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Stimulation of Cone and Seed Production In Pole-Size Loblolly Pine

BY
M. VICTOR BILAN

INTENSIVE FORESTRY and short rotations practiced by pulpwood growers require prompt regeneration of forest stands, which, in turn, depends to a great extent on an adequate and dependable seed supply. Large fluctuations in annual seed production of forest trees, therefore, present a serious problem.

Certainty of adequate seed production is particularly important in the southeastern United States. Here conditions favorable to seed germination and seedling establishment of southern pines deteriorate rapidly after cutting because of hardwood sprouting and increase of herbaceous vegetation. In this region seed supply often is insufficient because many pine stands are harvested for pulpwood when of pole size, and the remaining trees often are too young to produce enough seed for natural regeneration.

It is widely believed that seed production can be increased by girdling or strangulation of the stems as well as by exposure of the crowns to full sunlight. Girdling and strangulation are the oldest and most popular methods practiced by horticulturists, whereas crown release has been the only common practice used to stimulate fruitfulness in forest trees.

Girdling may consist of one continuous incision around the stem or two overlapping semi-circular incisions with a vertical separation of one to a few inches. Strangulation is carried out by winding a soft iron wire or a metal band tightly around the stem. As the diameter of the treated stem increases, the phloem becomes more

and more constricted, and the downward flow of assimilates is inhibited. Both girdling and strangulation result in accumulation of carbohydrates above the point of treatment, thus stimulating flower-bud initiation and fruiting.

Unlike orchard trees, forest trees often grow under crowded conditions, and release of crowns from competition usually has a pronounced effect on seed production. Crown release was familiar to early European foresters, who often made preparatory cuttings prior to the final harvest and natural regeneration of forest stands. Such preparatory cuttings were really preharvest crown releases, which improved light conditions in residual stands and resulted in prolific seed production.

Under the direction of Professor C. F. Korstian, an experiment was initiated in the Duke Forest in 1952 to determine the effectiveness of several methods of stimulating cone and seed production of pulpwood-size loblolly pine (*Pinus taeda* L.). This paper deals with the analysis of data

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collected during five years of experimentation and with physiological and silvicultural interpretation of the results.

Review of Literature

The fruiting of a tree involves several processes such as the formation of flower buds, blossoming, fertilization, seed development, and seed ripening. Each process can be profoundly affected by age, crown development and heredity of a tree as well as by the biotic and physical factors of its environment. Flower-bud formation alone, for example, is governed by such biotic factors of the plant as age, morphological development, inherited fecundity, correlation between vegetative and reproductive growth, and by environmental factors such as soil and weather.

The study of seed production of loblolly pine is made more difficult by the fact that the developmental cycle requires three growing seasons. Flower buds, young cones, and maturing cones are found on the same tree, and frequently even on the same twig. This overlapping of three periods of sexual reproduction and their superimposition on annual growth cycles complicates the study of nutrient requirements and the metabolism of fruiting.

The earliest known attempt to stimulate seed production in forest trees by horticultural methods was made by Busse (1924) in Germany. He claimed that, by breaking off the tips of young shoots in 19-year-old Scotch pine (*Pinus sylvestris* L.) in early spring, he was able to increase flower bud production for three consecutive years. However, most of the work dealing with stimulation of fruiting in forest trees has been done during the last two decades.

Stimulation of fruiting in forest trees by girdling and strangulation was reported by Pond (1936), Jensen (1942, 1943), Arnborg (1946), Stefansson (1948), Holmes and Matthews (1951), Wenger (1953), and others. Bergman (1955) and Hoekstra and Mergen (1957) reported an increased production of female flowers in pine as a result of strangulation and

girdling in combination with root pruning and/or fertilization. Most investigators agree that increased flower production is evident two to three years after the treatment.

Failure of girdling and strangulation to stimulate seed production in spruce and pine was reported by Vincent (1940) and Girgidow (1956). Girgidow also stated that glucose injection and root and crown pruning failed to increase seed production.

The Forestry Research Institute in Moscow¹ reached the following conclusions after 20 years of experimentation on stimulation of seed production in forest trees. Girdling, bark ringing, wiring, and banding decreased vigor of trees and resulted in the death of most treated trees in 4 to 6 years following treatment. Crown and root pruning decreased fruiting of experimental trees, and 4 to 5 years were required for seed production of treated trees to catch up with that of control trees. Exposure of entire crowns to full sunlight gave the best results. During 20 years, released trees produced 6 to 8 times as much seed as did unreleased trees. The trees in released stands began to bear seed when they reached an average d.b.h. of 3 inches, while trees in unreleased stands did not bear seeds until they were at least 6.3 inches.

The effect of full crown release on seed production of forest trees has been observed and studied by many workers in this country and abroad. Because of the extensive literature, this review will be limited to studies dealing mainly with crown release in loblolly pine.

Chapman (1923) and Forbes (1939) observed that residual loblolly pines on cut-over areas produced more cones than did trees in uncut stands. Shelterwood cutting (Pomeroy and Korstian, 1949) and alternate strip cutting (Trousdel, 1950) resulted in increased seed production of residual pines. Positive effect of crown release on seed production in loblolly pine was reported by Wenger (1954), Easley

¹Personal correspondence, December 1956.

(1954), and others. Many studies show that the stimulating effect was noticed in the first flower-bud formation following crown release and it continued for several years.

Field Experimentation

Site Conditions

The experimental area was located in the Duke Forest, Durham, North Carolina. The predominant soil type was Appling sandy loam with 14 to 34 inches of topsoil underlain by a friable sandy clay subsoil. The site index for loblolly pine was 85 feet, an excellent upland site.

The average annual precipitation in the vicinity, based on a 25-year record, is 42.5 inches, with the maximum in July and the minimum in November. Droughts may occur any time between March and October (U. S. Weather Bureau, 1929-54).

Although the average annual temperature is about 51°F, extremes of -10°F and 107°F have been recorded. The temperature reaches the maximum in July and the minimum in January. The average length of the frost-free season is approximately 200 days.

The experimental stand was planted in 1932 with a 7- by 7-foot spacing. It was given a crown thinning in 1948 when 5 cords of pulpwood were removed per acre. The trees were 21 years old when the experiment was initiated in the early spring of 1952.

Design and Establishment of the Experiment

On an area of about 50 acres, 220 dominant loblolly pines were selected and numbered consecutively. On one half of the experimental area crowns of 110 selected trees were exposed to full sunlight by removing all other trees whose crowns were within 6 feet. The remaining 110 selected trees were allowed to grow in a closed stand.

The experimental trees were divided into 44 blocks of 5 trees each. Within each block one tree was used for each of the three treatments and two untreated trees

were selected at random as controls. Thus each block consisted of one partially-girdled, one wired, one banded, and two control trees. All treatments were imposed on the tree trunks 6 feet above the ground during the first two weeks in April, 1952.

Partial girdling consisted of two semi-circular incisions completely encircling the stem with $\frac{1}{2}$ -inch overlap and two inches apart vertically. The incisions were made with a timber scribe by cutting through the phloem to the outer xylem. Wiring treatment consisted of wrapping a stem with 14-gauge galvanized steel wire. Two double strands of wire, approximately 1 5 inches apart, were tightened around the stem with pliers and a piece of iron rod. For the banding treatment an aluminum band $\frac{1}{16}$ inch thick and 1.5 inches wide was wrapped around the stem. The ends of the band overlapped 2 to 4 inches. The band was then fixed tightly in place by a double strand of 14-gauge galvanized steel wire. The trunks of control trees were left undisturbed.² Before the wires and bands were applied the rough outer bark of each stem was shaved until only a thin layer of bark remained at the points of treatment.

The experiment was set up to be analyzed as two sets of randomized blocks, one containing released trees and the other the unreleased trees. The double number of control trees, as compared with trees in any other treatment, was intended to provide a strong test for the effect of the treatments.

Effects of Treatments on Cone and Seed Production

Methods

Cone counts were made with binoculars in the spring of 1952 (crop of 1951) and in autumns of 1952, 1953, and 1954. Counts were made simultaneously and independently by two ground observers, who moved around the trees and attempted to count all visible cones. Averages of these two re-

²The wires and bands were removed in the winters of 1954-55 and 1955-56, respectively

corded counts were used in analysis of data. In 1954, 1955, and 1956, trees were climbed with a ladder and cones were then counted.

During the counting period in 1955 cone samples were collected from each bearing tree to determine the number of viable seeds per cone. Samples were selected from a branch in the third whorl from the tip on the northwest side of the crown. When the corresponding branches in the third whorl were barren, a sample was collected from the second whorl from the tip. When cones were borne on branches below the fourth whorl from the tip, a second cone sample was collected from the lowest bearing branch on the northwest side of the crown.

Care was taken to collect cone samples from the same exposure and same position on the crown because it had been shown by Acatay (1938) that in Scotch pine the number of viable seeds per cone changed with exposure and position of cones in the crown.

After storage of cone samples at room temperature for two months, the seeds were extracted and their viability determined by cutting. Seeds which contained white endosperm were considered to be viable.

Results

Cone production, 1954-55. Average annual cone production per tree during the period of experimentation is presented in Figure 1. Only the summation of data for 1954 and 1955 was subjected to analysis of variance because the crop of 1953 was a total failure due to a late freeze in the spring of 1955.

Full crown release of 21-year-old pines considerably increased cone production during the third and fourth growing seasons following the treatments. In 1954 and 1955 average cone production per tree was 93 for the released and 20 for the unreleased trees.

Although the number of cones produced per tree in the released portion of the stand during the period 1954-1955 was highest

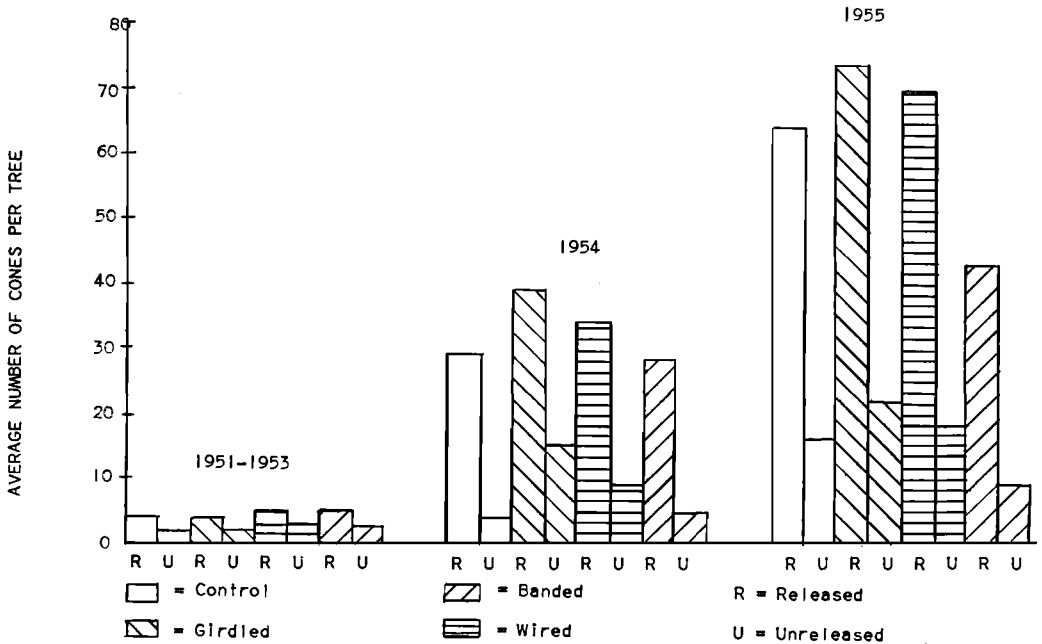


FIGURE 1. Average annual cone production per tree in 1951-1955.

for the girdled trees and successively less for the wired, control, and banded trees, the differences were not statistically significant.

Cone production of treated trees in the unreleased portion of the stand followed the general pattern of the released trees but the number of cones produced was much lower. In this instance, however, the decreased production by the banded trees was more conspicuous; the difference between the banded and control trees as well as between the banded and girdled trees was significant at the 5-percent level.

Viable seeds per cone. Full crown release increased the number of viable seeds per cone by 67 percent (Table 1). While the girdled, wired, and control trees in the released stand produced 46, 47, and 45 viable seeds per cone, respectively, the banded trees bore only 24 viable seeds per cone, a 50 percent reduction. This difference was significant at the 1-percent level.

In the unreleased portion of the stand the control trees produced an average of 27 viable seeds per cone, while the trees in each of the three remaining treatments bore an average of only 19 viable seeds per cone. The difference was significant at the 10-percent level.

The number of viable seeds per cone borne on the third whorl from the tip or above was consistently at least 30 percent higher than the number of viable seeds per cone borne on the branches below the fourth whorl from the tip. This relationship was constant for all treatments in the released portion of the stand. The difference was statistically significant at the 1-percent level. It could not be determined if a similar relationship existed in the unreleased part of the stand, because most unreleased trees bore cones only at the crown tips.

For the cone crop of 1955 no significant correlation existed between the number of cones per tree and the number of viable seeds per cone. This relationship held for both the released and unreleased portions of the stand.

TABLE 1. Average number of viable seeds per cone in 1955.

Treatment	Released trees		Unreleased trees	
	Mean	Standard error	Mean	Standard error
	Seeds			
Girdled	46.0	± 5.5	19.1	± 5.0
Wired	47.4	± 6.0	19.2	± 4.8
Banded	24.2	± 5.7	19.4	± 5.2
Control	44.5	± 4.0	26.6	± 3.3

Number of viable seeds per cone-bearing tree. Only 80 percent of unreleased trees bore cones in 1955 as compared with 100 percent for released trees. The average released, cone-bearing tree produced six times as many viable seeds as the average unreleased bearing tree (Table 2). Although banded, released trees did not lag in cone production, they did so in seed production due to a low number of viable seeds per cone.

In the unreleased portion of the stand girdled trees produced the highest number of viable seeds while banded trees bore the fewest. These differences were not statistically significant due to a very high variation in the number of cones per tree and the number of viable seeds per cone.

TABLE 2. Average number of viable seeds per cone-bearing tree in 1955.

Treatment	Released trees		Unreleased trees	
	Mean	Standard error	Mean	Standard error
	Seeds			
Girdled	3,531	± 857	1,101 ²	± 371
Wired	3,976	± 925	690	± 358
Banded	1,426 ¹	± 878	384	± 384
Control	3,396	± 621	559	± 245

¹Significantly lower than any other treatment.

²No significant difference among the treatment means.

Effect of Treatments on Tree Growth, 1952-1956

Total height, d.b.h., crown length, and crown width of each experimental tree were recorded at the beginning of the experiment in 1952 and at its termination in the autumn of 1956. The 1952-data are summarized in Table 3, while the changes during 1952-1956, adjusted for the differences existing in 1952, are presented in Table 4.

During six years of study, the average released tree grew in d.b.h. 1.9 inches as compared with 1.4 inches for the average unreleased tree. Significant reductions in diameter growth were caused by girdling

and wiring unreleased trees. No other treatments affected diameter growth significantly. It is believed that in 1952, and probably in 1953 also, diameter growth of released girdled and wired trees was below that of released control trees, but by 1956 these differences were offset by the high rate of growth in the released portion of the experimental stand.

Height growth from 1952 to 1956 amounted to 6.0 feet and 7.8 feet for released and unreleased trees, respectively. Neither girdling nor strangulation affected height growth of released or unreleased trees.

In the spring of 1952 the average live-crown ratio was 44 percent for the released

TABLE 3. Average total height, diameter at breast height, crown ratio, and lateral crown area of experimental trees at the beginning of the experiment in 1952.

Treatment	Total height in feet	D.b.h. in inches	Live-crown ratio	Lateral crown area in square feet
<i>Girdled</i>				
Released	56	10.3	44	201
Unreleased	56	9.9	43	227
<i>Wired</i>				
Released	54	9.5	44	198
Unreleased	57	9.8	43	240
<i>Banded</i>				
Released	55	9.9	46	200
Unreleased	56	9.5	43	232
<i>Control</i>				
Released	54	9.5	44	195
Unreleased	56	9.6	42	219

TABLE 4. Summary of average growth and development of the experimental trees during the period 1952-1956.

Treatment	Released trees				Unreleased trees			
	Control	Girdled	Wired	Banded	Control	Girdled	Wired	Banded
Height growth (feet)	5.6	6.3	5.4	5.9	8.4	7.9	7.4	8.0
D.b.h. growth (inches)	1.91	1.93	1.74	1.96	1.41	-1.11**	1.22*	1.48
Change in percentage of live-crown ratio	+2.9	+5.3*	+5.0*	+4.3	-5.3	-4.4	-7.5*	-6.6
Change in lateral crown area (square feet)	+129	+150	+121	+127	-16	-19	-48**	-28

**Difference from control significant at the 1-percent level.

*Difference from control significant at the 5-percent level.

and 42 percent for the unreleased trees, but by the autumn of 1956 the live-crown ratio of released trees increased to 47 percent, while that of unreleased trees decreased to 37 percent. Wiring significantly increased the live-crown ratio of released trees, but it decreased live-crown ratio of unreleased trees. Girdling increased live-crown ratio of released trees, but it did not seem to affect the live-crown ratio of unreleased trees.

At the beginning of the experiment, average lateral crown area per tree was 193 and 219 square feet for released and unreleased trees, respectively. By the end of 1956 the average lateral crown area for released trees increased to 318 square feet, while that for unreleased trees decreased to 206 square feet. Except for the significant decrease in lateral crown area of wired unreleased trees, stem treatments did not affect lateral crown area of either released or unreleased trees.

Effect of Treatments on Food Reserves

Methods

Twig samples for determination of total nitrogen and of stored carbohydrates were collected in the late winter of 1954-55. Samples consisted of 1- to 2-year-old twigs from branches growing in the third whorl from the tip on the northwest side of the crown. It was assumed that only food stored in the bark and wood tissue of the young twigs could affect cone production, since extensive studies by Curtis (1920) indicated that carbohydrates translocated to the main stem or roots were used close to the place of storage, and did not return to the shoots.

Twig samples were dried at 90° C for 72 hours. The needles were then discarded and the stems ground in a Wiley mill using a 40-mesh screen. The ground material was stored in glass containers at room temperature until the summer of 1956 when the chemical analyses were made.

Total nitrogen was determined by a modified Kjeldahl method (Emerson,

1925). Reserve carbohydrates, including starch, sugars, and their intermediate products, were hydrolyzed to glucose with the commercial enzyme preparation "Clerase." The amount of glucose in the final solution was determined by the method of Whittmeyer-Hassid which involves titration against 0.01N solution of ceric sulfate using Setopaline C indicator (Joslin, 1950). Total nitrogen and reserve carbohydrates were expressed as percentage of oven-dry weight.

Results

One- to 2-year-old twigs of released control trees contained about 5 percent less reserve carbohydrates than did corresponding twigs of control unreleased trees (Table 5). It is assumed that the relatively low carbohydrate reserves in the released trees were primarily caused by the drain of increased seed production.

There was no indication that either girdling or strangulation affected the amount of reserve carbohydrates. The values for individual trees ranged between 6.0 and 11.7 percent for both released and unreleased trees, but were grouped usually between 8 and 9 percent.

Total nitrogen in twigs of released trees averaged 22 percent higher than in twigs of unreleased trees. The highest and the lowest values were 0.60 percent and 0.30 percent for the released and 0.52 percent and 0.15 percent for unreleased trees. Stem treatment did not affect amount of total nitrogen in twigs of released or unreleased trees.

The average carbon-nitrogen ratios for released and unreleased trees were 19 and 25 respectively, ranging between 14 and 30 for released trees and between 13 and 56 for unreleased trees.

Effect of Crown Release on Available Light and Soil Moisture

Methods

Light intensity was measured with a Weston illumination meter under the crown canopy of each fifth tree on July 11, 1956, which was sunny. Four measurements,

TABLE 5. Stored carbohydrates and total nitrogen in 1- to 2-year-old twigs expressed as percentage of oven-dry weight.

Treatment	Stored carbohydrates in percent	Total nitrogen in percent	Carbon-nitrogen ratio
<i>Girdled</i>			
Released	8.33	0.441	19.3
Unreleased	8.59	0.376	23.6
<i>Wired</i>			
Released	8.13	0.460	17.9
Unreleased	8.55	0.358	26.2
<i>Banded</i>			
Released	8.19	0.429	19.7
Unreleased	8.46	0.370	23.5
<i>Control</i>			
Released	8.18	0.436	19.1
Unreleased	8.57	0.357	26.1

distributed evenly on the edge of the crown projection and 5 feet above the ground, were made hourly between 9:30 am and 3:35 pm. While light measurements were taken under the crown canopy, full light intensity was recorded hourly in an open area adjoining the experimental stand.

In the spring of 1955 one Bouyoucos moisture block was buried 6 inches deep in the soil under the southwest edge of the crown projection of each fifth tree. This design made it possible to place a moisture block under one of the five trees in each experimental block with random representation of the treatments.

Soil moisture measurements were made weekly with a Wheatstone bridge from the beginning of June to the end of September during 1955. When dry periods occurred soil moisture content was measured every few days in an effort to record the number of days when soil moisture was at or near the wilting percentage.

Results

Light. Light intensities under the crowns of released and unreleased trees are given in Table 6. Between 8:30 am and 3:30

pm on a clear day in July the light intensity under released trees averaged 58 percent of the light intensity recorded in an open field. Light intensity under unreleased trees averaged 42 percent of the intensity in an open field. The difference between average light intensity under the canopy of released and unreleased trees was

TABLE 6. Variations in light intensity under tree crowns at various times of the day on July 11, 1956. Light intensities expressed as percentage of the light intensity in an open field.¹

Time interval	Released trees	Unreleased trees
	Percent	Percent
8:43- 9:52 am	60.2	37.0
10:10-11:15 am	60.9	43.8
11:34 am-12:51 pm	63.5	52.9
1:10-2:11 pm	68.1	48.0
2:38-3:26 pm	46.1	29.8
8:43 am-3:26 pm	58.0	42.3

¹Each value represents an average of four readings under 22 trees.

23 percent points between 8:30 and 9:30 am, it decreased to 10 percent points between 12 noon and 1:00 pm and gradually increased again in the afternoon up to 16 percent points between 2:30 and 3:30 pm.

The extreme light intensities under individual crowns were 44 and 73 percent for the released trees and 27 and 61 percent for the unreleased trees.

Soil moisture. Variations in soil moisture content under the crown canopy of experimental trees over a period of 110 days during the summer of 1955 are given in Table 7. The soil in the released and unreleased portion of the stand was at or above field capacity only immediately after rain or during a prolonged rainy spell. At other times the soil moisture was consistently higher in the released than in the unreleased portion of the stand. The dif-

TABLE 7. Variations in soil moisture content at a 6-inch depth on different dates. Observations taken under the same crown canopy during the summer of 1955.¹

Date (1955)	Soil moisture (percent of oven-dry weight)	
	Released trees	Unreleased trees
	Percent	Percent
June 13	6.6 ²	6.5
June 17	4.8	3.2
June 22	6.5	6.6
July 1	3.2	2.5
July 5	2.5	2.3
July 13	3.8	3.2
July 20	6.0	5.8
July 27	2.8	2.4
Aug. 1	6.3	6.4
Aug. 8	3.0	2.5
Aug. 22	11.0	11.0
Aug. 30	10.2	10.0
Sept. 30	10.8	10.8

¹Each value represents an average of 22 observations.

²Approximate field capacity = 10 percent; approximate wilting percentage = 2.5 percent.

ferences were particularly great during dry periods.

In general, unreleased trees were exposed to much greater fluctuation in available soil moisture than were released trees. During the 110 days of observation 6 inches of top soil under released trees remained at field capacity for 79 days, at intermediate moisture conditions for 26 days, and at or near wilting percentage for 5 days. The corresponding values for unreleased trees were 74, 26, and 9 days.

Only under 9 of 22 released trees did the soil moisture ever reach the wilting percentage, while the roots of 18 out of 22 unreleased trees remained for 4 or more days in soil at the wilting percentage. Soil moisture under several released trees remained at or near field capacity during the entire growing season. On the other hand the soil under some unreleased trees remained at or near the wilting percentage for 23 days. It should be noted that these 23 days represent the cumulative value for the entire growing season and were distributed over three dry periods in July and early August.

Tree Characteristics Correlated with Cone Production

Methods

The logarithm of the combined 1954 and 1955 cone crops of each tree was considered as dependent variable y , while the following seven tree characteristics were analyzed as independent variables:

X_1 = Logarithm of the number of cones produced in the period 1951 to 1953

X_2 = Diameter at the breast height in April, 1952 in inches

X_3 = Lateral crown area in April, 1952 in square feet

X_4 = Percentage of nitrogen in bark and wood tissue of 1- to 2-year-old shoots, collected in winter of 1954-55 from the third whorl from the tip and expressed on the basis of oven-dry weight of analyzed tissue

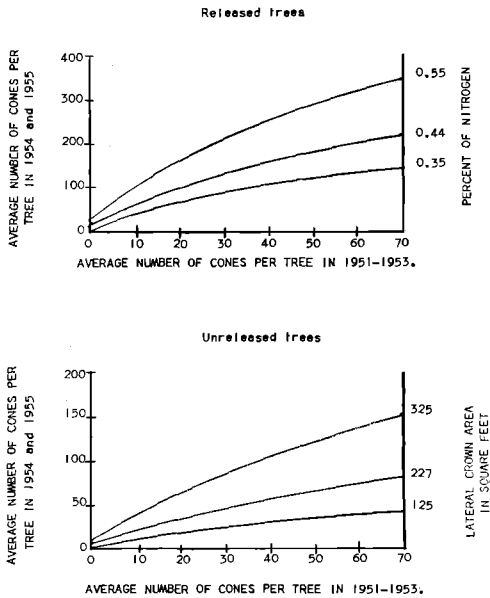


FIGURE 2. Tree characteristics correlated with cone production in 1954-1955.

X_5 = Percentage of carbohydrate reserves in winter of 1954-55 in the 1- to 2-year-old shoots expressed in terms of glucose on the basis of oven-dry weight of the analyzed tissue

X_6 = Ratio of X_5 to X_4 (carbon-nitrogen ratio)

X_7 = Ratio of the diameter one inch above the treatment to diameter at breast height in autumn of 1956

Results

Multiple regression analyses revealed that X_1 and X_4 were significantly correlated with cone production of released trees, while X_1 and X_3 were significantly correlated with cone production of unreleased trees. The resulting equations were as follows:

$$\text{Released trees: } \log(y + 1) = 0.534 + 0.543X_1 + 1.789X_4$$

$$\text{Unreleased trees: } \log(y + 1) = -0.062 + 0.700X_1 + 0.0029X_3.$$

Cone production of released and unreleased trees during 1954-1955 was highly

correlated with previous fruitfulness (Fig. 2.). In addition, cone production of the released trees was correlated with the amount of nitrogen in bark and wood tissue of 1- to 2-year-old shoots in the upper part of the crown, while cone production of the unreleased trees was correlated with the lateral crown area of the trees.

Discussion

A sevenfold increase in cone production of released trees during the third growing season and a fourfold increase during the fourth growing season, following crown release is attributed to the modified environment induced by the treatment. The entire crowns of the released trees were exposed to high light intensity. The roots had more growing space and consequently larger areas supplying them with mineral nutrients, nitrogen, and soil moisture. The reduced root competition also increased the amount of available soil moisture per tree, while the rapidly decomposing slash and litter probably increased the amount of nitrogen and minerals available to the released trees.

Thus the released trees were benefited by higher light intensities, more available soil moisture, by fewer and shorter periods of critical soil moisture, and probably by a higher amount of available nitrogen and mineral nutrients. Since loblolly pine requires full sunlight (Kramer and Decker, 1944) and adequate soil moisture (Kozlowski, 1949) for maximum rates of photosynthesis, the released trees were able to synthesize enough food for luxurious vegetative growth and abundant seed production. The abundance of food in the released trees during the period of experimentation was manifested by almost a doubling of the average lateral crown area, a high rate of diameter growth, and a relatively high production of cones. Supposition that insufficient reserve of nitrogen rather than of carbohydrates was the limiting factor in cone and seed production of released trees is supported by findings of

Potter and Phillips (1930), who concluded that carbohydrate levels of normally exposed plants are not critical for growth and fruiting, provided a certain amount of nitrogen is available.

Decreased light intensity and frequent shortage of available soil moisture in the unreleased portion of the stand probably resulted in a relatively low rate of photosynthesis and subsequent shortage in food. The inadequacy of food supply in unreleased trees was reflected in the decreased live-crown ratio and lateral crown area. It appears that unreleased trees were not able to synthesize enough food for both vegetative growth and prolific seed production. Consequently, any increase in the lateral crown area of the unreleased trees was accompanied by increased production of cones and seed. It is therefore assumed that food shortage was the limiting factor in cone production of the unreleased trees in 1954 and 1955.

The results of this experiment are in close agreement with the findings of Barrett (1940), Pomeroy and Korstian (1949), Trousdell (1950), Wenger (1953 and 1954), Lotti (1953), Easley (1954), and Girgidow (1956). These investigations emphasized the immediate effect of crown release on flower-bud formation manifested by abundant cone crops in the third growing season following treatment.

Girdling and strangulation interfere with normal physiological processes in the trees, and are believed to stimulate fruiting by concentrating carbohydrates in the upper parts of trees. Stimulation of fruiting is supposed to be proportional to the degree of interference with the downward flow of food in the phloem and should decrease in the order of girdling, wiring, and banding. Indeed, though statistically not always significant, cone production of released and unreleased trees followed the expected pattern, being highest for the girdled and lowest for the banded trees.

Girdling and strangulation favor seed production at the expense of vegetative

growth and development. Regirdling and severe strangulation cause starvation of the roots, decrease vegetative growth, and eventually cause death of treated trees. In the present experiment the death of one banded and two wired trees probably was the result of dehydration caused by inadequate absorption by starved roots.

The inhibitory effect of wiring and girdling on growth was particularly noticeable in the unreleased portion of the stand where carbohydrates and soil moisture supply were more critical than in the released portion. By the end of 1956 wired, unreleased trees had the smallest crown area and the lowest live-crown ratio of all experimental trees. More growth suppression resulted in wired trees than in girdled probably because the wires which were tightened in 1952 remained on the trees until the winter of 1954-55, while the incisions on the girdled trees were fully overgrown by the end of 1953 growing season.

The detrimental effect of girdling and strangulation on growth and development of trees was reported by Arnborg (1946), Bergman (1955), and Girgidow (1956).

In 1954 trees banded and released produced as many cones as did untreated released trees, but in 1955 they lagged considerably behind all other trees in cone and seed production. Banding, moreover, suppressed cone and seed production of unreleased trees. Holmes and Matthews (1951) also reported that metal bands failed to stimulate flower-bud formation in Corsican pine during the first growing season following treatment, but they caused peculiar coloration of the bark. The effect of banding on cone production and other aspects of tree physiology deserve further study.

The large number of viable seeds per cone in released trees probably resulted from an abundance of pollen as well as a high degree of cross-pollination. The amount of pollen in the unreleased portion of the stand was relatively small, and the chance of cross-pollination was also small

because of the few flowering trees and interference with free movement of pollen by the dense crown canopy.

The higher number of viable seeds per cone in the upper part of the crowns is believed to be the result of the abundance of pollen in general and of the greater chance of cross-pollination in the upper crowns. Rempe (1937) demonstrated that in forest stands the amount of pollen in the air decreased very rapidly from the tree tips toward the crown bases. Dengler (1932), and Plym-Forshell (1953) reported on the superior viability and germination of Scotch pine seed originated from the cross pollination, while Acatay (1938) found that seeds collected from the tips of Scotch pine trees had higher germination percentage than seeds from other parts of crowns.

Possibly some loblolly pine trees have inherited capacity for high seed production while others do not have this capacity. Regardless of treatment, in the present experiment, cone production of pine trees in 1954-55 was highly correlated with cone production during the three previous years. Several trees produced over 300 cones each although their morphological development was only average or even less. One released tree with a well developed crown and higher than average diameter did not produce a single cone during 6 years of observation. Pomeroy and Korstian (1949) and Grano (1958) also concluded that some loblolly pine trees had an inherent capacity for abundant seed production.

Generally, only well developed crowns and root systems insure abundant and continuous production of viable seed. The best long-term increase in seed production is achieved by heavy thinnings, which allow the crowns to develop more fully than in closed stands.

Application of Results in Silvicultural Practice

Cone and seed production of pulpwood-size loblolly pine trees can be increased considerably by full crown release a few years prior to final harvest cutting. A 25-

year-old loblolly pine tree 9 to 10 inches d.b.h. may produce up to 3,400 viable seeds in some years if its entire crown had previously been exposed to full sunlight for at least three growing seasons. In young loblolly pine stands the earlier that full crown release occurs, the higher the seed production.

Girdling and strangulation are less effective in stimulating seed production in pulpwood-size loblolly pine trees than is full crown release. When used as a supplement to crown release, girdling and strangulation are likely to be more harmful than helpful. Their beneficial effect on seed production is negligible, and the risk of losing trees to storm breakage or root starvation is high.

Full crown release may be considered a biologically sound and economically profitable silvicultural practice because it not only increases seed production but also accelerates growth. This practice makes it possible to grow loblolly pine on a pulpwood rotation and still benefit from the advantages of natural regeneration without additional cost.

Preharvest crown release can readily be combined with thinning at least three years prior to the final harvest for pulpwood. Even when a thinning has not been made before the harvest cutting, about 15 trees per acre could be released several years prior to harvest. The increased growth of released and of adjoining trees may in a few years offset the volume removed. Under normal conditions the removed trees would be merchantable and would provide an early income, while the better developed crowns and root systems of the released trees would insure better and more prompt seed production as well as a minimum risk of losing the seed trees from natural causes.

In selecting young trees of loblolly pine for preharvest crown release, their previous fruitfulness, crown size and crown density are the best indicators of their future seed productivity.

The present work indicates that fifteen

25-year-old seed trees per acre, when given ample growing space 4 years before harvest would be capable of producing 100,000 viable seeds in two years, an amount usually considered adequate to assure a satisfactory restocking of loblolly pine on average sites (Barrett 1940, Pomeroy and Korstian 1949, Trousdell 1950).

Summary

Beginning in 1952 a 5-year study was initiated on effects of crown release, partial girdling, wiring, and banding of stems on cone production of pulpwood-size loblolly pine trees.

Full crown release was the most successful method of stimulating cone and seed production. It resulted in a sevenfold increase in cone production the third year after release and in a fourfold increase the fourth year. Crown release almost doubled the number of viable seeds per cone and increased diameter growth and crown development.

Available light and soil moisture conditions were improved to a great extent in the released portion of the stand. The soil in the unreleased portion of the stand remained at the wilting percentage approximately twice as long as did the soil in the released portion of the stand.

Partial girdling and wiring of stems did not contribute significantly to cone and seed production of released or unreleased trees, but such treatments decreased diameter growth and reduced the live-crown ratio of unreleased trees. Banding suppressed cone production of released and unreleased trees and reduced by one-half the number of viable seeds per cone in the released trees.

In released trees cones borne on branches in the third whorl from the tip and above had more viable seeds per cone than did cones borne on the branches below the fourth whorl from the tip.

Regardless of treatment, cone production of experimental trees in 1954-55 was positively correlated with cone production in 1951-53. In addition to previous fruitfulness, cone production of released trees in

1954 and 1955 was also positively correlated with the amount of nitrogen in the bark and wood of the 1- to 2-year-old twigs in the upper part of the crown. The lateral crown area was positively correlated with cone production by unreleased trees in 1954 and 1955.

Neither the total amount of carbohydrate reserves in the bark and wood of 1- to 2-year-old twigs in the upper part of the crowns, nor the carbon-nitrogen ratio during the winter of 1954-55 was significantly correlated with cone production in 1954 and 1955.

Application of results in silvicultural practice was discussed, and preharvest crown release was recommended as a biologically sound and economically profitable silvicultural practice for stimulation of seed production in pole-size loblolly pine.

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