

SHORTLEAF PINE SEED PRODUCTION FOLLOWING PARTIAL CUTTING IN THE OUACHITA MOUNTAINS

Robert F. Wittwer and Michael G. Shelton¹

Abstract—Seed production is one of the principal determinants of successful natural regeneration of shortleaf pine (*Pinus echinata* Mill.) in both uneven-aged and even-aged silvicultural systems. In this paper, we describe the amount and periodicity of shortleaf pine seed production observed in a number of stands with monitoring periods of up to 8 yr. Results were compiled from: (1) two replicated research studies testing hardwood retention in uneven-aged and even-aged reproductive cutting methods in the eastern part of the Ouachitas, and (2) eight operational-level stands, which were mostly located in the western part of the Ouachitas. The following generalities can be drawn from the combined results: (1) seed production is highly variable, ranging from zero in some years to over 3 million sound seeds per ac in others, (2) reduced seed production occurs during some years in stands where midcanopy hardwoods are present but the effects are not consistent from year to year, (3) seed production tends to decrease in older stands and in overstocked stands, and (4) the western part of the Ouachitas tends to have more failures and fewer good seed crops. Results indicate that seed production will usually be adequate for natural regeneration of shortleaf pine within most of the Ouachita Mountains.

INTRODUCTION

Although the most widespread of the southern pines, the greatest concentration of shortleaf pine (*Pinus echinata* Mill.) is in the Ouachita Mountains of central Arkansas and eastern Oklahoma (Lawson 1990). Within this region, shortleaf pine is the most important commercial species, and it is the dominant naturally occurring pine species. Shortleaf pine can be successfully regenerated by both artificial and natural methods. One of the most critical determinants of successful natural regeneration of shortleaf pine is an adequate seed supply (Baker 1992, Lawson 1986). Some silvicultural strategies, such as retaining fruitful trees and promoting their general vigor, can be used to enhance seed production within a stand, but these techniques are overshadowed by the uncontrollable influences of seed and cone consumers and weather. Considering these restrictions, resource managers relying on natural regeneration of this important species should be familiar with the periodicity of seed crops.

The timing of an adequate seed supply with a receptive seedbed and low levels of competing vegetation is the greatest challenge to managers relying on natural reproduction cutting methods (Shelton and Cain, in press). In this paper, we compile data on shortleaf pine seed-production from two research studies and eight operational stands; all sites are located in the Ouachita Mountains. This information will provide land managers with knowledge about the periodicity of seed crops within the Ouachitas and the extent to which they can enhance seed production through silvicultural manipulations.

The Pine Reproductive Cycle

For shortleaf and the other southern pines, the total time between strobili initiation and seed dispersal is over 2 yr. The wide variation observed in annual shortleaf pine seed crops can be attributed to several factors. Flower production in an old-field stand was observed to vary by a factor

of eight times over a 6-yr period in the Virginia Piedmont (Bramlett 1972). Flower initiation is influenced by the interaction of physical environmental factors (nutrients, moisture, light, temperature) and physiological processes (Barnett and Haugen 1995).

Subsequent mortality is caused by spring frosts, insects, and physiological abortion. Spring frosts, late enough to damage new juvenile leaves on hardwoods, have been observed to damage female flowers (Campbell 1955, Hutchinson and Bramlett 1964). Male flowers seem less susceptible to frost damage. Overall survival of flowers to mature cones varied from 3 to 65 percent and averaged 29 percent over a 6-yr observation period (Bramlett 1972). Greatest losses occurred between May and September during the first year of cone development. Mortality during the second year was attributed to squirrels and insects. Yearian and Warren (1964) found 39 insect species to be associated with shortleaf and loblolly pine (*Pinus taeda* L.) conelets and cones in Arkansas; *Dioryctria clarioralis* (Walker) and *D. amatella* (Hulst) were the most destructive. Seed sampling in 22 stands included in the Phase I, Ecosystem Management Research pilot study found about 12 percent of the seed to be damaged by seed bugs (Mangini and others 1994); *Leptoglossus corculus* (Say) and *Tetyra bipunctata* (Herrich-Schaffer) caused the most damage.

Shortleaf pine seed yields have been found to vary from failures to over two million per acre in previous studies (Wittwer and Shelton 1992). Three long-term studies have been previously conducted: (1) a 10-yr study in the Piedmont region of the Carolinas and Georgia in the eastern portion of the natural range (Bramlett 1965), (2) a 10-yr study in east Texas in the southwest portion of the range (Stephenson 1963) and (3) a 9-yr study in the Ozark and Ouachita Mountains of Arkansas, Missouri, and Oklahoma in the northwestern portion of the natural range (Shelton and Wittwer 1996). In general, all studies recorded three or four

¹ Professor, Department of Forestry, Oklahoma State University, Stillwater, OK 74078-6013; and Research Forester, USDA Forest Service, Southern Research Station, Monticello, AR 71656-3516, respectively.

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good seed crops during the study periods. In the southeastern Piedmont, seed yields were observed to decrease with increasing latitude (Bramlett 1965). In the Ozark/Ouachita Mountain study, yields were lower in the western portion of the region, an area representing the northwestern limit of shortleaf's natural range (Shelton and Wittwer 1996). Good seed crops may not be distributed at regular intervals; two successive years with good yields may be followed by three or four poor years.

Seed quality, expressed as the percentage of the total crop that is sound, appears to increase with the higher yields. Bramlett's (1965) 10-yr study in the Piedmont found 57 percent sound seed in the three good seed crops and 41 percent for the other seven crops. In east Texas, Stephenson (1963) found sound seed to average 61 percent for the four years with good crops during the 10-yr study. Shelton and Wittwer (1996) found the percentage to range from about 30 percent in poor seed years to 70 percent for bumper seed crops. Intensive cone sampling from two Ouachita Mountain stands in a year with a mediocre seed crop found between 30 and 50 percent of the seeds to be sound (Wittwer and others 1997).

METHODS

Study Areas and Treatments

Study 1 (uneven-aged pine-hardwoods)—This study was installed in the Winona Ranger District of the Ouachita National Forest in Perry County, AR (Shelton and Murphy 1997). 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. Slopes of individual plots ranged from 8 to 21 percent. 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 yr and ranged from 53 to 64 ft, which is typical of upland sites in the Ouachita Mountains (Graney 1992). Annual precipitation averages 52 in., and temperature averages 40° F in the winter and 79° F in the summer (U.S. Department of Commerce 1968). Winter is the wettest season and autumn is the driest. Water deficits typically develop during the summer.

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). Overstory basal area (trees > 3.6 in. d.b.h.) averaged 90 ft² per ac for shortleaf pine and 32 ft² per ac for hardwoods before study implementation. Oaks accounted for 84 percent of the total hardwood basal area. Overstory pines and oaks in the initial stand ranged in age from 30 to over 110 yr (Shelton and Murphy 1991); dominant pines averaged 76 yr old, while dominant oaks averaged 70 yr old. No silvicultural treatments had been applied within a decade of study installation.

Sixteen square 0.50-ac plots were established and surrounded by a 58-ft isolation strip that was treated in an identical manner. Plots were arranged in a randomized complete block design with four replicates. One plot per

block was designated as a control that was not treated in any manner. The pine component for the treated plots was reduced to a target basal area of 60 ft² per ac using uneven-aged marking guidelines for single-tree selection (Baker and others 1996). An average of 81 percent of residual pines were > 10 in. d.b.h., which is usually accepted as the minimum size for high-seed producing potential (Shelton and Wittwer 1995). Plots were harvested during the winter of 1988-89. Imposed treatments were three targeted levels of retained overstory hardwoods (0, 15, and 30 ft² per ac in trees > 4 in. d.b.h.). Hardwoods (> 0.6 in. d.b.h.) that were not designated for retention were controlled with stem-injected herbicide.

Within each plot, four 0.9-ft² seed traps (Cain and Shelton 1993) were located about 30 ft from the center of the plot in a square pattern and about 100 ft from the outer boundary of the plot. Seed collections were generally made during the middle and end of each October-to-February period, which is the normally accepted period for dispersal of shortleaf pine seed (Wittwer and Shelton 1992). Monitoring began in October 1988 for the treated plots and in October 1990 for the untreated control, and the last collection was made in March 1997.

Study 2 (shelterwood pine-hardwoods)—This study area was located about 0.5 mile from study 1, and both were very similar in stand and site conditions (Shelton 1997). Elevations ranged from 640 to 810 ft above sea level. Slopes of individual subplots ranged from 5 to 26 percent. Soils were mapped as the Carnasaw and Pirum series. Site index for shortleaf pine averaged 60 ft at 50 yr, ranging from 56 to 65 ft, and the dominant pines averaged 66 yr old. No silvicultural treatments had been applied within a decade of study installation. Pre-treatment overstory basal area averaged 74 ft² per acre for shortleaf pine and 41 ft² per acre for hardwoods. Oaks accounted for 92 percent of the hardwood basal area.

Eight rectangular 1.7-ac plots were established and surrounded by a 60-ft isolation strip that was treated in an identical manner. Plots were arranged in a randomized complete block design with four replicates. The pine component on all plots was reduced to a basal area of 30 ft² per ac in trees selected principally for their potential as seed trees; all trees were > 10 in. d.b.h. Retention of overstory hardwoods was 0 and 15 ft² per ac in trees > 4 in. d.b.h. All merchantable pines were harvested during the winter of 1989-90, and merchantable hardwoods not designated for retention were harvested during the spring and summer of 1990. After harvesting was completed, plots were split into halves, and two control methods for submerchantable hardwoods (0.6 to 3.5 in. d.b.h.) were imposed (chain-saw felling with and without a stump-applied herbicide). Three 0.9-ft² seed traps were located along the center line of each split plot; traps were at least 120 ft from the untreated stand and 100 ft from adjacent whole plots. Monitoring began in October 1990, and the last collection was made in March 1997.

Operational stands—A 3-ac area within an operational seed-tree stand was selected for monitoring in the eastern Ouachitas. The area was located about 2 miles from studies

1 and 2 and was similar to those studies in soil and site conditions. Elevations ranged from 520 to 600 ft. The seed-tree cut was made in 1985, and hardwoods were controlled by chain-saw felling. Nine 0.09-ft² seed traps were systematically located within the area. Monitoring began in October 1993 and the last collection was made in March 1997.

Five natural stands on the Ouachita National Forest (ONF) and two stands on Choctaw National Forestry (CNF) lands in eastern Oklahoma were selected for monitoring (October 1989 through February 1997). Stands were 22 to 40 ac in area. The ONF stands were 60-80 yr old when sampling began and had been subjected to even- or uneven-aged reproduction cutting methods. The CNF stands were 45-50 yr old when sampling began; one was thinned while the other was not. Stands on the ONF were in LeFlore County, OK, while those on CNF lands were in Latimer County, OK. Elevations ranged from 800 to 1200 ft above sea level. The Carnasaw and Bengal soil series were common in the stands, although other series were present. All soils were moderately deep or deep and moderately well-drained or well-drained. Texture of the surface horizon ranged from stony- to fine-sandy loams. Annual precipitation averages approximately 45 in., and temperature averages 43°F in the winter and 80°F in the summer (U.S. Department of Commerce 1968). Seed production was sampled with six to ten, 2 by 2-ft wood-frame and wire mesh traps in each stand (Scholtens 1979).

Seed Processing

Coarse litter was generally removed from the seed traps in the field, and fine litter and seeds were brought into the laboratory for separation. Collected material was refrigerated until processed. Seeds were counted, and viability was generally determined by cutting 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 seeds. Although ineffective for stored seeds, the cut test can be accurate when applied to fresh seeds (Bonner and others 1994). To confirm validity of the cut test in our studies, a subsample from the 1993 and 1994 collections for studies 1 and 2 totaling 1,800 seeds was germinated under controlled conditions following 30 days of cold/moist stratification. At the end of the 30-day germination periods, a cut test revealed that only 3.5 percent of the ungerminated seeds were full, indicating that virtually all of the full seeds collected in our studies were viable. Because of the large number of seeds to be processed from the Oklahoma stands in 1993, seeds were considered sound if they sank in ethanol (Krugman and Jenkinson 1974). A subsample of these seeds was cut and yielded the same results as the float test.

Data Analysis

Means were calculated for each plot or subplot for study 1 and 2 and for the entire stand for the operational stands. For study 1, data were analyzed using analysis of variance for a randomized, complete block design. Differences among treatment means were isolated by using the Ryan-Einot-Gabriel-Welsch Multiple Range Test at a probability level (*P*) of 0.05. This procedure, which is one of the most powerful step-down, multiple-range tests available, controls the experiment-wise error rate (SAS Institute 1989). For

study 2, data were analyzed by analysis of variance for a 2 by 2 factorial, split-plot randomized complete block design using the SAS procedure GLM (SAS Institute 1989). Since there were only two levels for each factor, means were not separated but were presented with the associated mean square error (MSE) and *P*. Significance was accepted at *P* < 0.05.

RESULTS AND DISCUSSION

Seed Yield

Seed yields exhibited wide annual variation, ranging from complete failures in some stands for some years to over 3 million sound seeds per ac in the pine-only shelterwood stands in 1993 (tables 1, 2, and 3). In the eastern Ouachitas, five of the eight seed crops sampled in both shelterwood and uneven-aged stands produced generally good yields (tables 1 and 2). An adequate seed crop to successfully regenerate shortleaf pine has usually been specified as being in excess of 80 thousand seeds per ac (Baker 1992, Haney 1962, Shelton and Wittwer 1996). Suitable conditions for germination and seedling establishment may be present for three years after site preparation, perhaps longer on poor sites and less on more productive sites (Shelton and Wittwer 1992). In the eastern Ouachita Mountain stands, an adequate crop was produced at least once within any three year interval.

Hardwood retention generally had a negative influence on shortleaf pine seed production, but the effects varied from year to year. In the uneven-aged stand where hardwoods were retained, seed production was significantly decreased during 1993 and 1994 and for the 6-year mean (table 1). A similar significant decrease occurred in the shelterwood stand during three seed crops (1993, 1994, and 1996) and for the 7-yr mean (table 2). The negative effects of hardwoods on seed production were usually greatest for the better seed crops. The method of controlling submerchantable hardwoods did not significantly affect seed production in the shelterwood stand.

The importance of reducing shortleaf pine basal area was apparent in the uneven-aged stand in 1992 and 1996 (table 1). The harvested plots with high hardwood retention produced three times more seeds than the unharvested controls in 1992 and five times more in 1994. These two areas had about the same hardwood basal area, but the pine basal area was about 30 ft² per ac lower in the harvested plots. Overall, the harvested plots with no hardwoods produced about twice the sound seeds as the unharvested controls over the 6-yr period when both areas were monitored.

There was wide stand-to-stand variation for the operational stands sampled in the western Ouachita region for the 8-yr period from 1989 through 1996 (table 3). Only 1993 can be characterized as producing a good seed crop, but even then, three of the seven stands in the western Ouachita region exhibited failures. This trend agrees with a 9-yr study of seed production throughout the Interior Highlands of Arkansas, Missouri, and Oklahoma from 1965 through 1973 (Shelton and Wittwer 1996). Seed crops were only adequate in the western Ouachitas during 1966 and 1967, when bumper seed crops occurred throughout the rest of the region.

Table 1—Annual shortleaf pine seed production after the initial harvest implementing uneven aged silviculture in a shortleaf pine hardwood stand in the Ouachita Mountains (study 1)

Seed year	Hardwood retention ^a			Untreated control	Mean square error	P > F
	None	Medium	High			
	- - - thousands of sound seeds per acre ^b - - -					
1989	197	144	200	—	6.78E3	0.58
1990	3	3	3	—	3.48E1	1.00
1991	75	75	68	31	8.05E2	0.16
1992	166	260	122	44	2.44E4	0.32
1993	2,654a	1,912ab	1,590ab	964b	3.73E5	0.02
1994	310a	75b	128b	20b	4.36E3	< 0.01
1995	0	6	0	0	1.31E1	0.09
1996	2,313	1,915	1,796	1,596	3.59E5	0.43
Mean ^c	920a	707ab	617ab	442b	3.37E4	0.03

^a After harvest, merchantable basal areas (trees >3.6 inches d.b.h.) in 1988 averaged 62 square feet per acre for shortleaf pine and 0, 16 and 31 square feet per acre for none, medium, and high hardwood retention treatments, respectively. Unharvested control plots averaged 94 and 32 square feet per acre for pine and hardwood basal areas, respectively, in 1990, and there were also 8 square feet per acre of understory hardwoods (0.6 to 3.5 inches d.b.h.).

^b Row means followed by different letters are significantly different.

^c Means are from 1991 to 1996 so that control plots could be compared to treated plots.

Table 2—Annual shortleaf pine seed production in shelterwood stands with two overstory compositions and two control treatments for submerchantable hardwoods (study 2)

Seed year	Pine only ^a overstory		Pine hardwood ^a overstory		Overstory composition		Submerchantable hardwood treatment	
	Manual	Chemical	Manual	Chemical	MSE	P > F	MSE	P > F
	- - - thousands of sound seeds per acre - - -							
1990	67	50	21	17	2.71E3	0.23	2.50E2	0.23
1991	33	25	17	37	5.28E2	0.87	3.66E2	0.54
1992	142	171	121	175	3.48E3	0.80	3.70E3	0.22
1993	3,442	3,484	2,295	2,291	1.27E5	0.01	1.27E5	0.94
1994	1,431	1,596	517	572	3.14E5	<0.01	5.35E5	0.38
1995	8	17	0	4	6.38E1	0.08	2.26E2	0.44
1996	1,888	2,378	1,652	1,694	3.34E4	0.02	9.32E4	0.13
Mean	1,002	1,103	660	684	4.59E3	<0.01	1.57E4	0.36

^a After harvesting in 1990, shortleaf pine merchantable basal area (trees >3.6 inches d.b.h.) averaged 28 square feet per acre, and hardwoods averaged 16 square feet per acre when retained.

Seed Quality

The percentage of sound seed was positively related to total seed production in the sampled stands (fig. 1). Values ranged from < 20 percent in years with the lower seed production (< 100,000 seeds per ac) to over 60 percent in good seed years. A 9-yr study conducted between 1965 and 1973 found sound seed to be about 30 percent of total production in poor seed years and 70 percent of total production in years with good crops (Shelton and Wittwer 1996). Void and defective seeds result from several factors, which are not greatly affected by management in natural stands. These

factors include lack of pollen, lethal gene combinations, self-pollination, insect damage, and climatic factors (Fatzinger and others 1980).

CONCLUSIONS

Shortleaf pine seed production is highly variable for natural stands in the Ouachita Mountains. Annual production of sound seed during the 8-yr observation period from 1989 through 1996 ranged from zero to over 3 million seeds per ac. The influence of retained hardwoods varied from year to year. For the better seed crops, stands with retained

Table 3—Annual production of shortleaf pine seed from 1989 through 1996 for operational stands representing a range of residual shortleaf pine basal areas in the Ouachita Mountains

Stand	Shortleaf pine basal area <i>ft² per acre</i>	Sound seed production by year							
		1989	1990	1991	1992	1993	1994	1995	1996
		----- thousands of sound seeds per acre -----							
ST ^a	8	NS	NS	NS	NS	188	22	0	1,058
ST	17	0	0	0	20	4	0	0	8
SW	48	0	6	0	12	1,183	0	1	20
UEA	43	NS	39	33	NS	361	0	0	33
UEA	45	NS	2	0	4	96	0	2	15
UEA	51	NS	0	0	2	87	0	2	5
THN	62	265	0	1	NS	0	1	0	0
UTHN	98	272	0	2	NS	0	0	2	2

ST = Seed tree regeneration harvest; NS = not sampled; SW = shelterwood regeneration harvest; UEA = even-aged stand harvested to implement uneven-aged silviculture; ST, SW, and UEA stands were 70 to 80 years old; THN = a 50-year old stand thinned to the specified basal area; UTHN = an unthinned 50-year old stand.

^aThis stand is in the eastern part of the Ouachita Mountains; all others are in the western part.

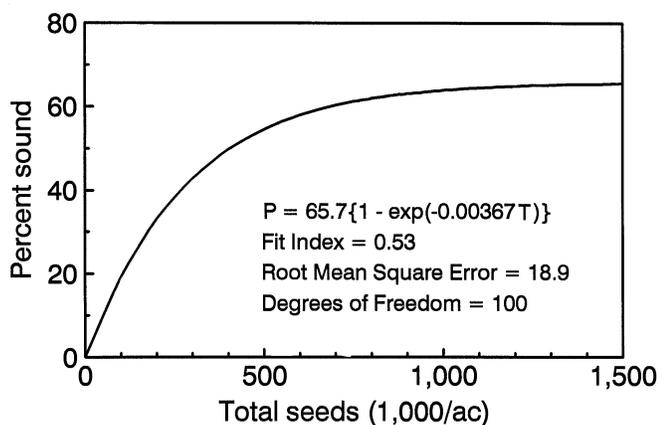


Figure 1—Relationship between sound seed percentage (P) and total seed production (T) for shortleaf pine in the Ouachita Mountains.

hardwoods tended to produce less seeds, but the difference was less evident in years with poor and mediocre seed crops. Seed production for a shelterwood stand equaled or exceeded that of a nearby uneven-aged stand, even though there was a higher basal area in trees of seed-producing sizes in the uneven-aged stand. Results of this study and previous work suggest that shortleaf pine stands in the eastern part of the Ouachita Mountains should produce adequate seed crops for successful natural regeneration using both even-aged and uneven-aged methods.

Results from this study support earlier reports of the sparse and sporadic seed crops in the western Ouachita Mountains and suggest that regional climatic factors near the western limit of shortleaf's natural range are the overriding influence. Where seed production limits the success of natural regen-

eration, managers should pay careful attention to: (1) retention of an adequate density of trees with a high potential for seed production, (2) individual tree characteristics related to seed production, such as crown class, vigor, size (d.b.h. > 10 in.), and presence of old cones, (3) preparatory cutting to stimulate tree vigor, and (4) limiting the amount of retained hardwoods. Perhaps the best option is to monitor shortleaf pine's reproductive structures over the 1.5 yr period from pollination to the beginning of seed dispersal. Particular attention should be paid to the amount of maturing cones during the summer before seed dispersal (Shelton and Wittwer 1995). Monitoring can forecast when adequate seed crops are most likely to occur, and site preparation treatments can be timed to coincide.

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LITERATURE CITED

- Baker, James B. 1992. Natural regeneration of shortleaf pine. In: Brissette, John C.; Barnett, James P., comps. Proceedings of the shortleaf pine regeneration workshop; 1991 October 29-31; Little Rock, AR. Gen. Tech. Rep. SO-90. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station: 102-112.
- Baker, James B.; Cain, Michael D.; Guldin, James M. [and others]. 1996. Uneven-aged silviculture of the loblolly and shortleaf pine forest types. Gen. Tech. Rep. SO-118. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 65 p.
- Barnett, James P.; Haugen, Ronald O. 1995. Producing seed crops to naturally regenerate the southern pines. Res. Pap. SO-286. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station. 10 p.

- Bonner, F.T. 1974. Seed testing. In: Schopmeyer, C.S., tech. coord. Seeds of woody plants in the United States. Agric. Handb. 450. Washington, DC: U.S. Department of Agriculture: 136-152.
- Bonner, F.T.; Vozzo, J.A.; Elam, W.W.; Land, S.B., Jr. 1994. Tree seed technology training course. Gen. Tech. Rep. SO-107. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station. 171 p.
- Bramlett, David L. 1965. Shortleaf pine seed production in the Piedmont. Res. Note SE-38. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. 4 p.
- Bramlett, David L. 1972. Cone crop developmental records for six years in shortleaf pine. *Forest Science*. 18:31-33.
- Cain, Michael D.; Shelton, Michael G. 1993. Modification of GSA metal wastebaskets for use as seed and litter traps. *Engineering Field Notes*. 26(3): 65-69.
- Campbell, T.E. 1955. Freeze damages shortleaf pine flowers. *Journal of Forestry*. 53: 452.
- Fatzinger, Carl W.; Hertel, Gerard D.; Merkel, Edward P. [and others]. 1980. Identification and sequential occurrence of mortality factors affecting seed yields of southern pine seed orchards. Res. Pap. SE-216. Asheville, NC; U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. 41 p.
- Graney, David L. 1992. Site index relationships for shortleaf pine. In: Brissette, J.C.; Barnett, J.P., comps. Proceedings of the shortleaf pine regeneration workshop; 1991 October 29-31: Little Rock, AR. Gen. Tech. Rep. SO-90. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station: 142-157.
- Guldin, James M.; Baker, James B.; Shelton, Michael G. 1994. Midstory and overstory plants in mature pine-hardwood stands on south-facing slopes of the Ouachita/Ozark National Forests. In: Baker, J.B., comp. Proceeding of the symposium on ecosystem management research in the Ouachita Mountains: Pretreatment conditions and preliminary findings; 1993 October 26-27; Hot Springs, AR. Gen. Tech. Rep. SO-112. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station: 29-60.
- Haney, Glenn P. 1962. Seedbed scarification aids regeneration of shortleaf pine. *Journal of Forestry*. 60: 400-402.
- Hutchinson, Jay G.; Bramlett, David L. 1964. Frost damage to shortleaf pine. *Journal of Forestry*. 62: 343.
- Krugman, S.L.; Jenkinson, J.L. 1974. *Pinus* L. pine. In: Schopmeyer, C.S., tech. coord. Seeds of woody plants in the United States. Agric. Handb. 450. Washington, DC: U.S. Department of Agriculture: 598-638.
- Lawson, Edwin R. 1986. Natural regeneration of shortleaf pine. In: Murphy, Paul A. (ed.). Proceedings of a symposium on the shortleaf pine ecosystem; 1986 March 31-April 2; Little Rock, AR. Monticello, AR; University Arkansas Cooperative Extension Service: 53-63.
- Lawson, Edwin R. 1990. *Pinus echinata* Mill. shortleaf pine. In: Burns, R.M. and Honkala, B.H., tech. cords. Silvics of North America: Volume 1. Conifers. Agric. Handb. 654. Washington, DC: U.S. Department of Agriculture: 316-326.
- Mangini, Alex; Carlton, Chris; Perry, Roger W.; Hanula, James 1994. Seed, cone, regeneration, and defoliating insects in forest ecosystem management. In: Baker, J.B., comp. Proceeding of the symposium on ecosystem management research in the Ouachita Mountains: Pretreatment conditions and preliminary findings; 1993 October 26-27; Hot Springs, AR. Gen. Tech. Rep. SO-112. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station: 154-159.
- SAS Institute. 1989. SAS/STAT user's guide. Version 6. 4th ed. Cary, NC: SAS Institute, Inc. 846 p.
- Scholten, John R. 1979. A practical seed trap for pine stands of coastal South Carolina. *Southern Journal of Applied Forestry*. 3: 112-113.
- Shelton, M.G.; Cain, M.D. [In press]. Regenerating uneven-aged stands of loblolly and shortleaf pines: current state of knowledge. *Forest Ecology and Management*.
- Shelton, Michael G. 1997. Development of understory vegetation in pine and pine hardwood shelterwood stands in the Ouachita Mountains—the first 3 years. Research Paper SRS-8. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 18 pp.
- Shelton, Michael G.; Murphy, Paul A. 1991. Age and size structure of a shortleaf pine-oak stand in the Ouachita Mountains—implications for uneven-aged management. In: Coleman, S.S.; Neary, D.G., comps. Proceedings of the 6th biennial southern silvicultural research conference; 1990 October 30-November 1; Memphis, TN. Gen. Tech. Rep. SE-70. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station: 616-629.
- Shelton, Michael G.; Murphy, Paul A. 1997. Understory vegetation 3 years after implementing uneven-aged silviculture in a shortleaf pine-hardwood stand in the Ouachita Mountains. Research Paper SO-296. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 13 p.
- Shelton, Michael G.; Wittwer, Robert F. 1992. Effects of seedbed condition on natural shortleaf pine regeneration. In: Brissett, J.C.; Barnett, J.P., comps. Proceedings of the shortleaf pine regeneration workshop; 1991 October 29-31; Little Rock, AR. Gen. Tech. Rep. SO-90. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station: 124-139.
- Shelton, Michael G.; Wittwer, Robert F. 1995. Forecasting loblolly and shortleaf pine seed crops. In: Edwards, M. Boyd, comp. Proceedings of the eighth biennial southern silvicultural research conference; 1994 November 1-3; Auburn, AL. Gen. Tech. Rep. SRS-1. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station: 605-612.
- Shelton, Michael G.; Wittwer, Robert F. 1996. Shortleaf pine seed production in natural stands in the Ouachita and Ozark Mountains. *Southern Journal of Applied Forestry*. 20: 74-80.
- Stephenson, George L. 1963. Ten years of shortleaf pine seed crops in Texas. *Journal of Forestry*. 61: 270-272.
- U.S. Department of Commerce. 1968. Climatic atlas of the United States. Washington, DC: U.S. Department of Commerce; Environmental Science Service Administration. 80 p.
- Wittwer, R.F.; Shelton, M.G. 1992. Seed production in natural shortleaf pine stands. In: Brissett, J.C.; Barnett, J.P., comps. Proceedings of the shortleaf pine regeneration workshop; 1991 October 29-31; Little Rock, AR. Gen. Tech. Rep. SO-90. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station: 113-123.
- Wittwer, R.F.; Tauer, C.G.; Huebschmann, M.M.; Huang, Y. 1997. Estimating seed quantity and quality in shortleaf pine (*Pinus echinata* Mill.) cones from natural stands. *New Forests*. 14: 45-53.
- Yearian, W.C.; Warren, L.O. 1964. Insects of pine cones in Arkansas. *Journal of the Kansas Entomological Society*. 37: 259-264.