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LONG-TERM CHANGES IN FLOWERING AND CONE PRODUCTION BY LONGLEAF PINE

William D. Boyer[1]

Abstract-Cone production by longleaf pine has been followed for up to 30 years in regeneration areas at five to nine coastal plain sites from North Carolina to Louisiana. A rapid increase in the size and frequency of cone crops has occurred sin& 1986 following 20 years of relative stability. Cone production for the last 10 years averaged 36 cones per tree versus 14 cones per tree for the preceding 20 years. This change was evident at most sites, including the Escambia Experimental Forest where longleaf pollen shed has been recorded since 1957 and counts of female flowers in regeneration areas since 1970. Although pollen production was cyclic, no long-term change was evident. The recent increase in cone production seems due to both an increase in flower production and an increase in the fraction of flowers surviving to become mature cones.

INTRODUCTION

Longleaf pine *(Pinus palustris* Mill,) is a poor seed producer compared to other southern pines, and seed crops large enough for adequate natural regeneration are relatively rare. Most information on the size of longleaf pine seed crops in the past is anecdotal. Wahlenberg (1946) noted that good seed crops may occur every 5 to 7 years. Heavy seed crops may occur over much of the longleaf range once in 8 to 10 years (Maki 1952). Longleaf seed years have been characterized by relative terms such as failure, light, medium, heavy, or bumper, but these terms have not been tied to actual numbers such as cones per tree or seeds per acre.

In order to achieve satisfactory natural regeneration, the available seed supply must feed all the many predators with enough left over to establish a satisfactory seedling stand, An average of 360 cones per acre is needed to provide for the first seedling. A minimum of 750 and preferably 1,000 or more cones per acre is usually needed for successful regeneration (Boyer and Peterson 1983). The size of longleaf pine cone crops varies greatly from year to year, and also from place to place (Boyer 1987). This irregularity in seed production by longleaf pine is a major problem for the natural regeneration of this species (Croker and Boyer 1975).

Long-term records of lbngleaf pine cone production were obtained from natural regeneration trials initiated between 1966 and 1969. The tests included nine coastal plain sites from North Carolina to Louisiana, plus two in the montane longleaf forests of central Alabama. Cone production records from these tests, covering the 20-year period from 1966 through 1985, were reported earlier (Boyer 1987). Cone production records for the following 10 years, through 1995, are included in this report.

METHODS

Cooperative operational tests of longleaf pine natural regeneration were established at 11 sites within the southeastern longleaf pine belt. One test site is the Escambia Experimental Forest, Escambia County, AL. Four sites are on national forests in Louisiana, Mississippi, Alabama, and Florida. Three sites are on State forests in Florida, South Carolina, and North Carolina. Two sites are on private lands in Alabama and Georgia, and one is on a military reservation in Florida.

At each of IO sites, two tests were established within stands ranging in size from 16 to 128 acres and averaging 64 acres. One was a test of the two-cut and the other the three-cut sheltetwood method of natural regeneration (Croker and Boyer 1975). Several tests of the two-cut method only were established on the Escambia Experimental Forest. All tests were located in maturing stands of longleaf pine nearing a saw log rotation.

Twenty-five sample points were established within each test area. Two seed trees nearest each sample point were marked for annual springtime binocular counts of female flowers and conelets (first- and second-year pistillate strobili) using the method described by Croker (1971). Cones produced by each sample tree the preceding fall were also counted. This count included all the cones on the ground under each sample tree plus a binocular count of the cones remaining in each tree. Sample trees were not replaced. when removed by cutting or natural mortality, so their number has declined over the years.

Counts ended in 1974 at three sites, two in the montane longleaf type and one on the coastal plain in Mississippi, when the parent overstory was removed following successful regeneration of both tests at each site. Cone count data from the two montane longleaf sites have been omitted due to exceptionally high cone production there as compared to monitored coastal plain sites. For the 8-year period from 1967 through 1974, the montane sites averaged 6.3 times as many cones per tree as five coastal plain sites with records covering the same period of time.

Counts ended at three additional coastal plain sites following 1978, 1979, and 1987 cone crops. Counts were resumed at these three sites, in new sheltetwood stands, beginning in 1991, 1992, and 1994. Five coastal plain Sites (one each in South Carolina, Georgia, Florida, Alabama, and Louisiana) have nearly complete cone count records,

[1] Research Forester, USDA Forest Service, Southern Research Station, G.W. Andrews Forestry Sciences Laboratory, Auburn University, AL 36849.

with 142 of 144 year-site cells filled. Eight cells at three sites were filled by estimates derived from springtime counts of enlarging conelets. Years of record at each coastal plain site, for both cone and flower counts, are given in table 1. The. years listed for flower counts include only those with follow-up cone counts from the same sample trees.

Annual pollen shed by longleaf pine has been monitored on the Escambia Experimental Forest since 1957, using the method described by Grano (1958).

Annual cone counts on regeneration test sites were made to determine the size of cone crops normally needed for satisfactory natural regeneration, and also the frequency of their occurrence at different locations. Binocular counts of flowers and conelets were made to determine their potential value as predictors of cone crop size and so provide some lead time to prepare for an approaching good cone crop.

RESULTS

Long-Term Cone Production

Records of cone production by longleaf pine on coastal plain sites now cover the 30 years from 1966 through 1995. Average annual cone production for all years of record at each location ranged from 7.3 to 37.8 and averaged 21.2 cones per tree (table 2). These results suggest that longleaf pine cone production may increase with increasing distance from the coast.

Table l-Coastal plain sites and years of record for flower and cone counts

State and county	Flower counts		Cone counts	
	Started (flower yr)	Years counted	Started (cone yr)	Years counted
NC				
Bladen	1969	7	1968	15
SC				
Chesterfield	1970	23	1969	27
GA				
Decatur	1968	23	1967	29
FL				
Santa Rosa	1968	24	1967	29
Okaloosa	1969	12	1968	22
Leon	1967	7	1966	16
AL				
Escambia	1970	25	1966	30
MS				
Perry	1967	6	1966	9
LA				
Grant	1968	18	1967	27

Table 2-Average annual cone production on coastal plain sites

State	County	Cones/tree (average)
North Carolina	Bladen	18.2
South Carolina	Chesterfield	37.8
Georgia	Decatur	10.9
Florida	Santa Rosa	14.3
	Okaloosa	7.3
	Leon	19.6
Alabama	Escambia	22.4
Mississippi	Perry	14.2
Louisiana	Grant	36.2
Average		21.2

Year-to-year variation in cone production for all sites combined was very high, ranging from a low of fess than one cone per tree in 1966 to a high of 65 cones per tree in 1987 (fig. 1). A minimum of 750 cones per acre is usually needed for adequate regeneration- This means cone production must average 30 or more cones per tree given 25 residual seed trees per acre in a shelterwood stand.

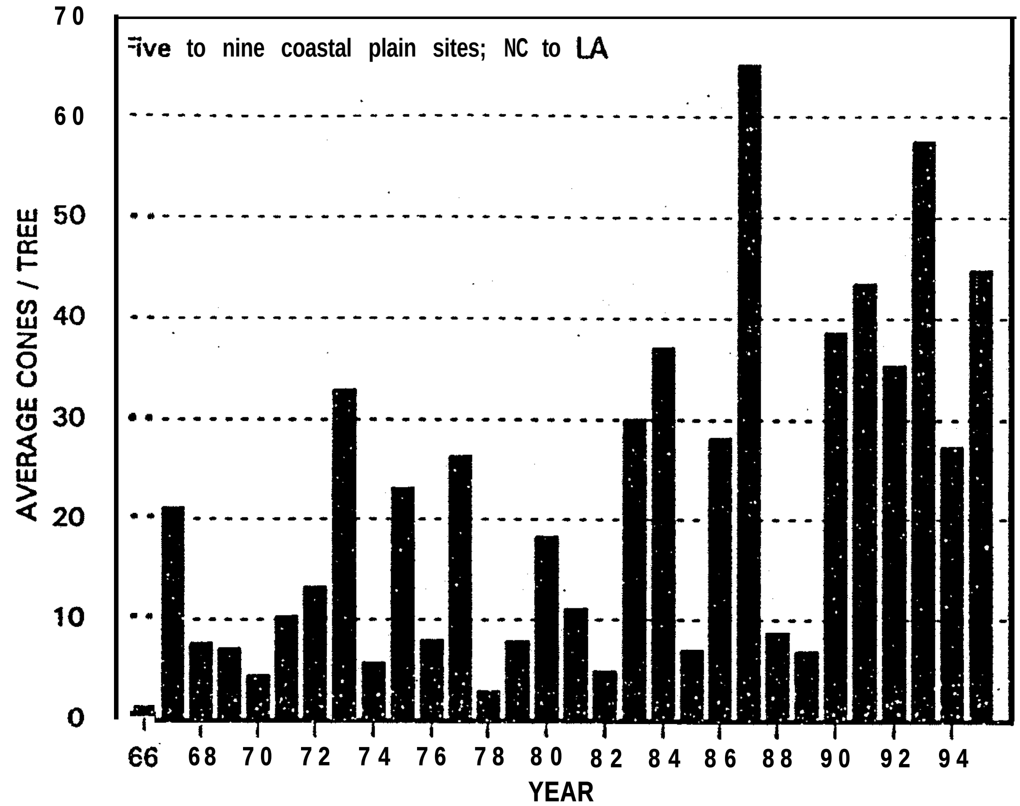
Both the size and frequency of monitored longleaf pine cone crops have increased substantially during the last 10 years. Cone production for all sites from 1986 through 1995 averaged 35.6 cones per tree. The average for the preceding 20 years was 14.0 cones per tree. For all sites combined, the frequency of cone crops adequate for regeneration (30 or more cones per tree) has changed from an average of once per 6.7 years before 1986 to once per 1.7 years since. A 5-year moving average for cone production at all sites illustrates the change (fig. 2). An apparent region-wide heavy longleaf cone crop in 1996 could push the 5-year average above 50 cones per tree.

Longleaf Flowering and Cone Production

A good iongleaf pine cone crop depends on initiation of a large number of female flowers. Although a good female flower crop always precedes a good cone crop, a good cone crop does not always follow a good female flower crop. Pollen supply is another critical factor and. based on 9 years of observation, cone crop size was also closely related to pollen density in the flower year (Boyer 1974). However, large crops of both female and male (staminate strobili) flowers do not necessarily coincide. Weather conditions that promote production of female flowers in southern pines may not be the most favorable for production of male flowers (Boyer 1981).

Escambia Experimental Forest

The Escambia Experimental Forest is the only site where longleaf pine pollen supply has been monitored over a long period of time. This, along with counts of female flowers, permits some exploration of the role of both in year-to-year variations in cone production.



Fii i-Average annual cone production per Lee for all coastal plain sites.

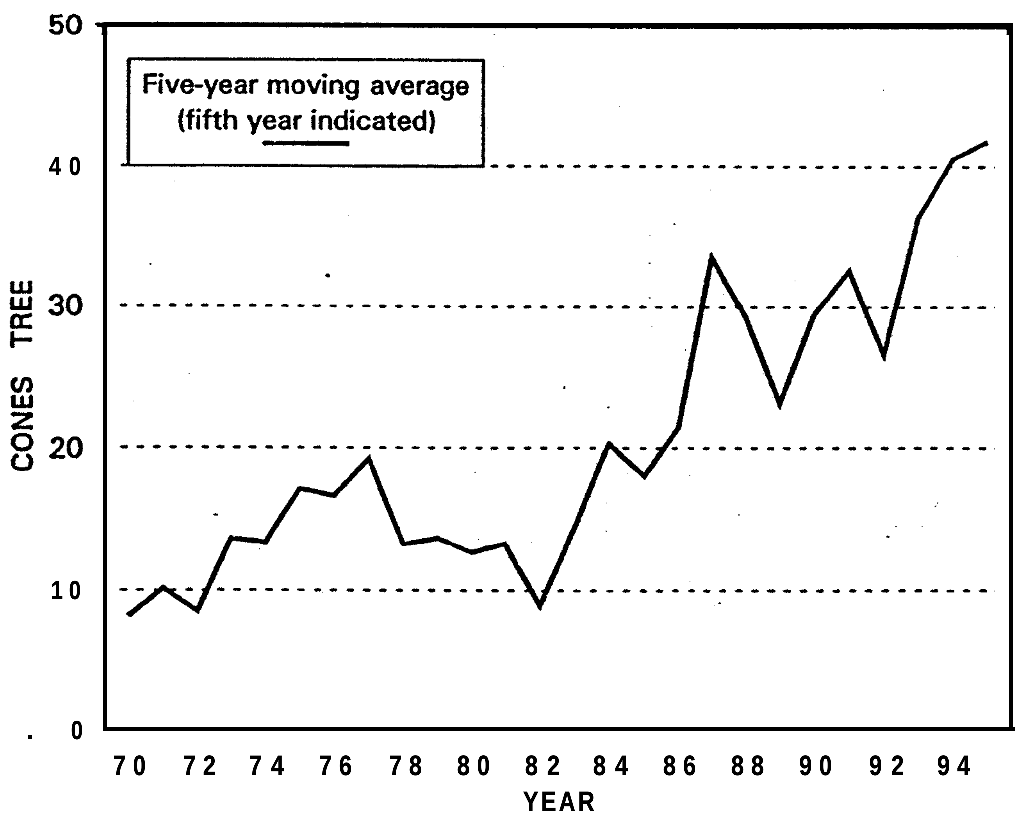


Figure 2-The 5-year moving average of cones per tree for all coastal plain sites.

Cone production by longleaf pine on Escambia Experimental Forest over a 38-year period (1958-95) ranged from a low of 0.2 cones per tree in 1989 to 128.1 cones per tree in 1993, with an overall average of 21 .O cones per tree (fig. 3). The average cone production for the 28 years before 1986 was 16.6 cones per tree. For the 10 years from 1986 through 1995, the average was 33.1 cones per tree, an increase of nearly 100 percent. The increase can be entirely attributed to the heavy cone crops in 1987 and 1993. Omit these 2 years and the average for the remaining 8 becomes 12.4 cones per tree.

Annual pollen supply over 40 years of record (1957-96) has ranged from 0.6 to 24.5 and averaged 7.4 thousand grains per square centimeter (cm^2). While cyclic, there is no indication of any long-term increase in pollen supply (fig. 4). Pollen supply averaged 8.4 thousand grains per cm^2 over the first 20 years, and 6.3 during the last 20 years. In 1957 and 1966, the pollen supply exceeded 20 thousand grains per cm^2 leading to a higher average for the first 20 years.

Flower counts on sample trees over the 27 years from 1970 through 1996 ranged from 0.2 to 80, and averaged 30.6 per tree (fig. 5). Flower production, both male and female, was less variabie from year to year than cone production. Considering only the 25 years with matched flower and cone counts from the same sample trees, the coefficient of variation for annual flower counts was 67.9, and for cone counts 138.0 percent. The coefficient of variation for pollen supply over the same 25-year period was 58.2 percent.

Pollen supply for the 38 years from 1957 through 1994 was related to subsequent cone production (1958-95), although it was not a strong relationship, with a coefficient of determination (r^2) of 0.43. An adequate pollen supply, however, seemed necessary for a good cone crop. Cone production for the 16 years with pollen supply less than 5 thousand grains per cm^2 averaged 7.0 cones per tree. For the 12 years with pollen supply in excess of 10 thousand grains per cm^2, cone production averaged 45.1 cones per tree.

Flower counts were more closely related to subsequent cone production, with an r^2 of 0.66. Adding pollen supply increased the r^2 value only to 0.68. There was also a relatively weak relationship between flower counts and pollen supply over 27 years of record, with an r^2 of 0.46.

The large year-to-year variability in pollen supply, flower counts, and cone production on the Escambia Experimental Forest was reduced by 5-year moving averages for all three variables (fig. 6). All values are tied to the year of cone maturity, so that pollen supply and flower counts for the spring of one year are shown under the following year, when these flowers matured into cones. Both the high and especially the low points in the cycles for all three variables generally coincided. After 1986. however, the gap between flower counts and subsequent cone production closed, indicating a rather sharp reduction in the number of flowers per mature cone. Before 1986. there was an average count of 2.1 flowers per cone which declined to 1 .O for the years 1986 through 1995. Flower

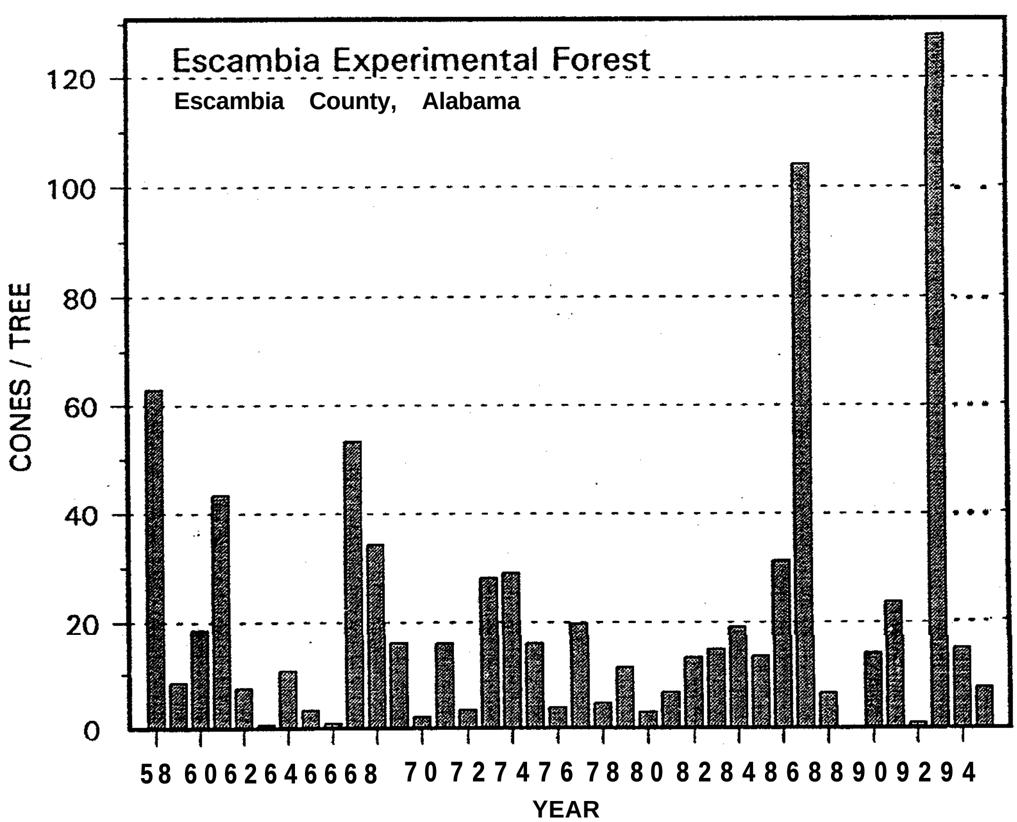


Figure 3-Average annual cone production per tree on the Escambia Experimental Forest.

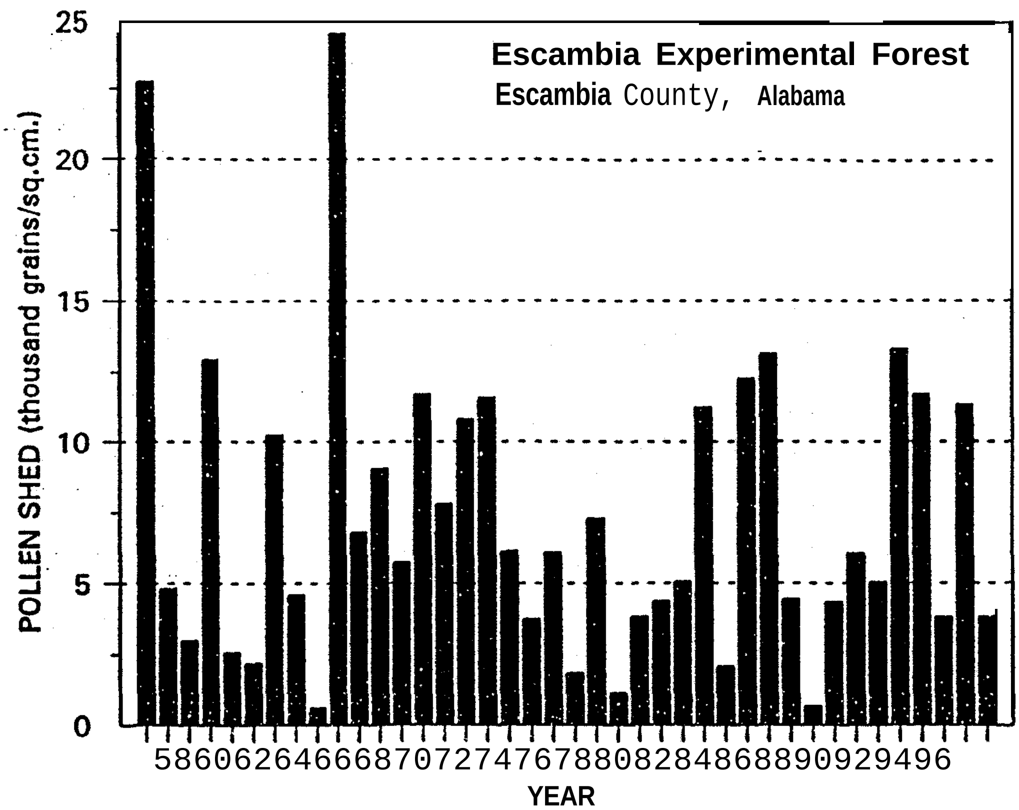


Figure 4-Annual pollen shed by longleaf pine on the Escambia Experimental Forest.

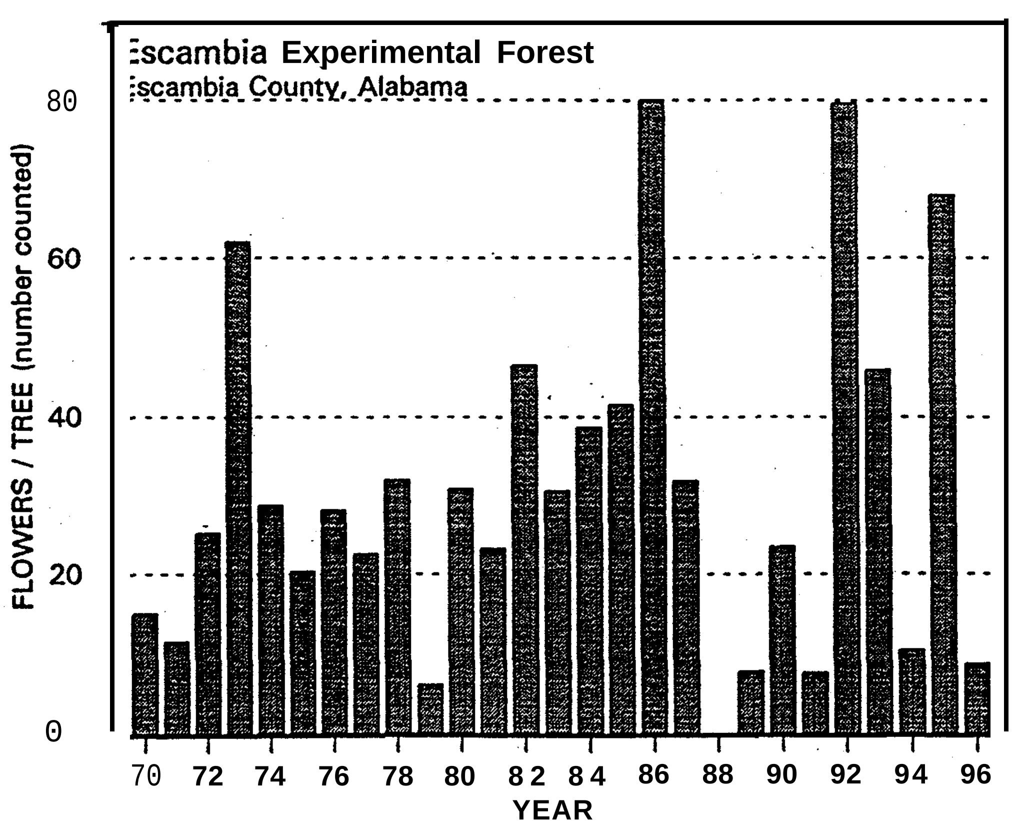


Figure 5—Average annual flower counts per tree on the Escambia Experimental Forest.

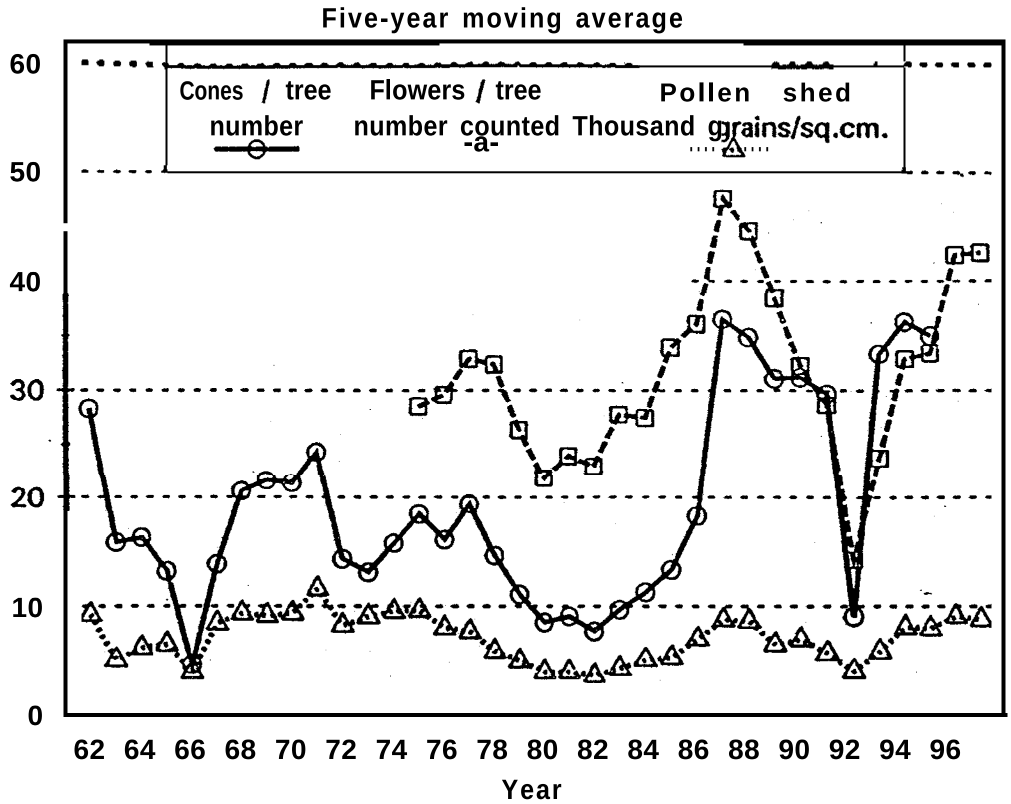


Figure 6—The 5-year moving averages for cone production, flower counts, and pollen supply on the Escambia Experimental Forest.

counts averaged 28.1 per tree before 1986 and 32.9 per tree after. an increase of only 17.1 percent Cone production for the same trees over the same 25-year period averaged 13.4 per tree before 1986 and 33.1 per tree after, an increase of 147 percent! On the Escambia Experimental Forest, at least, it seems that the large increase in cone production observed after 1985 was due in small part to an increase in production of female flowers, but in larger part to an increase in the number of flowers that survived to become mature cones.

Five Coastal Plain Sites

All five coastal plain sites, induding the Escambia Experimental Forest, that were monitored over a relatively long period of time showed increases in flower counts and cone production after 1985 compared to the average for all earlier years. Based on average flower and cone counts per tree for all five sites combined, flower counts increased by 59 percent and cone production by 110 percent (table 3).

The 17.1 percent increase in flower production for the Escambia Experimental Forest was the smallest. Increases in flower counts on the remaining four sites ranged from 40 to 211 percent Cone production for these same sites increased from 30 to 1.175 percent. At four of the five locations, increases in cone production exceeded the increases in flower counts, suggesting that a larger fraction of flowers survived to become mature cones. The exception was Grant Parish, LA, where an increase of 40 percent in flower counts was greater than the 30 percent increase in cone production.

The average percent increase in flower counts since 1984, for all five coastal plain sites, was 75.1, while the increase in cone production was 337.6. The average for percent change greatly exceeded the increase based on average flower and cone counts for crops in 1986 and later versus the earlier years, since the greatest percentage increases ware at locations with the lowest average cone production before 1986. The log of percent increase in cone production at the five sites was strongly related to average size of cone crops before 1986, with an r^2 of 0.88.

Average flower counts and, to a greater extent, cone counts were much less variable among the five coastal plain sites for cone crop years after 1985 than for the earlier years. The coefficient of variation for flower counts declined from 33 to 22 percent, and for cone production from 75 to 25 percent.

DISCUSSION AND CONCLUSIONS

The average size of longleaf pine cone crops on monltored coastal plain sites over the 10 years from 1986 through 1995 was more than double the average size for the preceding 20 years. This change appears due to both an increase in the number of female flowers per sample tree and to an increase in the number of flowers that survived to become mature cones. The relative contribution of these two factors varied among locations.

Table 3—Changes in flower counts and cone production on five coastal plain sites for cone aop years of 1985 and earlier versus I986 and later

		Flower counts per tree			Cone counts per tree		
State	County	Earlier years	Later years	Change	Earlier years	Later years	Change
		···· Average ····		Percent	···· Average ····		Percent
SC	Chesterfield	34.0	48.5	42.6	33.4	54.2	62.3
GA	Decatur	16.1	50.0	210.6	2.8	35.7	1,175.0
FL	Santa Rosa	21.5	35.6	65.6	7.6	28.4	273.7
AL	Escambia	28.1	32.9	17.1	13.4	33.1	147.0
IA	Grant	43.3	60.5	39.7	39.4	51.2	29.9
All sites		28.6	45.5	59.1	19.3	40.5	109.8

Longleaf pollen shed, recorded at only one location, was cyclic over a 40-year period with no evident long-term change. An adequate pollen supply along with a good female flower crop appeared necessary requirements for a good cone crop.

Among the five locations with relatively continuous records, the increase in cone production was greatest at the three central Gulf Coast sites. less at the Atlantic Coast and West Gulf sites. Cone production at the Gulf Coast sites was much lower than the other two sites over the first 20 years. The percent increase in cone production was closely related to the average size of pm-1986 cone crops. The site with the largest gain (Decatur, GA) was that with the smallest average pre-1986 cone crop size, and the site with the smallest gain (Grant, LA) was that with the largest average pre-1986 cone crop size. The order is the same for the remaining three sites. Cone production since 1985 at the three Gulf Coast sites is still lower than at the other two sites, but the diierences are much smaller.

The sudden and dramatic increase over the last 10 years in the size and frequency of good longleaf pine cone crops certainly suggests some favorable changes in environmental condiins associated with the cone production process. What these changes may be is open to speculation. In view of the regional scale of its occurrence, the most likely cause is some change in climatic conditions. Whether this is a permanent change, or only part of some iong-term cycle, remains to be seen, provided flower and cone production records can be continued into the future.

LITERATURE CITED

Boyer, W.D. 1974. Longleaf pine cone production related to pollen density. In: Kraus. J., ed. Seed yield from southern pine seed orchards: Proceedings of a colloquium: 1974 April 2-3; Macon, GA: Georgia Forest Research Council: 8-14.

Boyer, W.D. 1981. Pollen production and dispersal as affected by seasonal temperature and rainfall patterns. In: Franklin. EC., ed. Pollen management handbook Agric. Handb. 587. Washington, DC: U.S. Department of Agriculture: 2-9.

Boyer, W.D. 1987. Annual and geographic variation in cone production by longleaf pine. In: Phillips, D.R., comp. Proceedings, fourth biennial southern silvicultural research conference; 1986 November 4-6; Atlanta, GA. Gen. Tech. Rep. SE-42 Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station: 73-76.

Boyer, W.D. ; Peterson, D.W. 1983. Longleaf pine. In: Bums, R.M., tech. comp. Silvicultural systems for the major forest types of the United States. Agric. Handb. 445. Washington, DC: U.S. Department of Agriculture: 153-156.

Croker, T.C., Jr. 1971. Binocular counts of longleaf pine strobili. Res. Note SO-127. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station. 3 p.

Croker, T.C., Jr.; Boyer, W.D. 1975. Regenerating longleaf pine naturally. Res. Pap. SO-105. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station. 21 p.

Grano, C.X. 1958. A timesaving slide for trapping atmospheric pollen. Forest Science. 4(l): 94-95.

Maki, T.E. 1952. Local longleaf seed years. Journal of Forestry. 50(4): 321-322.

Wahlenberq, W.G. 1946. Longleaf pine. Washington, DC: Charles Lathrop Pack Forestry Foundation in cooperation with U.S. Department of Agriculture, Forest Service. 429 p.