

EFFICIENCY OF SEED PRODUCTION IN SOUTHERN PINE SEED ORCHARDS

David L. Bramlett¹

ABSTRACT.--Seed production in southern pine seed orchards can be evaluated by estimating the efficiency of four separate stages of cone, seed, and seedling development. Calculated values are: cone efficiency (CE), the ratio of mature cones to the initial flower crop; seed efficiency (SE), the ratio of filled seeds per cone to the seed potential; extraction efficiency (EE), the ratio of extracted seeds per cone to the total seeds; and germination efficiency (GE), the ratio of germinated seeds per cone to the filled seeds. The product of these four efficiency values is the overall seed orchard to nursery efficiency (SO-NE). With SO-NE, the orchard manager can compare the actual yield of seedlings produced from the orchard to the maximum biological potential of a given flower crop to produce viable seeds. The two approaches to increasing production of seed orchards are to increase flower production and to increase CE, SE, EE, or GE values. Computation of efficiency values pinpoints major types of seed losses and shows where corrective actions should be concentrated.

The tree improvement program in the South now has many thousand acres of established pine seed orchards. The seeds from these orchards contain the improved growth, wood quality, and pest resistance of a new generation of forest trees. To economically meet the demand for these seeds, it is important that each orchard produce seeds efficiently.

The reproductive process begins with initiation of flower primordia and ends with seedlings. In this paper, however, I discuss only the development and maturity of seed after the flowers have been formed. The primary stages of seed orchard production discussed are cone development, seed yield per cone, extraction of mature seeds, and germination of filled seeds.

¹Plant Physiologist, Southeastern Forest Experiment Station, USDA Forest Service, Macon, Georgia.

CONE DEVELOPMENT

Survival and normal development of a high percentage of cones is critical because loss of a cone means loss of its entire set of seeds. For a given flower crop in the seed orchard, cone development can be evaluated in terms of cone efficiency. This value is the ratio of the harvested cones to the original flower crop.

$$\text{Cone efficiency} = \frac{\text{Number of harvested cones}}{\text{Number of female flowers initiated}} \times 100\%.$$

The calculated cone efficiency value gives the overall survival of a flower crop but it does not identify specific causes of cone mortality. In shortleaf pine (*Pinus echinata* Mill.) studies in Virginia, the majority of mortality occurred during the spring and summer following pollination. The average cone efficiency for flower crops from 1963-1969 was 29 percent; 61 percent of the potential cone crop was lost in the first year and only 10 percent lost in the second year (Bramlett 1972). To evaluate seasonal losses, a periodic count is necessary. The Georgia Forestry Commission Seed Orchard has utilized a subsample of 10 tagged branches on randomly chosen sample trees. The cones on the tagged branches were counted a total of 10 times during the cone developmental period and flower and cone mortality were recorded (Godbee and others 1977). DeBarr and Barber (1975) charted the development of a flower crop and identified specific causes of cone mortality on life tables.

Since cone efficiency is the percent survival of an initial flower crop, the actual number of original flowers strongly influences cone efficiency. With a constant cone efficiency a greater number of flowers are lost as the size of the flower crop increases. Conversely, if the number of cones lost in each flower crop remains constant, then the cone efficiency decreases for small flower crops and increases for large flower crops. A further complication occurs when the previous cone crop influences the succeeding crop in terms of increasing mortality the year following a year with abundant flowering. This increase apparently is the result of an increase in insect populations from the preceding year. For example, cone efficiency of a natural stand of shortleaf pine was only 3 percent in 1964 as a result of a severe spring frost in 1963. The following year a large flower crop was produced with a correspondingly high cone efficiency of 65 percent. The flower production remained relatively high for the next two years, 1966 and 1967, but mortality in numbers of cones increased annually and the cone efficiency likewise decreased. Flower production was again low in 1968 but cone efficiency remained at 25 percent. Flower production increased to its highest level in 1969 and the projected cone crop (based on first-year survival) would give a cone efficiency of approximately 48 percent.

SEED YIELD PER CONE

Once the cones are mature and harvested, the seed yield per cone can be measured and compared to the capacity of the cone to produce seeds. Each pine cone contains a series of scales spirally arranged on a central axis. The cone scales can be counted and classified as fertile or infertile in a cone analysis technique developed by Bramlett and others (1977). Average values for total number of scales on sampled cones from 4 southern pines were 87 for shortleaf, 111 for Virginia (*P. virginiana* Mill.), 135 for loblolly (*P. taeda* L.), and 149 for slash pine (*P. elliottii* Engelm.) (Bramlett 1974). The total number of scales per cone, however, is not an accurate measure of the capacity of the cone to produce seeds. To quantify the seed production capacity, only the fertile or seed bearing scales should be counted (Lyons 1956). The fertile scales occur in the upper one-half to two-thirds of the cone and are distinguished from the lower, infertile scales by the presence of functional ovules or seeds. Also, fertile scales are wider at the base and in general larger than infertile scales.

Each fertile scale is capable of producing two seeds. Thus, for each cone, seed potential is:

$$\text{Seed potential} = 2 \times \text{number of fertile scales.}$$

Seed potential is the maximum number of seeds that the cone is biologically capable of producing. The seed potential observed in sample cones averaged 170 for slash pine, 155 for loblolly pine, 88 for Virginia pine, and 87 for shortleaf pine (Bramlett 1974).

Although the seed potential establishes the upper biological boundary for seed production from a given cone, the actual yield of filled seeds is the only product of value from the orchard. Seed efficiency is determined by comparing the yield of filled seeds per cone with the seed potential for that cone.

$$\text{Seed efficiency} = \frac{\text{Number of filled seed}}{\text{Seed potential}} \times 100\%.$$

Seed efficiency can be used to evaluate the seed performance of a given tree, clone, or seed orchard. For example, a sample of slash pine cones in 1972 yielded 28 filled seeds per cone. Since the seed potential was 170 seeds; the seed efficiency was $28/170 = 16$ percent. Comparable values for loblolly, Virginia, and shortleaf pine were 24 percent, 19 percent, and 14 percent for the samples evaluated.

SEED LOSSES

Seed efficiency values ranging from 14 to 24 percent seemed disappointing, and it was important to examine the causes of seed failure in the remaining 86 to 76 percent of the potential seeds. The cone

analysis procedure was used to place all ovulates and seeds on the extracted cone scales into four classes: (1) First-year aborted ovules, (2) second-year aborted ovules, (3) empty seed, and (4) filled seed. After the losses in each class were estimated, specific causes of seed losses were sought.

First-year aborted ovules.--First-year aborted ovules are potential seeds that abort during the first growing season. In mature cones, therefore, they are no larger than normal ovules after one year of development. The wing develops normally, however, and these ovules are "wings without seeds."

First-year abortion of ovules was a major type of loss in slash pine and loblolly pine.. In 1972 sample cones, slash pine lost 110 seeds per cone and loblolly pine lost 69 seeds as first-year aborted ovules. These losses represented 65 percent and 44 percent of the seed potential for these two species.

The high losses in this category made it very important to identify specific causes. Two causes were known: Pollination failure (Sarvas 1962, McWilliam 1959), and feeding by seedbugs, particularly Leptoglossus corculus (DeBarr and Ebel 1973). The early instars of this insect are able to penetrate the conelet, puncture the integument and extract large portions of the ovule. Feeding damage of this type can be identified macroscopically and confirmed by microscopic examination (Bramlett and Johnson 1975). When feeding of seedbug occurs for an extended period, the conelet may also abort (DeBarr and Kormanik 1975).

In addition to these established causes of first-year ovule abortion, other causes are suspected. Apparently, for unknown reasons, some pollinated ovules do not develop. Also, fungi may cause ovule deterioration (Miller and Bramlett 1975), but specific details are not yet established.

Second-year aborted ovules.--Second-year aborted ovules survive the first year of development but abort during the second year before the seedcoat is well formed. These ovules appear resinous, collapsed, or necrotic in early summer. Frequently, resin streaks are also visible in the vascular cells of the scale. In addition to the large necrotic ovules, some aborted ovules produce a small seed coat but are not as large as a fully developed seed.

Heavy losses of this type were observed on shortleaf and Virginia pines. Shortleaf pine averaged 41 second-year aborted ovules per cone (47 percent) and Virginia pine had 31 (36 percent) in samples from unprotected natural stands. Sample cones of loblolly and slash pine had 23 and 17 second-year aborted ovules per cone or 15 percent and 10 percent of the seed potential.

The major cause of second-year aborted ovules in pines is feeding by pine seedbugs on the developing cones. Krugman and Koerber (1969) described feeding damage of Leptoglossus occidentalis on ponderosa pine (P. ponderosa Laws.). DeBarr (1967) identified two seedbugs that damage southern pine seed. DeBarr and Ebel (1974) increased seed yield in shortleaf and loblolly pine with screen cages and described ovule damage associated with feeding of Leptoglossus corculus. Bramlett and Moyer (1973) were able to eliminate almost all second-year aborted ovules in Virginia pine with protective screen wire cages that excluded seedbugs prevalent in the area.

These observations show that seedbug damage is responsible for most second-year abortion of ovules. The cause of the smaller, hardened, aborted ovules is not known. Some preliminary indications associated this type damage with moisture or nutritional stress during development.

Empty seeds.--All seeds have some remnants of gametophyte tissue and/or a shriveled or damaged embryo. They were formerly classed as empty if they would float in 95 percent ethanol, and they are now usually recognized by X-ray detection. In a broad sense, seeds damaged by seedbugs or fungi, and seeds with abnormal development can be grouped as empty seeds.

In a well-managed seed orchard, 85 percent of the seeds should be filled. In the absence of protection from insects, values below 50 percent have been observed. Known causes of empty seeds include insects, fungi, and embryonic lethal alleles.

Insect attack and damage seed in the nearly mature or mature cone. Unlike cone-destroying insects such as Dioryctria spp., the leaf-footed pine seedbug and the shieldback seedbug feed on seeds without leaving external signs of damage on the cone. External damage on the seedcoat may also be minimal, even when the embryo is killed (DeBarr 1970).

Insects are not the only cause of empty seeds in pines. Even when protective screen cages are used to exclude seed insects, empty seeds are found in the sample cones (Bramlett and Moyer 1973; DeBarr and others 1975; DeBarr and Ebel 1973). Many studies have shown an increase in the percentage of empty seeds following self-pollination (Franklin 1970). These empty seeds are the result of recessive embryonic lethal alleles that cause embryo mortality soon after fertilization. Although pines may have polyzygotic embryony, selfing and other forms of inbreeding increase the probability of embryo abortion in the pine ovule. Empty seeds are the result (Bramlett and Popham 1971). Empty seeds also occur following cross pollinations or wind pollinations. Embryo mortality following cross pollinations (with screen cage protection) are apparently due to the random matching of the recessive embryonic lethals (Bramlett and Pepper 1974).

Other classes of seed loss or damage include seedworm (Laspeyresia spp.) damage, abnormality, fungal infection, and incompletely filled seeds. The cumulative total of these seed losses is usually less than 10 percent and normally is not a serious problem in the seed orchard.

Filled seeds.--Filled seeds have the potential to germinate; they have healthy, undamaged gametophyte tissue, a normal embryo, and no evidence of fungi or other destructive pests. They are the end product of the seed orchard and represents the final yield from an initial crop of female flowers. As previously stated, the ratio of filled seed to the seed potential gives the seed efficiency per cone. Seed orchard efficiency is calculated by combining seed efficiency and cone efficiency.

$$\begin{aligned}\text{Seed orchard efficiency} &= \frac{\text{Cone}}{\text{Flowers}} \times \frac{\text{Filled seed}}{\text{Seed potential}} \times 100\% \\ &= \text{Cone efficiency} \times \text{Seed efficiency} \times 100\%.\end{aligned}$$

Seed orchard efficiency can be used to evaluate seed orchard performance. For example, an initial crop of 8,000 flowers per acre in a slash pine seed orchard would have a biological potential of 8,000 X 170 (seed potential) for slash pine or 1,360,000 seeds. Based on an average of 13,500 cleaned seeds per pound for slash pine, this yield would equal ca 100 pounds of seeds per acre. The fate of these seeds is determined by the amount of loss occurring during the development period. For example, under intensive management approximately 75 percent of the initial flowers could become mature cones. Losses would include not only insect damage, but other abiotic factors such as unharvested cones, wind damage, trees lost to lightning, etc. With a 75 percent cone efficiency and a similar 75 percent seed efficiency, the orchard would produce 56 percent of the biological potential, or 56 pounds of seeds per acre. This value may represent the upper limit that can be expected in seed orchards even under excellent management.

Under typical management, a seed orchard may produce 50 percent cone and seed efficiencies, but since seed orchard efficiency is the product of these two values, the overall efficiency is only 25 percent. Under poor or no management, seed efficiency may be below 10 percent. Cone efficiency X seed efficiency in a natural stand of shortleaf pine ranged from 0.5 to 17.4 percent during 5 years of observations and averaged about 4 percent (Bramlett 1972).

SEED EXTRACTION

The percentage of seed removed by extraction can be important to the overall seed efficiency. The primary factor is the degree of cone opening after heating in the extraction kiln. Poor cone opening may be associated with cones harvested too early, fungal damage, insect damage, or case hardening during storage. These causes combined

represent a net loss of seeds supplied to the nursery. The quantity of seeds lost during the extraction process can be estimated by comparing number of seeds extracted to the total number produced by the cone. This value is the extraction efficiency.

$$\text{Extraction efficiency} = \frac{\text{Number of seeds extracted}}{\text{Total number of seeds/cone}} \times 100\%.$$

SEED GERMINATION

When a seed germinates and produces a seedling, the final link between generations is complete. Germination is the subject of considerable literature but for this paper will simply be considered as the percentage of filled seeds that germinate normally during a specified test period. Germination efficiency (percent germinated) is determined for each cone.

$$\text{Germination efficiency} = \frac{\text{Number of germinated filled seeds}}{\text{Total number of filled seeds}} \times 100\%.$$

Germination of a pine seedlot is normally between 70 and 90 percent. The average germination efficiency value can be combined with previous efficiency values to estimate overall seed orchard to nursery efficiency.

SEED ORCHARD TO NURSERY EFFICIENCY

The ability of a seed orchard to produce not only seeds but seedlings can be evaluated as a product of the four separate efficiency statements, cone efficiency (CE), seed efficiency (SE), extraction efficiency (EE), and germination efficiency (GE). Thus, seed orchard-nursery efficiency (SO-NE) is:

$$\text{SO-NE} = \text{CE} \times \text{SE} \times \text{EE} \times \text{GE}.$$

Using this combined efficiency value, the seed orchard manager can evaluate the overall performance of a given flower crop to produce seedlings for the nursery. With excellent seed orchard management and protection, efficiency values of 75 percent are possible for CE and SE and 90 percent for EE and GE. Thus, $\text{SO-NE} = 0.75 \times 0.75 \times 0.90 \times 0.90 = 0.45$. This value of 45 percent efficiency may approach the upper biological limit for an operational seed orchard. Levels of SO-NE below 45 percent indicate that some improvements may be possible.

Godbee and others (1977) used SO-NE to evaluate an insecticide spray program in a Georgia Forestry Commission seed orchard. The SO-NE averaged 17 percent on plots treated with the insecticide, compared to 6 percent in the control plots. This evaluation indicated that the spray program was increasing the seeds and seedlings produced

in the orchard, yet substantial losses were still occurring. Modifications in the insect control program have now been implemented to provide more effective control.

Evaluation of seed orchard performance by computing efficiency values suggests two general ways to increase the seed production of seed orchards. The first is to increase flower production while holding values for CE, SE, EE, and GE constant. The second is to reduce seed losses during one or more of the developmental stages. The logical approach to reduce seed losses is to first evaluate seed production efficiency and identify and quantify the specific causes of seed losses. Once the seed losses are known, control measures can be prescribed to prevent or reduce the losses. If the orchard manager knows the impact of a specific loss and the cost of the control, he can evaluate the projected increase in seed efficiency and seed yield.

LITERATURE CITED

- Bramlett, David L. 1972. Cone crop development records for six years in shortleaf pines. *For. Sci.* 18:31-33.
- Bramlett, David L. 1974. Seed potential and seed efficiency, In Seed Yield from Southern Pine Seed Orchards Colloquium Proc. John Kraus (Ed). p.1-7. Ga. For. Res. Council., Macon, Ga.
- Bramlett, David L., E. W. Belcher, Jr., G. L. DeBarr, G. D. Hertel, R. Karrfalt, C. W. Lantz, T. Miller, K. D. Ware, and H. O. Yates, III. 1977. Cone analysis of southern pines - a guidebook. USDA For. Serv. Gen. Tech. Rept. SE-13, Southeast. For. Exp. Stn., Asheville, N.C., and Southeast. Area S&PF, Atlanta, Ga. (In press).
- Bramlett, David L., and C. J. Johnson. 1975. Pollination in a slash pine seed orchard. In Thirteenth South. For. Tree Improv. Conf. Proc. 1975: 161-165.
- Bramlett, David L., and E. L. Moyer, Jr. 1973. Seed losses reduced in Virginia pine cones by screen wire cages. USDA For. Serv. Res. Note SE-192, 4 p. Southeast. For. Exp. Stn., Asheville, N.C.
- Bramlett, David L., and W. D. Pepper. 1974. Seed yield from a diallel cross in Virginia pine. In Seed Yield from Southern Pine Seed Orchards Colloquium Proc., John Kraus (Ed.). p. 49-55. Ga. For. Res. Council., Macon, Ga.
- Bramlett, David L., and T. W. Popham. 1971. Model relating unsound seed and embryonic lethal alleles in self-pollinated pines. *Silvae Genet.* 20:192-193.
- DeBarr, G. L. 1967. Two new sucking insect pests of seed in southern pine seed orchards. USDA For. Serv. Res. Note SE-78, 3 p., Southeast. For. Exp. Stn., Asheville, N.C.
- DeBarr, G. L. 1970. Characteristics and radiographic detection of seedbug damage to slash pine seed. *Fla. Entomol.* 53:109-117.
- DeBarr, G. L., and L. R. Barber. 1975. Mortality factors reducing the 1967-1969 slash pine seed crop in Baker County, Florida--a life table approach. USDA For. Serv. Res. Pap. SE-131, 16 p. Southeast. For. Exp. Stn., Asheville, N.C.

- DeBarr, G. L., and B. H. Ebel. 1973. How seedbugs reduce the quantity and quality of pine seed yields. In Twelfth South. For. Tree Improv. Conf. Proc. 1973: 97-103.
- DeBarr, G. L., and B. H. Ebel. 1974. Conelet abortion and seed damage of shortleaf and loblolly pines by a seedbug, Leptoglossus corculus. For. Sci. 20:165-170.
- DeBarr, G. L., D. L. Bramlett, and A. E. Squillace. 1975. Impact of seed insects on control-pollinated slash pine cones. In Thirteenth South. For. Tree Improv. Conf. Proc. 1975:177-181.
- DeBarr, G. L., and P. P. Kormanik. 1975. Anatomical basis for conelet abortion on Pinus echinata following feeding by Leptoglossus corculus (Say). Can. Entomol. 107:81-86.
- Franklin, E. C. 1970. Survey of mutant forms and inbreeding depression in species of the family Pinaceae. USDA For. Serv. Res. Pap. SE-61, 21 p. Southeast. For. Exp. Stn., Asheville, N.C.
- Godbee, John F., T. S. Price, and David L. Bramlett. 1977. Effect of an insecticide spray program on slash pine seed orchard efficiency. In Fourteenth South. For. Tree Improv. Conf. Proc. 1977: (In press).
- Krugman, S. L., and T. W. Koerber. 1969. Effect of cone feeding by Leptoglossus occidentalis on ponderosa pine seed development. For. Sci. 15:104-111.
- Lyons, L. A. 1956. The seed production capacity and efficiency of red pine cones (Pinus resinosa). Can. J. Bot. 34:27-36.
- McWilliam, J. R. 1959. Interspecific incompatibility in Pinus. Amer. J. Bot. 46:425-433.
- Miller, Thomas, and D. L. Bramlett. 1975. Plant pathogenic microorganisms may be reducing cone production in seed orchards. In Thirteenth South. For. Tree Improv. Conf. Proc. 1975:129.
- Sarvas, R. 1962. Investigations on the flowering and seed crop of Pinus silvestris. Commun. Inst. For. Fenn. 53:198 p.