DO CONES IN TOPS OF HARVESTED SHORTLEAF PINES CONTRIBUTE TO THE STAND'S SEED SUPPLY?

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Abstract--Because success of natural regeneration strongly depends on a stand's seed supply, we conducted a study to determine the potential contribution of cones in the tops of harvested shortleaf pines (*Pinus echinata* Mill.) if trees were felled after seed maturation but before dispersal was complete. Closed cones, collected in October 1998, were stored in wire cages with periodic removals over the following 9 months to determine the number and viability of extracted seeds. Storage sites were an opening in a seed-tree stand and a closed-canopy pine-hardwood stand. Of the initial average of 30 viable seeds per cone, 93 percent had dispersed in the open site and 83 percent in the closed-canopy stand by the end of February 1999, which is considered the end of the normal dispersal period from cones on standing trees. By May, virtually all viable seeds had dispersed from cones in both sites. Results indicate that cones in tops of trees cut during the 2-month period after seed maturation can make an important contribution to the stand's seed supply, especially in reproduction cutting methods where most of the trees are harvested.

INTRODUCTION

Because of lower establishment costs, natural regeneration is a viable option for shortleaf pine (*Pinus echinata* Mill.) that appeals to many landowners, and about two-thirds of the pine stands in the southeastern United States originated from natural seedfall (USDA Forest Service 1988). Most natural regeneration methods rely on retained trees to produce an adequate seed supply for regeneration. However, trees felled during reproduction cutting may also potentially contribute to the seed supply if felling took place after seed maturation but before complete dispersal. Wakeley (1954) recommended starting in mid-October when collecting shortleaf pine cones for seed extraction. However, Barnett (1976) reported that cones of other southern pines, such as loblolly pine (*P. taeda* L.) and slash pine (*P. elliottii* Engelm.), can yield viable seeds when collected 2 to 3 weeks before recommended dates, suggesting that shortleaf cones may yield viable seeds as early as late September. Shortleaf pine seed dispersal from standing trees is about 50 percent complete by late November and 90 percent complete by the first of January (Wittwer and Shelton 1992). Trees felled in reproduction cutting during the 2-month period from late September to late November have the potential to make a substantial contribution to the stand's seed supply if viable seeds disperse from cones in felled tops. Seeds from tops of cut trees would likely be most important to regeneration success in reproduction methods that remove most of the stand's trees, such as the seed-tree method or small clearcuts.

Although seed dispersal from shortleaf pine trees has been the subject of numerous studies (Stephenson 1963; Wittwer and Shelton 1992; Shelton and Wittwer 1996), we are aware of no earlier investigation of shortleaf pine seed dispersal from cones in tops of felled trees. Objectives of the study were: (1) to determine the potential for cones in the tops of felled shortleaf pine trees to contribute to the stand's supply of viable seeds and (2) to determine the possible fate of seeds dispersed during the growing season when cold, moist stratification that normally promotes germination would not occur.

METHODS

Study Area

The study was located on forest lands of the School of Forest Resources, University of Arkansas at Monticello. The study site is in the West Gulf Coastal Plain at 91 degrees 46 minutes West longitude and 33 degrees 37 minutes North latitude. Elevation is 98 meters with a rolling topography. The soil is a Sacul loam (clayey, mixed, thermic, Aquic Hapludult), a moderately well-drained upland soil with a site index of 21 meters for shortleaf pine at 50 years (Larance and others 1976). The growing season is about 240 days with seasonal extremes being wet winters and dry autumns. Annual precipitation averages 134 centimeters.

Two sites were located for cone storage. The closed-canopy site was located in a mature loblolly/shortleaf pine-hardwood stand. Basal area in trees $\leq$ 9.0 centimeters d.b.h. averaged 25.7 square meters per hectare for pines and 6.4 square meters per hectare for hardwoods; basal area was 2.8 square meters per hectare in trees 9.0 centimeters d.b.h. Light intensity at 1.37 meters in height

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averaged 7 percent of full sunlight at noon during a clear summer day, and the canopy exerted 97 percent ground coverage. The open site was in a 20-meter by 20-meter cleared area within a pine seed-tree stand with approximately 10 sawtimber-sized trees per hectare. This area intermittently received shadows from adjacent trees during the winter months but was mostly in full sunlight during the summer. The open site was 0.4 kilometers from the closed-canopy stand.

Field Procedures

Closed cones were collected from recently harvested shortleaf pines in a mature sawtimber stand in northern Louisiana (October 13, 1998) and a similar stand in southern Arkansas (October 26, 1998). About five tops were sampled in each stand. Immediately after collection, cones were transported to the two study sites and placed in storage frames designed to simulate logging tops but also to provide protection of cones and seeds from predators. The storage frames were 0.5-meter square and made of 1.3-centimeter mesh galvanized hardware cloth. They were held 0.5 meter above the forest floor by legs constructed of 0.6-centimeter diameter steel. This arrangement allowed wind movement around the frame, which we felt was representative of small branches in the top of a felled tree. A top constructed of 0.35-centimeter mesh hardware cloth covered each frame. Cones were attached to the inside surface of the top by intertwining cone-bearing branches through the hardware cloth. Cones were oriented in a downward angle that averaged 45 degrees. Ten cones from each stand were attached to each storage frame's top. The 16 frames at each location provided for up to four removals from field storage with four replicates. The first removal was scheduled for late winter 1999, but subsequent removals were based on observed results. Before seed extraction, cones were always removed from storage when closed; if required, cones were gently sprayed with water the night before removal to cause closure.

To provide field validation, additional cones were sampled in early March 1999 from shortleaf pine tops within a logged area about 0.4 kilometer from the open study site. This mature loblolly/shortleaf pine stand was lightly thinned during late September 1998.

To determine the possible fate of seeds dispersed later than normal, we deposited packets of seeds on the soil surface in the closed-canopy stand and the open site bimonthly beginning in April 1999 and continuing through October 1999. Seeds came from the cones collected in October 1998. After hand dewinging, filled seeds were separated from void seeds and debris by floating in a water bath for 4 hours and collecting the sinking (filled) seeds. Packets were made by uniformly spacing 40 seeds between two pieces of fiberglass window screen that were held in place by two pieces of 1.3-centimeter mesh hardware cloth while in field storage. The packets were intended to protect seeds from predation and to isolate seeds for reduced contamination from pathogens. Each packet measured 14 by 15 centimeters. There were 10 packets for each of the four bimonthly placements; four packets were placed in a prepared seedbed at the open and closed-canopy locations, and two packets were used for germination tests at each time of placement. Packets were stored in a National Weather Service instrument shelter located in the open site from November 1998 until placed on prepared seedbeds. Beginning in April 1999, packets were removed from the shelter bimonthly and placed on an exposed mineral soil surface; then finely ground surface soil from the area was sprinkled on packets until the seeds were lightly covered. Packets were periodically inspected after heavy rains, and soil was added as needed to keep the seeds lightly covered. Each seedbed area contained four packets representing a placement and was completely enclosed within 1.3-centimeter mesh hardware cloth to prevent predation.

To determine the natural pattern of opening and closing of cones, we randomly selected two groups of cones that matured in 1998 and placed them in the storage frames. The percentage openness of each cone was visually assessed just about daily from mid-May through June 1999. To determine cone temperature, a thermometer was inserted into a hole drilled in the base of a test cone and read after stabilization. Readings were also taken of the air temperature in a standard National Weather Service instrument shelter in the open site.

Laboratory Procedures

After removal from field storage, the 20 cones representing each replicate were allowed to air dry in cloth bags for several days until open. Seeds were then extracted by vigorously tumbling cones in a 20-liter plastic bucket. Cones were then lightly heated (33 degrees Centigrade) in a forced-draft oven for 24 hours and a second extraction was made. This process was repeated one additional time. About 90 percent of the seeds were obtained from the first extraction. Seeds were dewinged by hand. After counting, a germination test was conducted by using a subsample of seeds randomly drawn from each replicate. When ample seeds existed, the subsample was either two cups of 50 seeds each or one cup of 75 seeds. When the number of seeds declined below 75 per replicate, all seeds were used in the germination tests.

Test seeds were placed on moist, sterile sand in 10- by 10-centimeter plastic cups and stratified for 30 days at 4 degrees Centigrade. The 30-day germination test was conducted under 10 hours of full-spectrum fluorescent light and 14 hours of dark in accordance with published guidelines (Wakeley 1954). Temperature in the germination room was at 21 degrees Centigrade. A seed was considered to have germinated normally when the seed coat lifted off the sand. A designation of abnormal germination was based on guidelines described by Wakeley (1954). Seeds with fungi were removed immediately to reduce contamination; a cut test was conducted to determine if seeds were full or void (Bonner 1974). At the end of each germination test, a cut test was conducted on all ungerminated seeds; full seeds were classified as being decayed or potentially sound. A seed that germinated normally within the 30 days was considered viable; any full seed that did not germinate normally was considered nonviable.

In February 2000, all packets were removed from field storage, opened, and inspected to count the number of

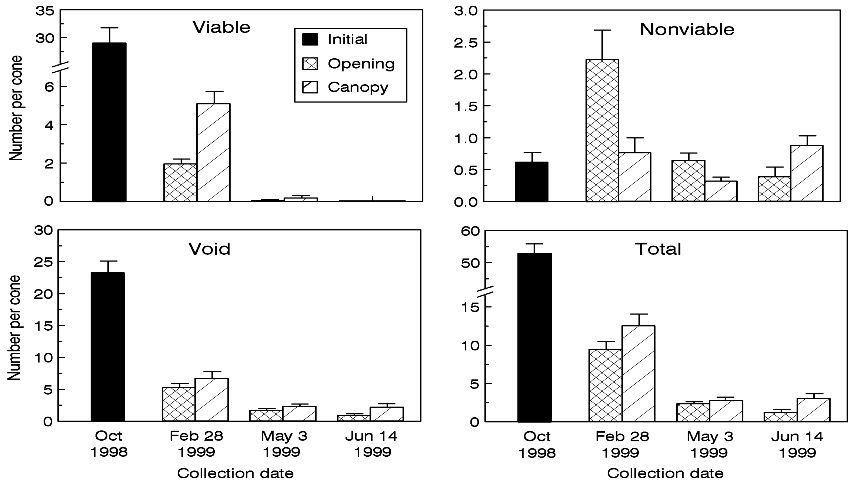

Figure 1—Number and viability of seeds (plus one standard error) observed over a 9-month period during field storage of shortleaf pine cones in an open site and a closed-canopy stand in southeastern Arkansas.

previously germinated seeds based on remnants of a radicle or a split seed coat. A germination test was conducted on all ungerminated seeds as previously described, except that stratification was reduced to 15 days.

Statistical Analysis

The homogeneity of treatment variances was determined by Bartlett's test (Steel and Torrie 1980). When the hypothesis of homogeneity of variance was rejected at $\alpha \leq 0.05$, data were square-root transformed, which provided homogeneity. Analysis of variance was conducted for a completely randomized, split plot in time and space. A split-plot design was used because each storage location and each time interval was singular. All factors were considered fixed. Replicates were considered the germination results of seeds extracted from the samples of 20 cones or from the 40-seed storage packets. Significance was accepted at $\alpha = 0.05$.

RESULTS AND DISCUSSION

Seed Dispersal

The shortleaf pine cones contained an average of 30 viable seeds per cone in October 1998 when they were fully mature (figure 1). This number is typical of years with good seed crops (Wakeley 1954). By late February 1999, viable seeds in the cones had declined by 93 percent in the open site and 83 percent in the closed-canopy stand, and the difference between the two areas was significant (table 1). Seed dispersal from standing shortleaf pines is normally considered complete by the end of February (Wittwer and Shelton 1992). Most of the viable seeds were apparently dispersed because there was no large increase in the number of nonviable seeds over this period.

The viable seeds present in late February (2 seeds per cone in the open site and 5 seeds per cone in the closed-canopy stand) were virtually all dispersed during early spring because few remained in May (<0.2 seed per cone in both the open site and closed-canopy stand). Most of the viable seeds were apparently dispersed because nonviable seeds did not increase over this period. Void seeds showed a similar decline over time as with viable seeds. Our results suggest that void seeds were retained to a greater degree than full seeds (viable and nonviable); void seeds represented 53 percent of the total seeds present in October 1998 but increased to an average of 72 percent in May and June 1999.

Table 1—Analysis of variance for the number of retained seeds in shortleaf pine cones over a 9-month period of field storage in an open site and a closed-canopy stand in southeastern Arkansas

Source of		Viable seeds		Nonviable seeds		Void seeds		Total seeds	
variation[a]	df [b]	MSE[c]	P>F	MSE[c]	P>F	MSE[c]	P>F	MSE[c]	P>F
Location	1	0.72	<0.01	0.18	0.16	0.69	0.03	0.96	0.02
Error I, RxL	6	0.03		0.07		0.08		0.10	
Time	2	7.33	<0.01	0.54	0.01	3.52	0.01	8.56	<0.01
Error II, RxT	6	0.04		0.05		0.08			0.08
LxT	2	0.41	<0.01	0.48	<0.01	0.06	0.41	0.13	0.20
Error III, RxLxT	6	0.02		0.03		0.06			0.06

[a] Location (L), replication (R), and time (T).
[b] Degrees of freedom (df).
[c] Mean square error (MSE) for square root transformed data.

The difference in dispersal pattern between the closed-canopy stand and the open site can be explained by differences in environmental factors, such as wind, temperature, dew, frosts, and humidity. These factors affect the drying of cones and thus the rate and degree of opening and closing. These factors also affect the environmental stresses that seeds are subjected to within cones. In May and June 1999, we observed that cones in the open site took an average of 2 days to open fully following a substantial rain (over 2 centimeters), while those in the closed-canopy stand took 6 days. Cones in the open site closed slightly during nights with heavy dew but fully reopened by midmorning of the following day. Dew did not visibly affect cone closure beneath the closed canopy. During midday, the temperature of cones in the open site averaged 7.5 degrees Centigrade higher than air temperature, while those in the closed-canopy stand were 2.2 degrees Centigrade below the open site's air temperature. The harsher environment of the open site resulted in a more rapid decline in seed viability. Although seeds initially had a 98 percent germination rate, germination of full seeds had declined to 87 percent by February 1999 in the closed-canopy stand and only 47 percent in the open site ($P<0.01$). By May and June 1999, germination of full seeds declined to an average of only 14 percent with no significant difference between the two sites ($P > 0.05$). Cain and Shelton (1997) reported a similar decline in viability for shortleaf pine seeds under field storage. There may be little operational significance of the slower decline in seed viability in the closed-canopy stand, as shade-intolerant shortleaf pine seedlings do not survive for long under such conditions. However, there may be microsites within an opening, such as in the shelter of tops or coarse woody debris, that could provide similar levels of protection.

Field Validation

To determine if the results in our protected storage frames were similar to that found in the field, we conducted additional cone sampling in nearby shortleaf pine stands that had been thinned during late September 1998. The initial base of viable seeds was not known but should have been similar to that of our study because the cones were from the same year. The number of viable seeds in early March 1999 for the thinned stand (9.1 seeds per cone) were very similar to that found in February in our study (5.1 seeds per cone in the closed-canopy stand). The night before the early March collection, a severe rain and wind storm broke the crowns or collapsed about 20 shortleaf pine trees in the stand that was being sampled for cones in logging tops. We collected current-year cones from those trees and confirmed the expected difference in dispersal pattern between standing trees and tops: 0.4 viable seed per cone from the storm-damaged trees compared to 9.1 seeds per cone from the tops ($P = 0.03$). The different seed dispersal pattern from cones of standing trees versus tops of felled trees undoubtedly reflects agitation and drying by the wind, both of which would affect cone openness. Cain and Shelton (1997) reported that a few pine seeds are held so tightly within cones that they may not be dispersed under normal circumstances.

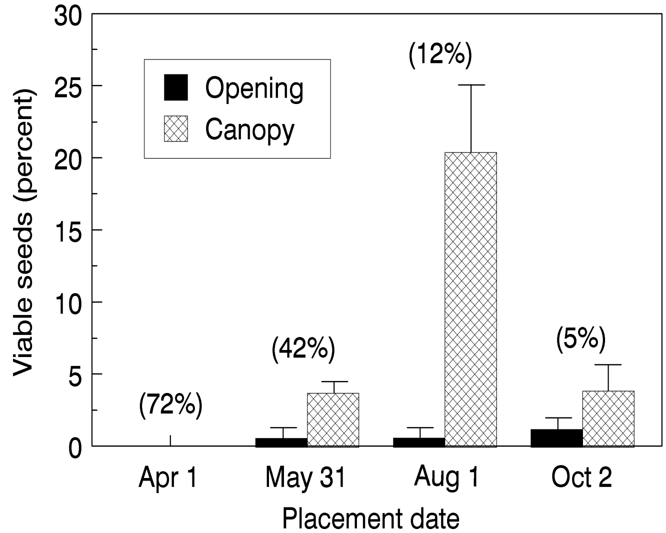

Figure 2—Viable shortleaf pine seeds (plus one standard error) at the end of field testing (February 2000) from packets that had been stored in the open site until placed on mineral soil seedbeds during 1999. The number in parentheses above each bar cluster is the percentage of viable seeds from a subset of packets that were tested for germination at the time of placement.

Seed Fate

Our results indicate that, in a good seed year, 2 to 5 viable seeds per cone could potentially be dispersed from tops after late February if shortleaf pines are felled after seed maturation but before dispersal is completed. Seeds dispersed outside of the normal pattern exhibited from standing trees would not receive the cool, moist stratification that promotes germination. To determine the possible fate of these seeds, seeds extracted from the October 1998 cone collection were placed into packets and were stored in a weather instrument shelter (open site only) awaiting periodic placement in prepared seedbeds. At the time of placement, seed viability declined linearly during the summer, averaging 72 percent for the placement on April 1 and 5 percent on October 2 ($P \leq 0.01$). These results generally agree with the decline in viability that was observed in the stored cones, suggesting that the seeds in the packets accurately represent seeds in cones that potentially could be dispersed.

All the seeds of the April 1999 placement either germinated or died as there was no germination when tested after removal in February 2000 (figure 2). When inspected in February 2000, 76 percent of the seeds from the April 1999 placement had remnants of radicles or had split seed coats. Subsequent placements during the summer and early autumn indicated potential carryover of viable seeds to the next growing season of about 1 percent in the open site and 4 to 20 percent under the closed-canopy stand ($P = 0.01$). The reason for the apparent anomaly in data for the August 1 placement, where germination appeared to increase through time, was not known. The higher potential carryover rates of pine seeds under the closed canopy probably reflected a less harsh environment than in the open site.

CONCLUSIONS

From the standpoint of natural regeneration, the importance of seeds dispersed from cones on felled tops is greater when more of the stand is cut than is retained; thus the potential is greatest in seed-tree stands and in small clearcuts. Our study showed that shortleaf pine cones in tops from an early autumn harvest could potentially disperse up to 93 percent of their viable seeds in time to germinate during the spring. Thus, the potential contribution of tops to a stand's seed supply is large. In addition, these seeds are probably dispersed close to the tops, where regeneration is difficult to obtain because the seedling-to-seed ratio is low (Grano 1949, Shelton and Murphy 1999). The contribution of seed-bearing cones in tops of felled trees is probably more important for regeneration during average seed crops than in good seed crops. Dispersal of seeds from cones in tops of felled trees appears to be enhanced by exposure to sunlight which promotes the drying and opening of cones. However, seed dispersal from cones in tops is prolonged when compared to that of standing trees. Up to 20 percent of the seeds dispersed from cones during the summer could potentially carry-over to the following growing season.

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