditions can be readily modified by site preparation, such as controlled burning and mechanical treatments. To some degree, seed production can be enhanced by retaining additional seed trees, but production principally varies in response to uncontrollable fluctuations in weather and pest populations. The availability of light and water is controlled by regulating the stocking of the merchantable stand through harvesting and by controlling understory composition through vegetation management, but uncontrollable variation in moisture can also strongly affect seedling survival during critical stages of development (Larson and Smith 1969, Trousdell and Wenger 1963). In addition, all of the determinants of natural regeneration interact, and deficits in one may be compensated for by surpluses in another (Becton 1936, Grano 1949, Trousdell 1950). However, unacceptable conditions in a single determinant, such as a poor seed crop or a severe drought, may result in a regeneration failure regardless of the suitability of the other factors.

Investigations of the seedbed requirements of shortleaf pine exist (Ferguson 1958, Haney 1962, Wood 1939, Yocom and Lawson 1977), but most of these studies have contrasted only disturbed and undisturbed seedbeds or have evaluated only a single seed crop. In this study, three of the determinants of natural regeneration of shortleaf pine—seed production, seedbed condition, and overstory competition—were evaluated. This research utilized an ongoing study designed to test the limits for hardwood retention within an uneven-aged silvicultural system that features shortleaf pine as the dominant species.

METHODS

Study Site

The study was located in the Winona Ranger District of the Ouachita National Forest in Perry County, AR. Plots were oriented along an east-west ridge, which is typical of the physiography of the Ouachita Mountains. Elevations ranged from 640 to 790 ft above sea level, a 150-ft difference in relief. Blocks were located on the following slope positions: lower, middle, and upper north slope and the upper south slope. Slopes ranged from 8 to 21 percent, and aspects ranged from north to northwest on the north-slope positions and from southeast to southwest on the south-slope position.

Soils of the study area are mapped as the Carnasaw and Pirum series, both Typic Hapludults. These are well-drained, moderately deep soils that developed in colluvium and residuum weathered from sandstone and shale. Natural fertility and organic matter are low, and the soils are strongly acidic.

Site index for shortleaf pine averaged 57 ft at 50 years and ranged from 53 to 64 ft, which is typical of upland sites in the Ouachita Mountains (Graney 1992). The lower north slope was slightly higher in site index than the other three slope positions (61 versus 56 ft). Site index averaged 53 ft at 50 years for white oak (*Quercus alba* L.) and 54 ft for black oak (*Q. velutina* Lam.).

Vegetation in the study area was typical of much of the forested landscape in the Ouachita Mountains, where upland forests are dominated by shortleaf pine and mixed oaks (Guldin and others 1994). Before treatment implementation, overstory basal area (trees

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≥3.6 inches in d.b.h.) in this mature, second-growth shortleaf pine-oak stand averaged 90 ft^2/acre for shortleaf pine and 32 ft^2/acre for hardwoods. Oaks accounted for 84 percent of the total hardwood basal area. White oak was the most prevalent hardwood, with lesser amounts of post oak (*Q. stellata* Wang.), black oak, blackjack oak (*Q. marilandica* Muench.), and southern red oak (*Q. falcata* Michx.). Overstory pines and oaks in the initial stand ranged in age from 30 to over 110 years (Shelton and Murphy 1991). However, most of the pines were 50 to 80 years old, and the oaks were 40 to 70 years old. The scarcity of young trees in the overstory indicated that regeneration and its subsequent development in both the pines and oaks had been limited for 30 to 40 years of stand development before study implementation.

The precipitation and temperature that occurred during the study were fairly typical of the normal conditions for this locale. Annual precipitation and temperature average 52 inches and 61.6 °F, respectively, at the nearby Alum Fork Weather Station (U.S. Department of Commerce, NOAA 1992). Precipitation occurring from October 1989 through September 1990 totaled 59.3 inches, and temperatures averaged 63.6 °F. Comparable values from October 1990 through September 1991 were 60.5 inches for precipitation and 61.6 °F for temperature. Precipitation that occurred during the period of germination was above normal for the 1989 seed crop and below normal for the 1991 seed crop (fig. 1). Monthly precipitation was about one-third below normal during June for the 1989 seed crop and during August for the 1991 seed crop.

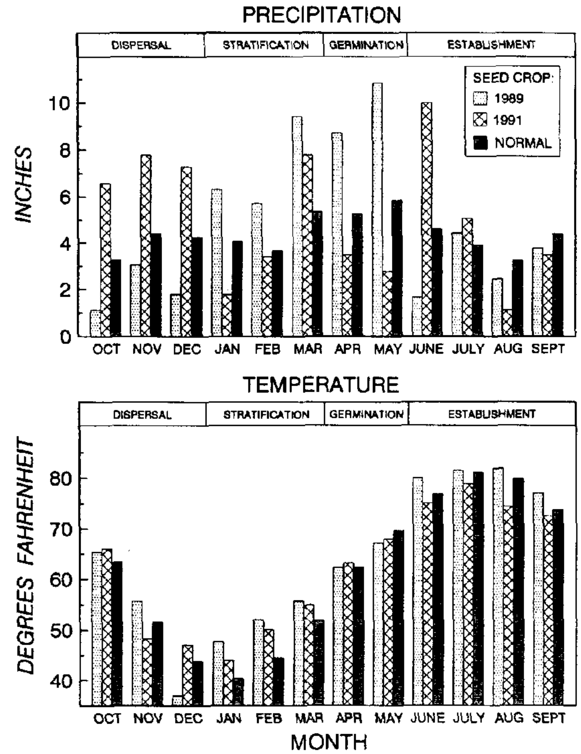

Figure 1.— *Precipitation and temperature occurring during the dispersal, stratification, germination, and establishment of the 1989 and 1991 seed crops compared to normal values. Data are for the nearby Alum Fork Weather Station (U.S. Department of Commerce, NOAA 1989–92).*

Study Design and Treatments

Overstory Treatments.—This seedbed study was superimposed within an ongoing study testing the limits for hardwood retention within an uneven-aged silvicultural system featuring shortleaf pine as the dominant species (Shelton and Baker 1992, Shelton and Murphy 1991). Twelve square, 1.6-acre plots were installed in 1988, and each consisted of an interior 0.5-acre plot that was surrounded by a 1.1-acre isolation strip (58.2 ft wide). The interior plot and isolation strip were treated in an identical manner. The basal area of overstory pines (≥3.6 inches in d.b.h.) was reduced to 60 ft^2/acre in all plots. Hardwood treatments were basal areas of 0, 15, and 30 ft^2/acre. Overstory treatments were assigned in a randomized, complete block design with four replications for each treatment.

The pine harvest was implemented using the basal area-maximum diameter-quotient method of single-tree selection (Farrar 1984). Targets were 60 ft^2/acre for basal area, 18 inches for maximum diameter, and a quotient of 1.2 for 1-inch diameter classes. Targets for maximum diameter and quotient were followed as closely as feasible because the stand lacked a balanced reverse-J structure. Hardwood retention favored the higher quality white and red oaks; these were typically the largest hardwoods in the study area.

Plots were harvested from December 1988 through early March 1989 using mules to skid logs to landings. Because no local markets existed for hardwoods, all hardwoods ≥1 inch in d.b.h. that were not specifically designated for retention were killed with stem-injected triclopyr during April 1989. Herbicide treatments were applied by contract crews following label directions; research crews did some followup injection work.

Seedbed Treatments.—Along the interior boundary of the isolation strip of each 1.6-acre plot, three 0.01-acre areas were selected where the existing forest floor had not been disturbed by logging. Areas were randomly assigned for establishment of seedbed treatments in 1989, 1990, and 1991.

During the early summer of the year designated for establishment, the ground vegetation was controlled within the area by a foliar application of glyphosate (2 percent in an aqueous solution) to the point of saturation. This treatment was done to ensure that initial levels of ground vegetation were equal in all overstory hardwood treatments and in all years. During the late summer, four contiguous, square subplots (10 ft on a side) were established and randomly assigned a seedbed treatment. The location of each subplot was permanently marked for identification. The following seedbed conditions were then created using hand tools:

(1) **mineral soil**—All organic materials were removed, which exposed the mineral soil surface. This treatment simulated areas where the forest floor had been scraped away by logging traffic and/or mechanical site preparation.

(2) **partial litter**—The surface litter, consisting principally of foliage deposited during the previous year, was removed, which exposed the older and more highly decomposed material. This treatment represented areas where litter had been disturbed but not completely removed during logging and/or site preparation.

(3) **undisturbed litter**—The existing forest floor was not disturbed.

(4) **enhanced litter**—The existing forest floor was enriched by the litter removed in seedbed treatments (1) and (2). This condition represented the piling of litter along the edges of skid trails, where the forest floor had been scraped from the center and displaced along the edges.

Twelve of these seedbed-treatment areas were established each year over a 3-year period, resulting in a total of 36 seedbed-treatment areas or 144 individual seedbed subplots. Subplots installed in 1989 and 1990 were prepared for the 1991 seed crop by treatment with a second application of glyphosate during the early summer of 1991 to control the ground vegetation that had developed since installation. The subplots were inspected later that summer to ensure that all existing pine seedlings had been killed.

Measurements

The forest floor material present before establishing seedbed treatments was determined by collecting three 0.9-ft^2 samples from just outside each seedbed-treatment area (a total of 36 samples per year). The relatively fresh litter that was principally deposited during the previous year (the litter layer) was collected separately from the older and more highly decomposed litter existing below (the fermentation layer). Very little humus material (dark, amorphous organic matter) was observed in these forest floors because of the rapid incorporation of organic material within the mineral soil; this condition was also noted by Shelton and Lawson (1994) elsewhere in the Ouachita Mountains. The observed boundaries between forest floor layers within these small sampling frames were also complied with when implementing the seedbed treatments. Samples were weighed after drying to a constant weight at 167 °F. Litter depth was also measured on each side of the sampling frames.

In 1989, 1990, and 1991, pine seed production was monitored from October through February of the next year in four 0.9-ft^2 seed traps (Cain and Shelton 1993) in each 0.5-acre plot. Seed traps were located about 30 ft from the plot center in a square pattern and were about 100 ft from the outer boundary of the 1.6-acre plot. Collections were made during the middle and the end of the October-to-February period. Viability was determined by splitting seeds and inspecting the contents (Bonner 1974). Seeds with full, firm, undamaged, and healthy tissue were judged to be potentially viable and were tallied as sound.

During the fall of the year following establishment, pine seedlings were counted on a milacre plot (3.72 ft in radius) centered in each of the seedbed subplots. Heights of the two tallest shortleaf pine seedlings, if present, were measured. Coverage of understory vegetation was ocularly estimated on milacre plots in 1990 and 1992 for the following groups: grasses, herbs, vines, shrubs, and hardwoods and for total coverage. Coverage was not evaluated in 1991. Pine seedlings were counted and measured for all installations in 1992.

The basal areas of pines and hardwoods for each of the 36 seedbed-treatment areas were determined using a 10-basal area factor prism. Litter depth was again evaluated in 1992 by taking 20 measurements across each of the 144 milacre plots where seedling counts were made. The seedbed treatments were 1 to 3 years old at this time.

Data Analysis

Analysis of variance for a split-plot, randomized complete block design was used to compare the effects of the overstory hardwood treatments and the seedbed treatments on the number of 1-year-old seedlings resulting from each seed crop. Overstory hardwood treatments constituted the main effects, and seedbed treatments were the subeffects. Differences among treatment means were isolated by the Ryan-Einot-Gabriel-Welsch Multiple Range Test (P=0.05). This test is one of the most powerful step-down, multiple-range tests available, and it controls the experiment-wise error rate (SAS Institute 1989).

A modeling approach was employed to combine the effects of all independent variables. This approach allowed greater flexibility in accounting for yearly variation in seed production and local variation in forest floor conditions and overstory basal areas. The concept of a potential and modifier function, which has widespread application in growth modeling, was employed to predict the number of 1-year-old seedlings resulting from a seed crop as follows:

$$Regeneration = Potential \times Modifier \quad (1)$$

Seed production represents the potential for obtaining regeneration in equation (1) that is modified by existing environmental conditions. The logistic function, which is constrained between the interval 0 to 1, was used as a modifier function. Several potential functions were examined, but none was found to be better than a fixed proportion of the sound-seed production. This conclusion may reflect the fact that evaluated seed crops had a fairly narrow range. For example, the best seed crop evaluated averaged 180,000 sound seeds per acre, whereas over a million seeds may be produced during bumper years (Shelton and Wittwer, in press). The resulting function was:

$$R = b_0 S / \{1 + \exp\,(b_1 + b_2 D + b_3 P + b_4 H)\} \quad (2)$$

where R is the number of 1-year-old seedlings per acre, S is the number of sound seeds per acre the preceding year, D is the depth of the litter in inches just before seed dispersal, P is the pine basal area in square feet per acre, H is the hardwood basal area in square feet per acre, and b_i's are coefficients to be estimated.

Data for fitting equation (2) were the seedling counts made each year following the annual installation of the seedbed treatments. Data also included the 1992 seedling counts of seedbed treatments installed in 1989 and 1990, when seedbed conditions had existed for 1 and 2 years, respectively, before dispersal of the 1991 seed crop. Litter depths for these treatments were evaluated in 1992 (the year following the 1991 seed crop) but were adjusted for a 1-year change in depth using equations that express the change in depth through time (equations (7) and (8) in the results and discussion section). Seed production was the mean of the four seedtraps located in each 0.5-acre plot, and pine and hardwood basal areas were those determined by prism for the specific seedbed-treatment area. Coefficients were calculated by nonlinear least squares regression using the SAS procedure MODEL (SAS Institute 1988). Variables were eliminated from the full model if their coefficient did not significantly differ from zero at a probability level of ≤0.05. Transforming the independent variables improved the fit index of equation (2). However, determining specific values for exponents was compromised by convergence problems in the regression procedure. Thus, square and square root transformations of independent variables were tested. If the fit index was improved, the transformation was retained; otherwise, it was dropped.

The following function was used for fitting the relationship between other response variables, such as seedling height and coverage of competing vegetation, and litter depth and overstory basal areas:

$$Y = \exp\,(b_0 + b_1 D + b_2 P + b_3 H) \quad (3)$$

where Y is the specific response variable, and the other symbols and fitting procedures are as previously described.

RESULTS AND DISCUSSION

Independent Variables

Annual seed production averaged 180,000, 3,000, and 74,000 sound seeds per acre for the 1989, 1990, and 1991 seed crops, respectively (table 1). The overall average was 86,000 sound seeds per acre. No significant differences were observed among the overstory hardwood treatments. Shelton and Wittwer (in press) reported that the long-term annual seed production for shortleaf pine within the Ouachita and Ozark Mountains averaged about 100,000 sound seeds per acre. Thus, the 1989 seed crop was above average, and the 1991 seed crop was slightly below average. The seed-crop failure in 1990 was a fairly common occurrence in shortleaf pine stands; about one-half of the seed crops within the region over a 9-year period were classified as failures (Shelton and Wittwer, in press).

The undisturbed forest floor of this stand weighed 15,000 lb/acre and had a mean depth of 0.9 inch. These values are typical of pine-hardwood stands within the Ouachita Mountains, for which Shelton and Lawson (1994) reported a regional mean weight of 17,000 lb/acre and a depth of 1.2 inches. The slightly higher regional means may reflect the difference in sampling times of the two studies; Shelton and Lawson sampled after the fall litter pulse, while forest floors were sampled before the pulse in this study. About one-third of the forest floor weight was in the litter layer or the relatively fresh material in the upper portion of the forest floor. A weak but significant negative relationship occurred between the undisturbed forest floor weight and the hardwood basal area (correlation coefficient=–0.37; $P>F$=0.02). A similar relationship reported by Shelton and Lawson (1994) was attributed to the higher decomposition rates of hardwood foliage when compared to pine foliage.

Establishing the seedbed treatments redistributed the original forest floor from one treatment to another, but mean values were not affected because all of the material was used. Litter weight for seedbed treatments ranged from 0 to nearly 60,000 lb/acre, and depth ranged from 0 to 3.7 inches (table 2). Establishing the seedbed treatments greatly increased the variability of litter weights and depths, and coefficients of

Table 1.— *Annual production of shortleaf pine seeds by overstory hardwood treatment after implementing uneven-aged silviculture in shortleaf pine-hardwood stands*

Seed crop year	Hardwood basal area* 0 ft²/acre	15 ft²/acre	30 ft²/acre	Mean square error†	*P>F*
	------ *Thousands of sound seeds per acre* ------				
1989	197	144	200	6.78E9	0.58
1990	3.1	3.1	3.1	3.48E7	1.00
1991	75.1	75.1	70.9	7.78E8	0.97

*No significant differences occurred among row means according to the Ryan-Einot-Gabriel-Welsch Multiple Range Test (P=0.05).

†In this table and elsewhere in this paper, values for mean square error are expressed in exponential notation; for example, 1.23E4 = 1.23×10^4 = 12,300.

variation were increased by four times when compared to the forest floors before disturbance. The mean weights of the seedbed treatments after establishment were 0, 9,700, 15,300, and 36,300 lb/acre for the mineral soil, partial litter, undisturbed litter, and enhanced litter treatments, respectively. Means for depth of the four seedbed treatments were 0, 0.6, 0.9, and 2.1 inches, respectively.

Overstory basal areas in the vicinity of the seedbed-treatment areas averaged 62 and 25 ft²/acre for pines and hardwoods, respectively (table 2). The mean basal area for pines was very close to the post-harvest target of 60 ft²/acre in the residual stand, but the mean basal area for hardwoods was higher than the treatment mean of 15 ft²/acre (that is, the mean of 0, 15, and 30 ft²/acre). The reason for this discrepancy is not known. It may have been due to locating the seedbed-treatment areas in the undisturbed portion of the stand; such areas may have had a higher hardwood component, which might have resulted in less logging disturbance. The wide range in basal areas of both pines and hardwoods indicates the high spatial variability that occurs in stands managed under guidelines for uneven-aged stands; canopy gaps of 0.1 to 0.2 acre in size can occur when such guidelines are implemented. There was no significant correlation between the basal areas of pines and hardwoods.

Seedling Density of Treatments

The density of seedlings resulting from a seed crop was affected by the size of the seed crop and the seedbed conditions when seeds were dispersed (fig. 2). The above-average 1989 seed crop resulted in an average of 3,040 seedlings per acre across all seedbed treatments, and the below-average 1991 seed crop resulted in an average of 790 seedlings per acre for the 0-year-old seedbed treatments. These values provided a mean seedling-to-seed ratio of 1.7 percent for the 1989 seed crop and 1.1 percent for the 1991 seed crop. The seed-crop failure that occurred in 1990 resulted in no seedlings. This result was expected because the carry over of pine seeds from one year to the next has been observed to be virtually nil (Barnett and McGilvray 1991, Little and Somes 1959). The mineral-soil seedbed yielded the greatest number of seedlings, generally followed by the partial-litter seedbed. Differences between the undisturbed and enhanced litter treatments

Table 2.— *Seedbed conditions and overstory basal areas existing after treatment implementation*

Property	Mean value	Standard deviation	Range Minimum	Maximum
	---------- *Seedbed conditions* ----------			
Litter weight (lb/acre)	15,320	14,130	0	59,990
Litter depth (inches)	0.87	0.82	0	3.70
	---------- *Overstory basal area** ----------			
Pine (ft²/acre)	62	24	20	120
Hardwood (ft²/acre)	25	23	0	80

*Determined by prism at each seedbed-treatment area.

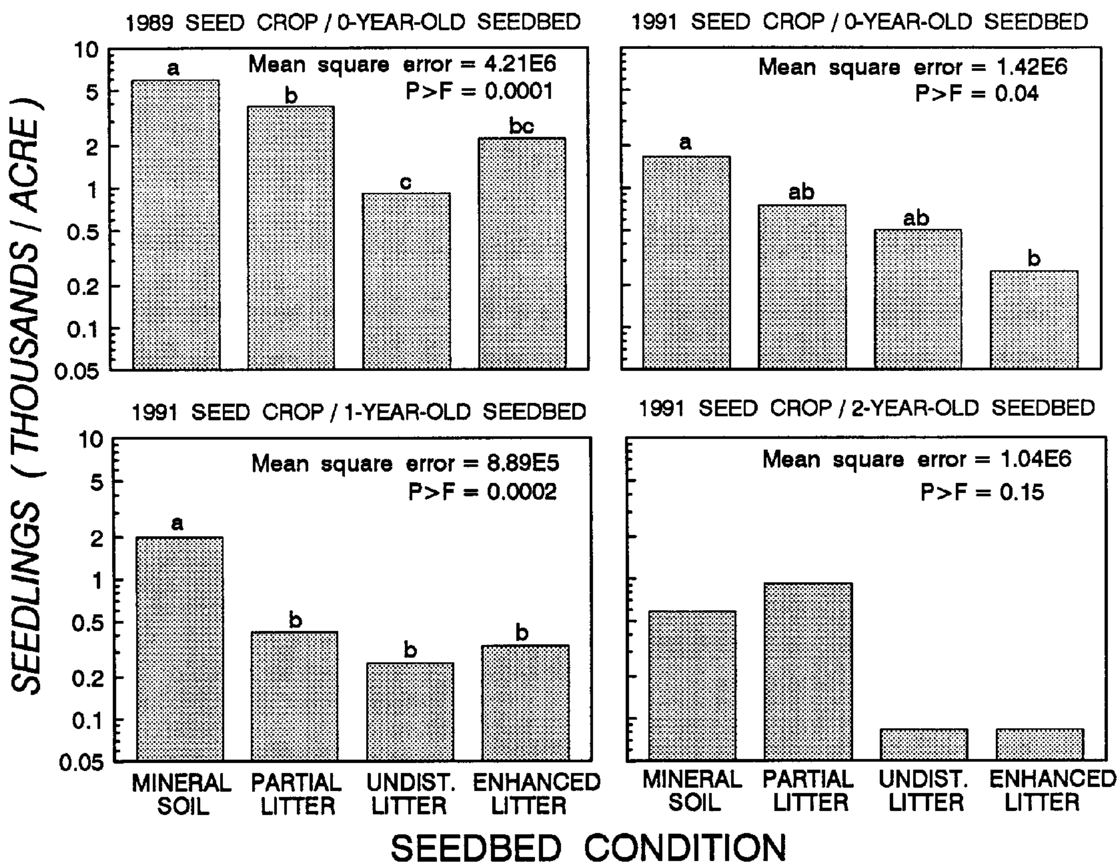

Figure 2.—*Density of 1-year-old shortleaf pine seedlings by seedbed treatment, seed crop, and seedbed age (time between treatment establishment and dispersal of the seed crop). Note that a logarithmic scale is used for seedling density. Bars with different letters are significantly different according to the Ryan-Einot-Gabriel-Welsch Multiple Range Test* (P=*0.05).*

were not significant for any seed crop or seedbed age. The favorable effects of a mineral-soil seedbed diminished through time; thus, the 2-year-old mineral-soil seedbed did not significantly differ from the other seedbed treatments for the 1991 seed crop. This occurs because the overstory trees had continued to produce litter, which eventually covered the exposed mineral soil.

The effects of overstory hardwood treatments are shown in table 3. Means for overstory treatments can be compared across all seedbed treatments because no significant interactions were observed between seedbed treatments and overstory hardwood treatments. For each seed crop and seedbed age, the seedling density was consistently greatest in the overstory treatment with no hardwoods, but differences were significant for only the 1991 seed crop and the 1-year-old seedbed. The lack of consistent significant differences reflects, to some degree, local variation in the basal area of overstory trees in the vicinity of the seedbed-treatment areas. This observation suggests that a modeling approach using the basal areas determined at each seedbed-treatment area would be more sensitive to this local variation.

Modeling Seedling Density

The following equation combines the effects of sound seed production (S in number per acre), litter depth (D in inches), and basal area of pines and hardwoods (P and H, respectively, in square feet per acre) on the density of 1-year-old seedlings (R in number per acre):

$$R = 0.1182S \,/\, \{1 + \exp\,(-3.151 + 1.074D^{0.5} + 0.5870P^{0.5} + 0.1364H^{0.5})\} \qquad (4)$$

where number of observations was 240, root mean square error was 1,183, fit index was 0.41, and mean R was 1,000 seedlings per acre. The coefficients of all independent variables were significant at the 0.05

probability level, and the model explained 41 percent of the variation in the resulting regeneration.

Seedling densities calculated from equation (4) are plotted in figure 3 for a seed crop of 100,000 sound seeds per acre and a reasonable range in values for litter depth and pine and hardwood basal areas. A single level of seed production is adequate for demonstrating trends in equation (4) because seedling density varies directly with the number of sound seeds; that is, doubling seed production doubles the number of seedlings and halving seed production halves the number of seedlings. This observation may have been an artifact of the relatively narrow range of seed production sampled over the 3-year monitoring period. However, some support for this finding exists in data reported by Cain (1991) for five pine seed crops and the resulting seedlings in uneven-aged pine stands in southern Arkansas. Calculated values for the seedling-to-seed ratios of a mineral-soil seedbed, coupled with hardwood control, were fairly narrow (ranging from 5 to 7 percent) for all seed crops except for a bumper seed crop of over a million sound seeds per acre, when the seedling-to-seed ratio was 20 percent.

Seedling density decreased with increasing litter depth (fig. 3). Grano (1949) reported a similar decline in seedling density with litter depth in uneven-aged loblolly-shortleaf pine stands in southern Arkansas, and Shelton (1995) described a similar relationship between the density of loblolly pine seedlings and litter weight. In addition, the decline in seedling density with increasing litter has commonly been observed for many species with small, wind-disseminated seeds. Seedling density decreases because: (1) litter modifies environmental conditions while seeds are dormant and germinating and as emerging seedlings become established, (2) litter acts as a physical barrier that interferes with development of the radicle and/or shoot, (3) litter teems with life, some of which may be unfavorable to dormant and germinating seeds, and (4) litter has distinctive chemical properties, some of which may be unfavorable to germination and seedling establishment (Shelton 1995).

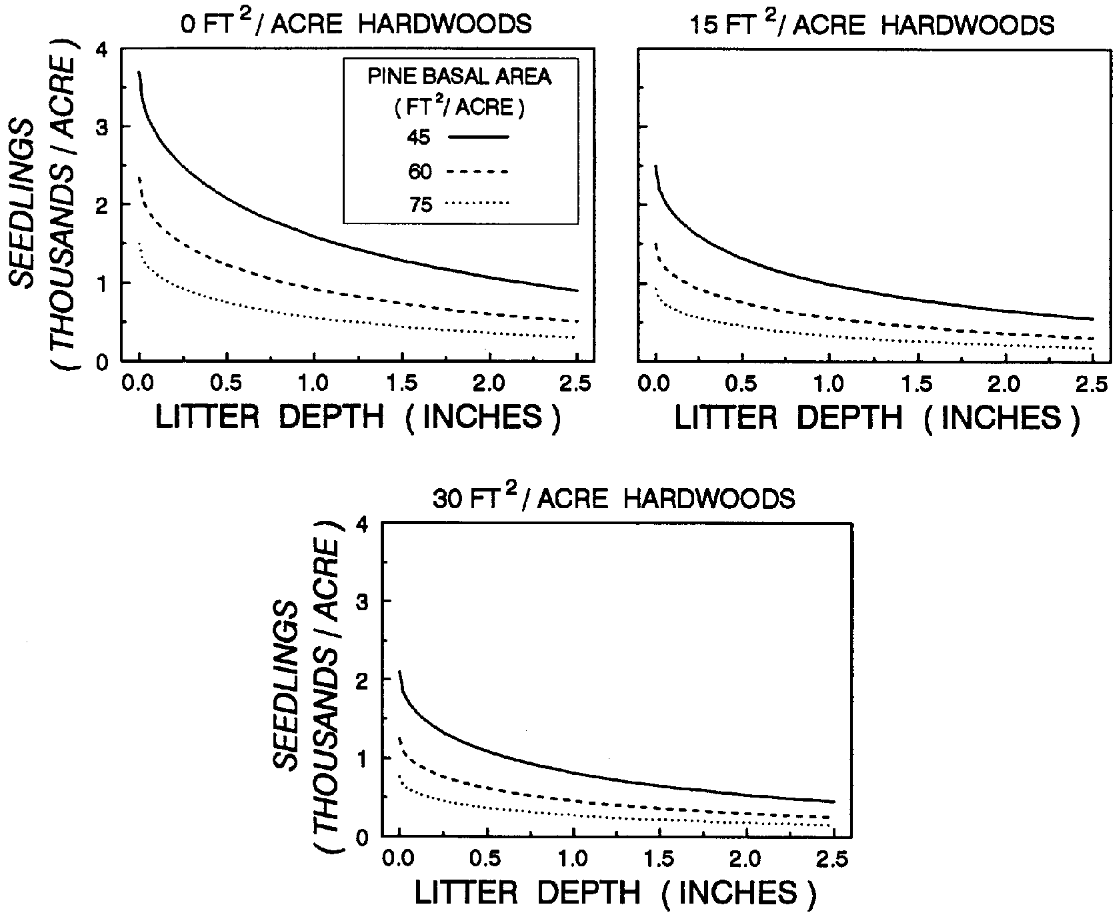

Figure 3.—*Effects of litter depth and overstory basal areas of pines and hardwoods on the number of 1-year-old shortleaf pine seedlings when the seed crop of the preceding year was 100,000 sound seeds per acre. Values were calculated from equation (4) in text.*

Table 3.— *Effects of overstory hardwood treatments on the number of 1-year-old shortleaf pine seedlings by seed crop and seedbed age*

Seed crop year	Seedbed age†	Hardwood basal area* 0 ft²/acre	15 ft²/acre	30 ft²/acre	Mean square error	*P>F*
	----- *Years* ----	-------- *Number of seedlings per acre* --------				
1989	0	5,560	1,000	2,560	8.60E7	0.16
1991	0	1,810	190	375	1.26E7	0.22
1991	1	1,940a	190b	125b	1.69E7	0.01
1991	2	1,120	125	0	6.08E6	0.11

*Row means followed by different letters are significantly different according to the Ryan-Einot-Gabriel-Welsch Multiple Range Test (P=0.05).
†Time from treatment establishment until seed dispersal.

The decline in seedling density with increasing overstory basal areas reflects a response of seedlings to levels of overstory competition for light and moisture. Guidelines for uneven-aged pine stands specify the upper and lower limits for basal area to keep overstory competition within acceptable bounds. Guidelines specify: (1) retention of a minimum of 45 ft²/acre of pine basal area to provide acceptable rates of merchantable growth and (2) never letting basal area exceed a maximum of 75 ft²/acre during a cutting cycle because regeneration will be adversely affected (Baker and others, in press). Although results of this study are too short term to confirm these guidelines, they do indicate that moderate litter depth (up to 1 inch) will not be a serious detriment to securing an adequate density of 1-year-old seedlings if: (1) seed production is at least near the regional average, (2) the total overstory basal area is reduced to specified guidelines and structural targets are imposed, and (3) understory hardwoods are controlled and ground vegetation is sparse. Because of the short-term nature of these results, they should not be extended to other situations or extrapolated to longer time periods.

Results seem to indicate that the composition of the overstory is not so critical in determining seedling density after the first growing season. This finding has also been observed in other studies in which the basal areas of overstory pines and hardwoods were reduced to near specified guidelines and understory hardwoods were controlled (Shelton and Murphy 1993, in press). Pine seedlings are apparently able to become established and subsist under fairly dense canopies for several years before dying (Becton 1936, Wahlenberg 1960). This observation suggests that newly established pine seedlings are moderately shade tolerant but become shade intolerant as the seedlings age. Bormann (1956) reported, for example, that the photosynthetic efficiency of loblolly pine seedlings at low light intensities declined substantially as secondary characteristics developed.

The subsequent development and survival of seedlings is not expected to continue where a substantial hardwood component exists. Hardwoods have been observed to produce about twice the amount of shade per unit of basal area as do pines because of their large crowns, broad leaves, and generally shorter heights (Tappe and others 1993). Based on this generality, an overstory composed of 60 ft²/acre of pines and 7.5 ft²/acre of hardwoods would produce the equivalent shade of a pure pine overstory at the upper limit specified for uneven-aged pine stands (that is, 75 ft²/acre). Thus, the opportunity for hardwood retention within uneven-aged shortleaf pine stands under single-tree selection appears to be low (Shelton and Murphy 1993).

The seedling-to-seed ratios for the values presented in figure 3 range from nearly 0 to 4 percent. (The number of seedlings in thousands is numerically equal to the seedling-to-seed ratio in figure 3 because it is for 100,000 sound seeds per acre.) These values are fairly typical of the seedling-to-seed ratios reported elsewhere for natural regeneration of shortleaf pine. Yocom and Lawson (1977), for example, reported a seedling-to-seed ratio of 0.4 percent for undisturbed areas within a seed tree stand in the Ouachita Mountains and 1.0 percent for disturbed areas. Haney (1962) reported a seedling-to-seed ratio of 0.3 percent for undisturbed areas and 2.0 percent for scarified areas in a sawtimber stand. In poorly stocked shortleaf pine stands, the seedling-to-seed ratio was 0.4 percent for untreated areas, 1.3 percent for burned areas, and 2.9 percent for areas where a brushcutter had been used (Maple 1965). In seed tree stands, Dale (1958) reported a mean seedling-to-seed ratio of 6.4 percent when the seedbed was bulldozed, 4.2 percent when disked, and 1.4 percent for the untreated control.

Seedling Height

The height of 1-year-old seedlings (*HT* in feet) was negatively correlated with the basal area of pines and hardwoods (P and H, respectively, in square feet per acre), as shown in the following equation:

$$HT = \exp(-0.7937 - 0.008401P - 0.01439H) \quad (5)$$

where number of observations was 71, root mean square error was 0.131, fit index was 0.29, and mean HT was 0.23 ft. The effect of litter depth was not significant. Calculated values for equation (5) are plotted in figure 4. The greatest heights occurred at the lowest basal areas, and then heights declined as the basal areas of both pine and hardwood increased. Heights ranged from 0.16 to 0.33 ft, which are typical of 1-year-old shortleaf pine seedlings on these poor sites (Shelton and Murphy, in press). This relationship simply reflects the increased competition from the overstory as basal area increases. Overstory competition is perhaps most easily demonstrated by the reduction in light intensity that results from increasing basal area. Tappe and others (1993), for example, reported a strong negative relationship between light intensity in the understory and the basal area of overstory pines and hardwoods. However, this relationship also undoubtedly involves competition for other resources such as soil moisture. Retained overstory trees in uneven-aged stands clearly suppress the growth of regeneration, but traditional guidelines for uneven-aged pine stands are designed to provide an acceptable environment for the survival and development of sufficient regeneration to sustain future harvests (Baker and others, in press).

Understory Vegetation

Coverage of herbs, vines, shrubs, and hardwoods averaged 3.7, 1.6, 0.3, and 1.1 percent, respectively, and did not vary significantly with litter depth or overstory basal area. By contrast, coverage of grasses (G in percent) was significantly related to litter depth (D in inches) and basal areas of pines and hardwoods (P and H, respectively, in square feet per acre) as shown in the following equation:

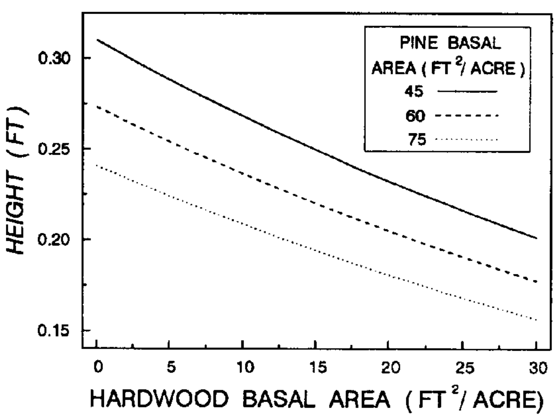

Figure 4.—*Effects of pine and hardwood basal areas on the height of 1-year-old shortleaf pine seedlings. Values were calculated from equation (5) in text.*

$$G = \exp(3.166 - 1.269D - 0.01021P - 0.04273H) \quad (6)$$

where number of observations was 192, root mean square error was 5.52, fit index was 0.25, and mean G was 2.8 percent. The effects of litter depth and overstory basal areas were negative, and the equation explained 25 percent of the variation in the coverage of grasses. Calculated values for equation (6) are plotted in figure 5. Coverage of grasses was about 15 percent for a mineral-soil seedbed with 45 ft^2/acre of pine basal area and no hardwoods. Values declined to near zero at the greater litter depths and the higher basal areas. Grasses observed in these seedbeds developed mostly from seeds because the herbicide application killed existing grasses. Seeds were stored in the soil and litter and were dispersed into the treated areas from outside the seedbed subplots.

The similar response of shortleaf pine seedlings and grasses indicates that these competitors have similar environmental requirements for germination and establishment. These results suggest that the favorable effects of a mineral-soil seedbed on the establishment of shortleaf pine seedlings need to be considered within the context of the entire understory community, especially where ground vegetation is not controlled with herbicides as was done in this study. Shelton (1995), for example, reported that loblolly pine seedlings developing on a mineral-soil seedbed were smaller than those developing on a seedbed where litter was present and attributed this result to the suppression of competing vegetation by litter. Thus, when the pine seed crop is good, litter seedbeds may actually be favorable to natural regeneration because of a reduction in herbaceous vegetation.

Changes in Seedbed Conditions Through Time

Litter production continues in stands that have been partially harvested; thus, the exposure of mineral soil through stand disturbance is short lived. In such areas, litter accumulates until a steady state occurs between rates of litter production and subsequent decomposition of the litter (Olson 1963). By contrast, areas with enhanced litter will decompose at higher rates than are supported by litter production, and depth of the enhanced litter will decrease through time until a steady state is attained.

Data collected in this study allowed calculating the recovery rates of the seedbed treatments. In the developed equations, D is the current depth expressed as a percentage of the depth before disturbance, T is the number of years since disturbance occurred, and H is the hardwood basal area in square feet per acre. The equation for the mineral-soil seedbed is as follows:

$$D = \exp(3.22 + 0.206T + 0.00629H) \quad (7)$$

where number of observations was 36, root mean square error was 12.9, fit index was 0.43, and mean D was 45.3 percent. The equation for the enhanced-litter seedbed is:

$$D = \exp(5.20 - 0.0983T + 0.00274H) \quad (8)$$

where number of observations was 36, root mean square error was 29.4, fit index was 0.27, and mean D was 161 percent. The above relationship for the partial-litter seedbed was not significant. For both the mineral-soil and enhanced-litter seedbeds, the hardwood basal area significantly influenced the recovery rate, but the pine basal area was not significant.

Values calculated from equations (7) and (8) are plotted in figure 6. For the mineral-soil seedbed, an increase in hardwood basal area and time since disturbance increased the recovery toward the depths existing before disturbance. After 3 years of recovery, litter depths in areas with exposed mineral soil were within 45 to 60 percent of the original depths before disturbance. The positive effects of hardwood basal area probably reflect the increased litter production associated with the higher basal areas. Hardwoods in the Ouachita Mountains have been observed to produce more litter per unit of basal area than shortleaf pine (Shelton and Lawson 1994).

Depth of the enhanced-litter seedbed decreased through time (fig. 6). After 3 years, depths were 135 to 150 percent of those occurring before disturbance. The effects of hardwood basal area on this relationship were positive, and thus, an increase in hardwood basal area retarded the recovery to undisturbed depths. This finding is consistent with the concept of higher litter production being associated with the greater hardwood basal areas.

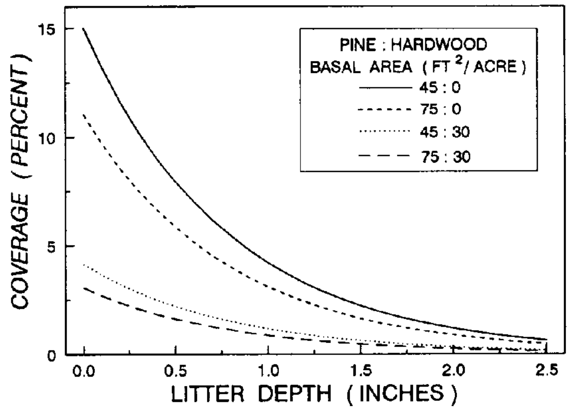

Figure 5.—*Effects of litter depth and overstory basal areas on the coverage of grasses 1 year after disturbance. Values were calculated from equation (6) in text.*

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Initial establishment of naturally regenerated shortleaf pine after implementing uneven-aged silviculture in pine-hardwood stands is affected by seed production, seedbed conditions, and overstory basal areas. The greatest uncertainty in the determinants examined in this study is seed production, which varies widely due to uncontrollable factors. However, seed

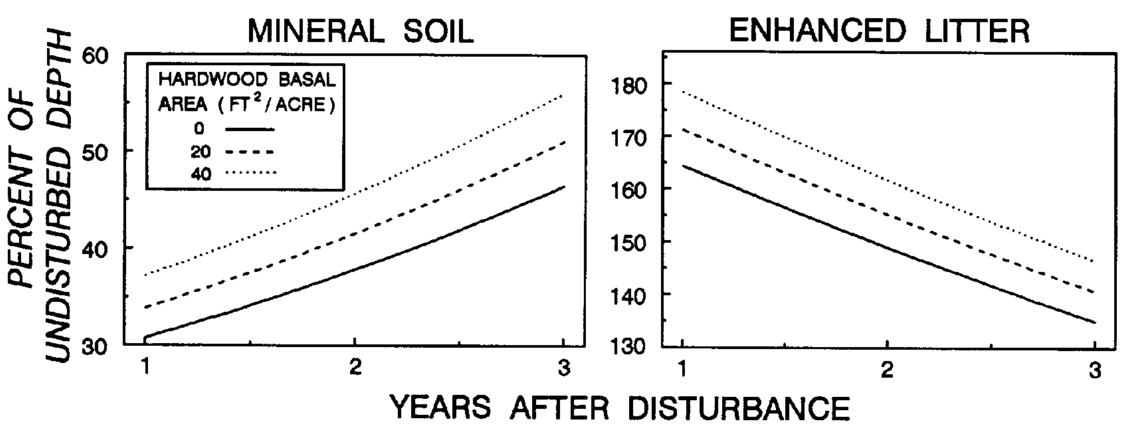

Figure 6.—*Recovery of mineral-soil and enhanced-litter seedbeds following disturbance. Values were calculated from equations (7) and (8) in text.*

production was adequate for obtaining regeneration in 2 of the 3 years of monitoring. The presence of litter inhibits the germination and early establishment of shortleaf pine, a finding that has strong support from the existing literature for many species with small, wind-disseminated seeds. Litter affects the complicated processes of germination and establishment through a number of environmental, physical, biological, and chemical mechanisms. However, the inhibiting effects of litter are far from complete; some seedlings in this study became established on the deepest litter seedbeds tested. Apparently, some suitable microsites for germination and establishment occur even within a generally unfavorable seedbed.

Although litter reduces seedling establishment, this relationship must be considered within the goal of securing a sufficient number of seedlings to successfully regenerate the stand. Results of this study indicate that seedbed conditions after implementing uneven-aged silviculture in shortleaf pine stands will not seriously limit adequate regeneration if: (1) seed production is at least near the regional average; (2) overstory basal areas are within guidelines for uneven-aged pine stands, and structural targets are imposed; (3) competition from understory hardwoods and ground vegetation is low; and (4) other environmental factors, such as moisture and temperature, are within acceptable limits. Seedbed conditions after harvesting of uneven-aged stands will be very heterogeneous and will range from exposed mineral soil to deep accumulations of litter and logging debris (Shelton and Wittwer 1992). Thus, all the seedbed conditions tested in this study will exist after harvesting; exposed mineral soil will occur where traffic scrapes litter away, and heavy litter accumulations will occur where this litter is deposited. The areal extent of each seedbed condition and the spatial distribution are the critical features affecting regeneration.

In most cases, the seedbed conditions after harvesting of uneven-aged stands will be suitable for shortleaf regeneration, and additional disturbance does not seem justified for seedbed preparation, although treatments may be needed to control competing understory vegetation. In addition, conventional seedbed-preparation treatments, such as prescribed burning and disking, are difficult to apply in uneven-aged stands because of the presence of residual trees and advanced regeneration. However, pre-harvest prescribed burning might be beneficial to control ground vegetation and reduce litter depths if few seedlings are present in the size classes susceptible to fire damage.

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Some of the factors affecting the establishment of shortleaf pine regeneration after the initial treatments implementing uneven-aged silviculture in shortleaf pine-hardwood stands are quantitatively described in this publication.

Keywords: Forest floor, natural regeneration, pine-hardwood stands, *Pinus echinata* Mill., site preparation, uneven-aged silviculture.