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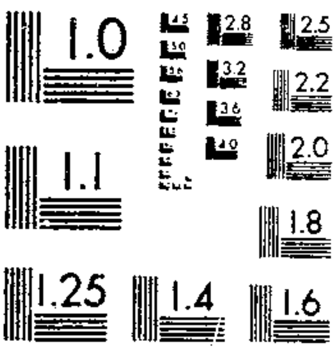

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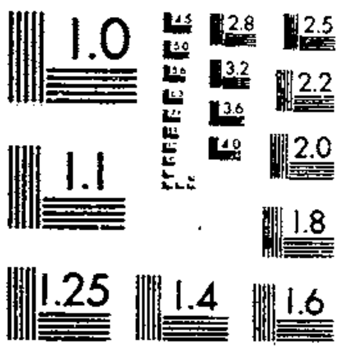

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Seed Crops of Forest Trees in the Pine Region of California

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CONTENTS

Seed Crops of Forest Trees in the Pine Region of California [1]

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To provide a better basis for silvicultural practices in the pine region of California, we are reporting the results of 28 years of study of seed crops. The study covered the development of cones, periodicity of cone crops, types of trees bearing cones, climatic and biotic factors affecting cone crops, and the dispersal of seed. The findings reported here should help foresters do a better job of planning silvicultural practices.

The pine forests in the pine region of California (fig. 1) contain about 11.2 million acres (*2*)[4] of commercial forest land on which ponderosa pine (*Pinus ponderosa* Laws.), sugar pine (*P. lambertiana* Dougl.), or Jeffrey pine (*P. jeffreyi* Grev. & Balf.), singly or in combination are the principal pine species. Mixed commonly with the pines are white fir (*Abies concolor* (Gord. & Glend.) Lindl.), incense-cedar (*Libocedrus decurrens* Torr.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and California red fir (*A. magnifica* A. Murr.).

Geographically, the pine forests occur in three subregions: (1) The Westside Sierra, where all species may be found in mixtures except that Douglas-fir is more common in the northern part and red fir in the higher altitudes; (2) the Eastside Sierra, where ponderosa and Jeffrey pines predominate and white fir and incense-cedar are associates; and (3) the Coast Range Pine, where ponderosa pine, sugar pine, white fir, Douglas-fir, and incense-cedar are found in mixture. The region has supplied the bulk of California's timber harvest, and it is certain to be a major source of timber in the State as forest management becomes more intensive.

After the period of clear cutting in the early part of the century, much of the cutting practice until recent years was based on a system of individual tree selection, utilizing the tree classes described by Dunning (*6*). Subsequently insect risk was shown in the Eastside pine type to be associated with recognizable vigor classes (*24*), and marking to remove the poorer risk trees was adopted rather generally. But further experience has now shown that individual tree selection is not an appropriate silvicultural method for the intolerant pines, particularly when regeneration cuts are made. Recognizing this shortcoming and the need for more positive silvicultural practices in the pine region, Dunning and his coworkers evolved the concept of Unit Area Control (*15*). Under this method, regeneration cuts in pine take the form of group selection, with definite provision made to

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[1] Submitted for publication April 13, 1956.

[2] The authors wish to acknowledge the participation in this study of a number of the present or former members of the staff of the California Forest and Range Experiment Station. Started by Duncan Dunning, formerly Chief of the Division of Forest Management Research, the study was continued under his general supervision until his retirement.

[3] Maintained at Berkeley, California, by the Forest Service, U. S. Department of Agriculture, in cooperation with the University of California.

[4] Italic numbers in parentheses refer to Literature Cited, page 47.

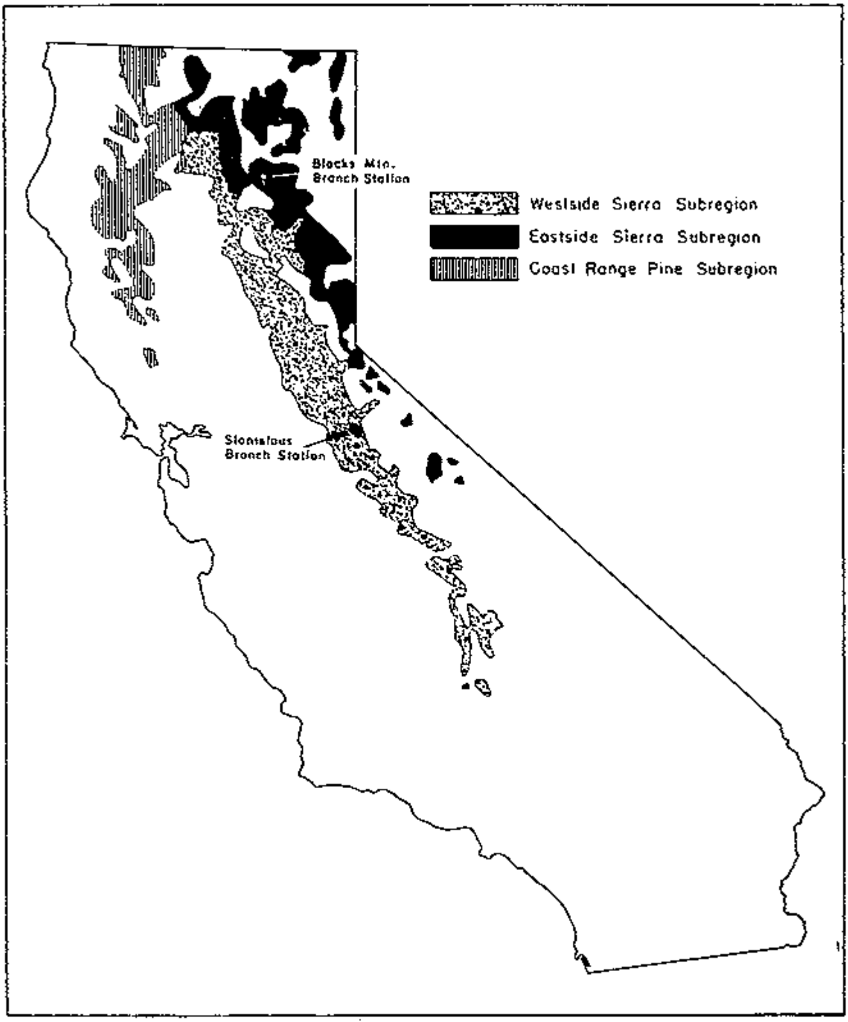

FIGURE 1.—The principal pine forests of California by subregions, with location of the study areas.

insure regeneration. With this added emphasis on providing for a new crop the forest manager must understand the seed-bearing characteristics in order that adequate seed trees be left. And for those older cutover areas not regenerating satisfactorily, knowledge of seeding habits provides clues to remedial measures needed to encourage regeneration.

This report presents the analysis of a great mass of data concerning the seed-bearing habits of trees, principally sugar pine, ponderosa pine, and white fir, on two study areas in the pine region. It summarizes for a 16-year period the number of cones borne on every ponderosa pine, sugar pine, and white fir on nearly 50 acres of plots in the Westside Sierra. No information is available for Douglas-fir which did not occur in the plots. All told, nearly 1,200 trees bore cones and were examined in one or more years. Inferences about cone crops were drawn from additional data for another 12 years. The report also summarizes the seed fall for 8 years in the same plots. During 4 years about 660 seed traps were exposed each year and in one year more than 1,000 seed traps were set out on these and additional temporary plots. In the second study area in the Eastside Sierra, as many as 840 seed traps in 1 year were used to measure the seed fall.

From this large quantity of data, perhaps the most comprehensive study of seed bearing to date in the United States, we can suggest the kind of trees, and how many, that should be reserved for seed trees. We are able to give some of the many reasons why seed crops fail, and in some instances, recommend how the losses may be avoided. And finally we estimate how much seed will be produced by certain trees or stands and how effective the seed might be in establishing reproduction.

These data contain measurement and population errors inherent in all such biological data. And so the silviculturist or land manager who follows the methods and practices presented should not expect to obtain results identical to ours even under similar conditions. This report, however, does provide much silvical knowledge essential to guiding better silviculture.

CONDUCT OF THE STUDY

Experimental Areas

Seed crops were observed chiefly in the vicinity of the Stanislaus Experimental Forest, Stanislaus National Forest, in the Westside Sierra subregion. The experimental forest is located at latitude 38° 10′ N., longitude 120°01′ W., at an elevation of 6,000 feet. Additional information was obtained at the Blacks Mountain Experimental Forest. Lassen National Forest, located at latitude 40°42′ N., longitude 121°10′ W., at an elevation of 5,700 feet, in the Eastside Sierra subregion.

Climatically, the Stanislaus study area is characterized by winters of heavy snow and a dry season extending usually from June to October. The annual precipitation averages about 35 inches, a large part of which falls as snow. The snow occasionally accumulates to 6 or 8 feet in depth. Summer maximum temperatures seldom exceed 95° F., and winter minimums may fall to −15°. Occasionally severe frosts occur in May or early June.

At Blacks Mountain Experimental Forest, the average precipitation is about 18 inches. The summer dry season may last from June to October, with maximum temperatures in the nineties and low relative humidity. Freezing temperatures often occur in June and early September. The temperature during the winter may drop as low as −25° F. and may never climb to 32° during some days. Snowfall is relatively light; an accumulation of 3 feet is about maximum.

Soils in the Stanislaus area are derived principally from diorite and grano-diorite and are classed principally in the Holland series. The ridgetops are usually capped with lava, from which Olympic soils have developed. At Blacks Mountain the parent material is largely andesite and lava-flow material, and the timbered soils fall in the Patterson series. These soils are common in the forests of the Westside Sierra and Eastside Sierra subregions.

The cover type in the Stanislaus study area is usually called "mixed conifer;" it contains ponderosa pine, sugar pine, white fir, and incense-cedar. Above 6,500 feet, Jeffrey pine and red fir are found with the other species. Site quality is classed (7) as I although small pockets may be rated as A and ridgetops as II or III (in this site scale, A is better than I and site V is poorest).

At Blacks Mountain ponderosa and Jeffrey pine predominate although on north slopes and higher elevations white fir may be fairly abundant. Incense-cedar is scattered throughout the forest. The site quality ranges from III to IV (7).

Both cone crops and seed dispersal were observed on the Stanislaus forest in permanent sample plots and in temporary plots on several cutover areas. Five permanent plots varying from 5.6 to 10.8 acres in size, were established to study the effect of cutting on stand development. All but a check plot were logged during the period 1923–29. The average stand in the plots before cutting was about 75,000 board-feet per acre. Different cutting systems gave reserve stands ranging from about 6,800 to 37,000 board-feet (table 1). Cutting reduced the proportion of pine in the stand and increased the white fir.

Seed dispersal was observed at Blacks Mountain on 21 experimental harvest-cutting plots established in the years 1938–41. Each plot was 20 acres in size. The cutting system and the average reserve volumes per acre for the series of plots cut during these 4 years were as follows:

Cutting method:	*Reserve volume per acre (board-feet)*
Silvicultural selection	14, 890
Sanitation-salvage	15, 550
Moderate partial cut	8, 260
Heavy partial cut	5, 090
Control (no cutting)	18, 380

TABLE 1.—*Reserve volume per acre by species and cutting method, Stanislaus National Forest plots*

Cutting method and plot number	Ponderosa pine	Sugar pine	White fir	Incense-cedar	Total
	Board-feet	*Board-feet*	*Board-feet*	*Board-feet*	*Board-feet*
Heavy partial cut—5	4, 410	4, 470	2, 630	240	11, 750
Heavy partial cut—9	1, 040	3, 700	3, 650	1, 470	10, 850
Economic selection—10	340	2, 270	27, 750	6, 680	37, 040
Very heavy partial cut—11	60	490	5, 400	750	6, 700
Control (no cutting)—12	16, 040	24, 480	40, 000	2, 060	82, 580

Cone bearing and seed dissemination were observed during a period of 28 years on the Stanislaus forest. The first observations were made in 1926 but this report covers mainly the period from 1933 to 1953, during which time cones were counted in 16 years. The project lapsed during the war years from 1943 through 1947. At Blacks Mountain Experimental Forest seed fall was first sampled in 1942 and again in 1945 and 1948.

Cone Counts

To obtain information on the periodicity of cone crops and on the types of trees bearing cones, trees in the Stanislaus plots were examined each summer, usually in August when aborted cones could be distinguished from normal cones. Every tree larger than 3.5 inches in diameter at breast height in these plots was numbered and described. With the aid of 6 x 30 binoculars, the cones in each tree were counted, along with cones freshly cut by squirrels and found on the ground. The number counted on the trees was multiplied by 1.5 on the assumption that two-thirds of the crown could be seen from a counting location, usually from the southern side of the tree for consistency.

Admittedly the counts and the use of the factor are subject to error. The error undoubtedly varied between species. The very large sugar pine cones are easy to see, and the adjusted counts are probably close to the actual number of cones on the tree. Ponderosa pine and white fir cones are smaller, and their habit of growing in clusters or densely packed along the twigs and limbs makes it very difficult to see all of them, particularly when cones are abundant. But the estimates are relative if not exact. Incense-cedar cones were not counted, because they are much too small and numerous to be counted with reasonable accuracy. Cone crops of incense-cedar were described as light, medium, or heavy for the entire stand.

Seed Trap Counts

Seed fall per acre was estimated from samples caught in seed traps. The traps, constructed of 1- by 4-inch lumber with ½-inch hardware cloth on the top and fly screen on the bottom, were approximately 2.8 feet square, inside dimension (fig. 2). The tops of the traps were solidly nailed to the frame and, to remove the seed, the traps were inverted and shaken over a canvas. The seeds from each trap were counted by species. Before 1936 all externally normal seeds were counted and reported. Beginning in 1936 all seeds were cut to determine soundness and only sound ones were included in the report of number of seeds per acre.

The intensity with which seed fall was sampled varied during the period of study. At the outset, about 2.5 traps per acre were placed on the Stanislaus plots. In 1937 the intensity of sampling in plots 9, 10, and 11 (table 1) was increased to 20 traps per acre, 2 traps being randomly located within each chain-square unit of the plot. This intensity of sampling continued as long as observations were made on these plots, through 1941, and required a great number of traps, 624 on the 3 plots. Seed fall on the other 2 Stanislaus plots was sampled from 1937 through 1941 at the original rate—2.5 traps per acre. In a study of seed fall on an experimental area cut over in 1948, seed traps were spaced mechanically at the rate of 10 traps per acre for estimates of seed fall in 1948 and 1952.

At Blacks Mountain the traps were distributed 1 chain apart in 5-chain lines. Two lines were located at random in each 5-acre subplot, and thus there were 40 traps per 20-acre plot. Trap locations were fixed on each plot so that each year the traps were placed in the

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FIGURE 2.—One of the seed traps used to sample seed fall.

same positions as in previous years. The traps were usually exposed until the middle of November.

During some or all years seed fell after the traps were picked up. Accordingly, figures on seed fall presented in this bulletin are somewhat less than the total fall.

Because of the differences in the intensity of sampling, seed fall estimates for the various years were computed by plots rather than by individual traps. Therefore, the fact that some plots had many more traps than others did not weight the estimate of the average towards the more heavily sampled plots.

DEVELOPMENT OF THE CONES

Flowering and Early Development

Knowledge of the time and rate of development of the flowers and cones can help the forester predict cone crops. Moreover, such information will help him understand some of the reasons why cone crops fail. The development of cones was studied for several years at the Stanislaus Experimental Forest. The dates of flowering and other stages of development which are reported from Stanislaus apply to that area and probably are not the same in parts of the pine region which differ phenologically.

The carpellate strobili of white fir were discernible in early May, and by middle or late May the conelets were almost 1 inch long.

Pollen shedding occurred during the last half of May. The cones were about 2 inches long by the first of July and reached full size in early August. They began to break apart and shed seed in late September or early October. A few cones, apparently sealed with resin, remained intact until December or later.

In ponderosa pine, the carpellate strobili were evident in the first part of June, appearing as distinct swellings at the base of the terminal bud of the shoot. At this time the staminate strobili were fully formed. By the last part of June, the conelets were about one-half inch long (fig. 3) and the pollen had been shed. The time of pollen shedding is in agreement with the dates of pollen collection reported by Duffield (*5*). The cones were almost 1 inch long by mid-July and grew to not much more than an inch in the fall. They continued development early the next spring, growing to more than 2 inches long by the middle of June. The cones reached full size in August and opened in late September or early October, shedding their seed.

The staminate strobili of sugar pine were apparent during the middle of June but no carpellate strobili were visible. By the middle of July the conelets were about ½ to 1 inch long, and pollen dissemination was starting (fig. 4). The pollen was shed by the first part of August, when the conelets were 1½ to 2 inches long. They grew to 2 to 3 inches at the end of the first year and developed rapidly the next year, reaching mature size in late August. Sugar pine cones shed their seed during the last of September or the first of October.

According to a few observations on the development of Jeffrey pine cones, they were about 1 inch long by the middle of July, by which time pollen had been dispersed. They attained a length of about 1½ inches in the fall and developed rapidly the second year, shedding their seed by the last of September or first of October.

Ripeness, Size, and Number of Seeds

For foresters who wish to collect seed, an index of ripeness, or cone maturity, is valuable. During the period of ripening, the cones slowly lose moisture, and as a result some measure of the weight may be used to indicate when the seeds are mature. The specific gravity is one measure that has been used. Freshly picked cones are placed in a liquid, such as kerosene, diesel fuel, or motor oil, of known specific gravity. If the cones float, their specific gravity is at least as low as the test liquid, and consequently the cones are considered ripe.

The specific gravity of ponderosa pine cones during the period when cones were judged to be ripe was 0.84. A density of 0.84 is in good agreement with the specific gravity of 0.86 reported to be the point at which ponderosa pine cones were ripe in the Northern Rocky Mountains (*18*). A solution of half kerosene and half linseed oil has a density of 0.86, suitable for this test.

Sugar pine cones were found to be ripe when the specific gravity had decreased to about 0.80 (*11*) or when the cones floated in kerosene. During the time the cones were ripening, the specific gravity decreased from 0.90 to 0.80 in a period of 1 month. Seed extracted from cones gathered at 3 dates in 1 month differed greatly in viability. The seed of the cones picked last was best.

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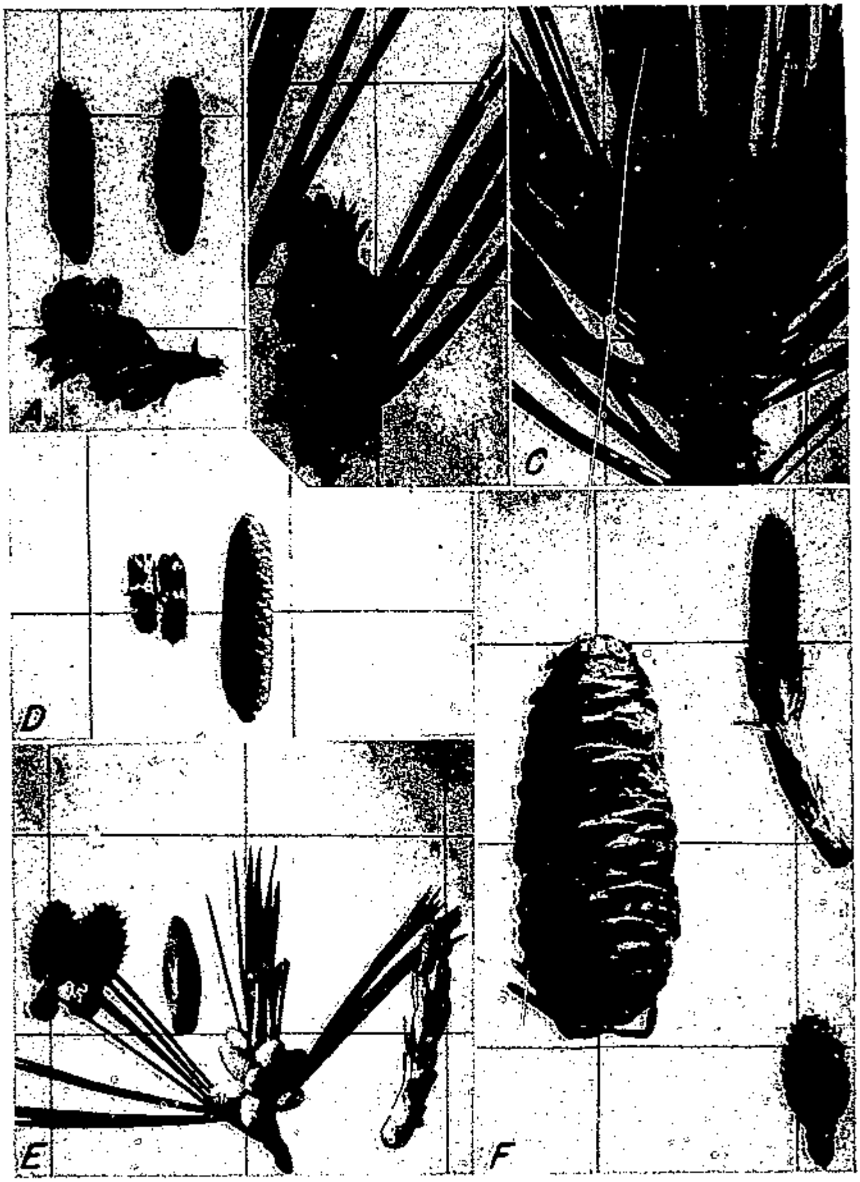

FIGURE 3.—Early development of white fir, ponderosa pine, and sugar pine cones (background grid is in 2-inch squares): *A*, June 2, 1938, white fir—*upper*, carpellate, *lower*, staminate strobili. *B*, June 2, 1938, ponderosa pine, carpellate strobili bud swelling at base of vegetative bud. *C*, June 2, 1938, ponderosa pine, staminate strobili. *D*, June 20, 1938, carpellate strobili—*left*, ponderosa pine, *right*, white fir. *E*, July 12, 1938, *left*, ponderosa pine carpellate strobili, *center*, sugar pine staminate strobili with carpellate strobili on either side. *F*, August 1, 1938, carpellate strobili—*left*, white fir, *upper right*, sugar pine, *lower right*, ponderosa pine.

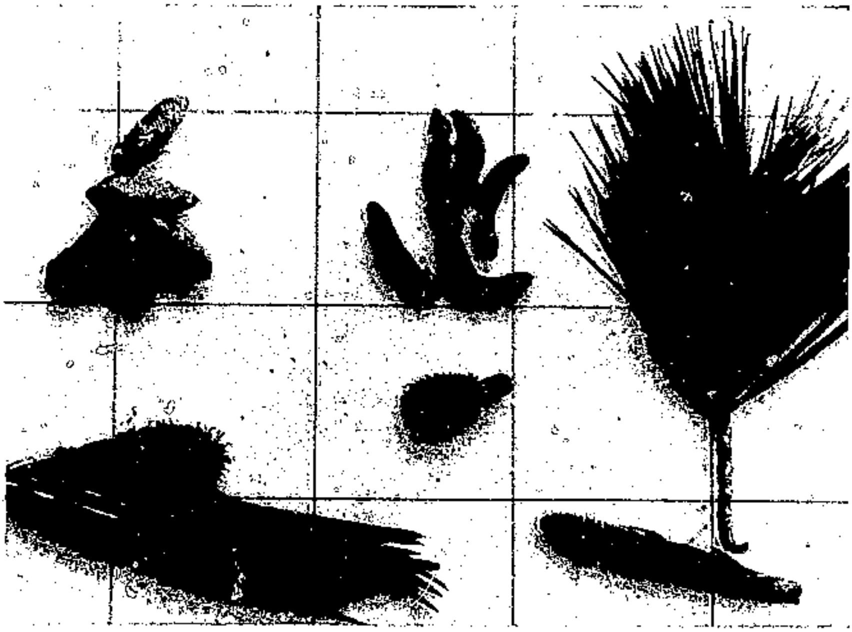

FIGURE 4.—Relative sizes of Jeffrey pine, ponderosa pine, and sugar pine strobili on July 12, 1937. *Upper*, staminate strobili, pollen already shed in Jeffrey and ponderosa pine. *Lower*, carpellate strobili.

Measurements of 100 white fir cones showed that the specific gravity was about 0.94 early in September, but no data are available as to what the specific gravity was in late September just before the cones broke apart.

Cone size varied greatly among species and within species. Mature sugar pine cones averaged 12.2 inches long; ponderosa cones, 4.1 inches; and white fir, 3.8 inches (table 2). Occasionally cones of sugar pine are found which measure 20 to 22 inches; ponderosa pine, 6 inches; and white fir, 5 inches. The cones were collected from several trees on any collection date and the data thus reflect variability within and between trees. For an additional estimate of cone size,

TABLE 2.—*Average length of mature cones of sugar pine, ponderosa pine, and white fir, California pine region*

Species and collection year	Length		Standard deviation	Basis
	Cm.	*Inches*	*Cm.*	*Number*
Sugar pine:				
1934	30.8	12.1	3.5	100
1941	31.2	12.3	4.1	212
1948	31.2	12.3	2.7	140
Ponderosa pine:				
1934	9.8	3.9	1.0	100
1940	10.8	4.3	1.3	279
White fir, 1940	9.7	3.8	1.0	100

cubic volumes of unopened cones were measured by water displacement as shown in the following tabulation:

Species:	*Volume per cone (cc.)*	*Standard deviation (cc.)*	*Basis (number)*
Sugar pine	871	114	382
Ponderosa pine	94	23	279
White fir	127	31	100

Seeds were extracted from cones of sugar pine, white fir, and ponderosa pine to obtain an estimate of the number of seeds per cone. The cones were picked from several trees. The numbers of developed seeds per cone are shown in the following tabulation:

Species:	*Collection year*	*Seeds per cone*	*Basis, number of cones*
Sugar pine	1934	209	100
Sugar pine	1941	[1] 219	185
Ponderosa pine	1934	69	100
Ponderosa pine	1940	[2] 73	204
White fir	1937	[3] 185	100

[1] Standard deviation 46; standard error 3.4.
[2] Standard deviation 23; standard error 1.7.
[3] Standard deviation 28; standard error 2.8.

On the basis of the number of scales which appeared to have carried seed, Fritz (*14*) estimated that sugar pine cones contained 230 seed apiece. His estimate agrees exceedingly well with those reported here in view of the different technique used in obtaining data.

For the amount of seed per bushel and the number of seed per pound, the Woody Plant Seed Manual (*33*) gives the following information:

Species:	*Seed per bushel of cones (ounces)*	*Cones per bushel (number)*	*Seed per pound (number)*
Sugar pine	25–32	20	1, 500– 3, 100
Ponderosa pine	9–32	200–300	6, 900–23, 000
Jeffrey pine	33	--------	3, 100– 5, 400
White fir	48–82	--------	8, 200–27, 200
Incense-cedar	32–48	--------	6, 400–29, 000

TYPES OF TREES BEARING CONES

An important feature of this study was the determination of the characteristics of trees which could be related to cone production. Characteristics studied were diameter, vigor, Dunning tree class, crown width, and crown length. Age was not studied as a separate variable but is reflected in the Dunning tree classes.

Cone Production and Tree Size

Cone production of the species studied varied considerably with tree size. Ponderosa pine and white fir generally began bearing cones at smaller sizes than sugar pine. About 13 percent of the ponderosa pines, and 4 percent of the white firs in the 3.6- to 7.5-

inch d. b. h. class bore cones, whereas none of the sugar pines in this diameter class produced cones (fig. 5). These percentages are all based on cone production in the 16-year period of record, during which each species had several very heavy seed years. Because of favorable conditions, then, all trees capable of producing cones had an opportunity to bear cones.

All of the ponderosa pines larger than 26 inches, and sugar pines larger than 30 inches bore some cones during the observation period. This was not true for white fir. One of the main reasons for the lack of cone production on the larger firs was the prevalence of fir American-mistletoe (*Phoradendron pauciflorum* Torr.) and western dwarfmistletoe (*Arceuthobium campylopodum* forma *abietinum* (Engelm.) Gill).

Not only did fewer small trees bear cones, but they bore fewer cones per tree per crop than larger trees. In computing the average size of crop per tree, we included only the years in which a tree bore cones. Thus the size of the crop was separated from the frequency of crops. Sugar pines under 14 inches in diameter averaged fewer than 8 cones per tree per crop during the 16-year period. At 22 inches the number of cones was 10 per tree. Only among trees about 30 inches and larger did cone production begin to increase significantly (fig. 6). The trend of cone production suggests that sugar pine cone crops may continue to increase in size with increase in diameter, an interpretation which is not correct when the trees become decadent.

For trees of the same diameter, ponderosa pine produced more cones than sugar pine. The average 16-inch ponderosa pine bore about 50 cones per crop, against 10 for a 16-inch sugar pine. At 38 inches the average crop for ponderosa pine was 200 cones, compared

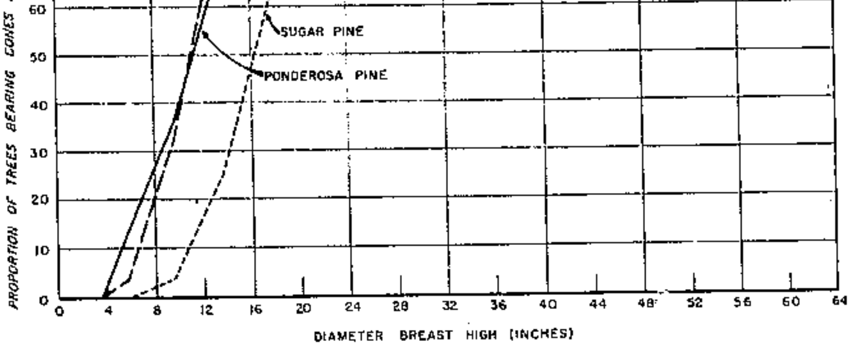

FIGURE 5.—Proportion of trees bearing cones by d. b. h. classes during an observation period of 8 to 16 years.

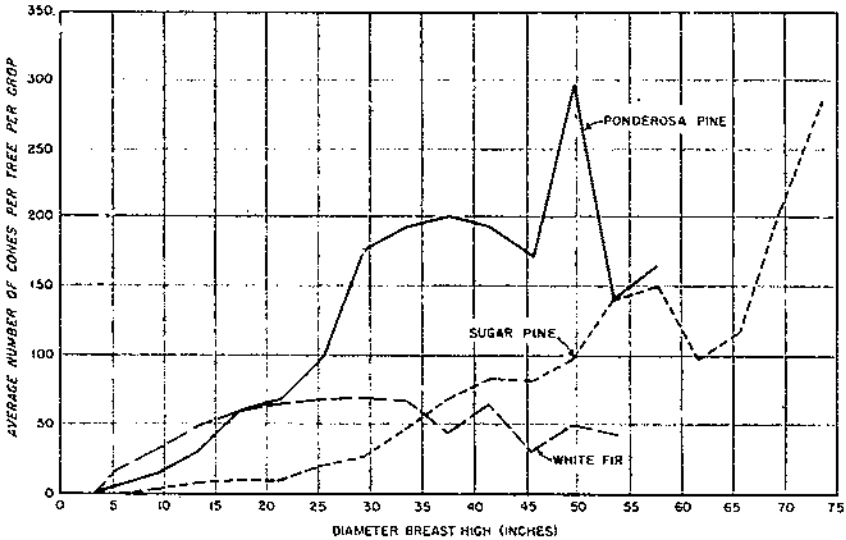

FIGURE 6.—Average number of cones per tree per crop by diameter classes and species on the Stanislaus National Forest (tree basis).

with 70 for sugar pine. Above 38 inches the spread between the two species decreased because cone production on ponderosa pine declined and sugar pine produced increasingly larger crops.

Small white fir trees produced larger average cone crops than the pines. In diameters less than 18 inches white fir produced more cones than ponderosa pine, and in diameters less than 36 inches it produced more cones than sugar pine. Beyond these diameters, cone production in white fir was much lower than in the pines. Cone production in white fir reached a peak at about 30 inches and then gradually dropped off with further increase in diameter.

The maximum number of sugar pine cones produced by an individual tree was 848 on a 48-inch tree in 1952 (fig. 7). This was equivalent to about 170,000 seeds, or about 85 pounds of seed, from a single tree. The second largest number of cones was 802 on a 58-inch tree in the same year. This latter tree, when 56 inches in diameter in 1936, bore 694 cones. Ponderosa pine bore even greater numbers of cones, for the maximum estimated was 2,250 on a 40-inch tree in 1926; the equivalent of about 160,000 viable seeds. The second highest number of cones on a ponderosa pine was 2,010 on a 35-inch tree, also in 1926. Individual white firs also produced large numbers of cones. The maximum recorded, on a 25-inch tree in 1948, was 987 cones containing approximately 190,000 seeds. The second highest was 741 cones on a 29-inch tree in 1948. Both of the white fir estimates probably are somewhat low because of the difficulty of counting all the cones during heavy crops.

As a measure of the yield of individual trees, the total cone production of single trees for 16 years was summed. The most productive sugar pine was a 55-inch tree which bore 2,370 cones in 16 years. A 36-inch ponderosa had 3,635 cones, and an 18-inch white fir had 1,663 cones in the same period.

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FIGURE 7.—A 48-inch d. b. h. sugar pine bearing an estimated 848 cones in 1952 on the Stanislaus National Forest.

The major source of pine cones was trees larger than 20 inches in diameter. None of the ponderosa pines less than 20 inches had 500 or more cones in the 16-year period, whereas 50 to 100 percent of the larger ones bore at least 500 cones (table 3). Sugar pines did not bear more than 500 cones until they were 28 inches. The sugar pines larger than 28 inches were also less productive than ponderosa pine. On the other hand, 5 percent of the white firs in the 11.6–15.5 inch diameter class bore 500 or more cones. In no case, however, did more than 23 percent of the firs in any diameter class produce more than 500 cones. In general, a larger proportion of the pines bore 500 or more cones than did white fir.

These general trends were also true for trees bearing at least 1,000 cones. A greater proportion of ponderosa pine than of sugar pine or white fir bore this number of cones; relatively few of the firs had more than 1,000 cones in the 16-year observation period. All in all, the best cone producers were the larger pines (20 inches and larger for ponderosa pine and 30 inches and larger for sugar pines) and the smaller firs (trees from 12 to 36 inches).

Table 3.—*Proportion of dominant trees that produced 500 or more and 1,000 or more cones in 16 years, by species and d. b. h. classes, Stanislaus National Forest plots*

D. b. h. class (inches)	Trees that produced 500 or more cones			Trees that produced 1,000 or more cones		
	Ponderosa pine	Sugar pine	White fir	Ponderosa pine	Sugar pine	White fir
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
3.0–7.5	0	0	0	0	0	0
7.6–11.5	0	0	0	0	0	0
11.6–15.5	0	0	5	0	0	0
15.6–19.5	0	0	11	0	0	1
19.6–23.5	50	0	14	7	0	5
23.6–27.5	70	0	16	40	0	5
27.6–31.5	100	7	23	73	0	5
31.6–35.5	89	25	20	89	0	3
35.6–39.5	90	50	3	60	17	0
39.6–43.5	71	50	17	57	12	0
43.6–47.5	75	50	7	25	12	0
47.6–51.5		57	8		43	0
51.6–55.5	100	100	0	50	67	0
55.6–59.5	100	75	0	100	50	0

Cone Production and Tree Condition

Cone production also varied with recognizable tree and crown classes and with foliage vigor and crown development. Trees in 3 of the 7 Dunning tree classes (fig. 8 and table 4) were the most consistent cone bearers and produced most of the cones; these were tree classes 1, 3, and 5. All class 3 and class 5 pines and all class 3 white firs bore at least 1 cone in at least 1 of the 16 years of record (table 5). Ninety-six percent of the class 5 white firs produced 1 or more cones. Among class 1 trees, 57 percent of the ponderosa pine, 46 percent of the sugar pine, and 63 percent of the white fir also bore some cones.

Most of the class 4 trees of all 3 species produced cones, but comparatively few of the sample pines were in this class. Among class 2 trees, which might be expected to be comparatively poor producers, 12 to 34 percent bore cones. Several class 6 and 7 trees, usually poor producers, also bore cones. But consistency of cone bearing alone was not a good measure of productivity. It was necessary to consider the actual number of cones per tree as well in order to show the effectiveness of certain types of trees in producing seed.

The class 1, 3, and 5 pines and class 1 firs bore the most cones. Twenty-five percent of the cone-bearing ponderosa pines, and 22 percent of the sugar pines, were class 3 trees. They bore about half

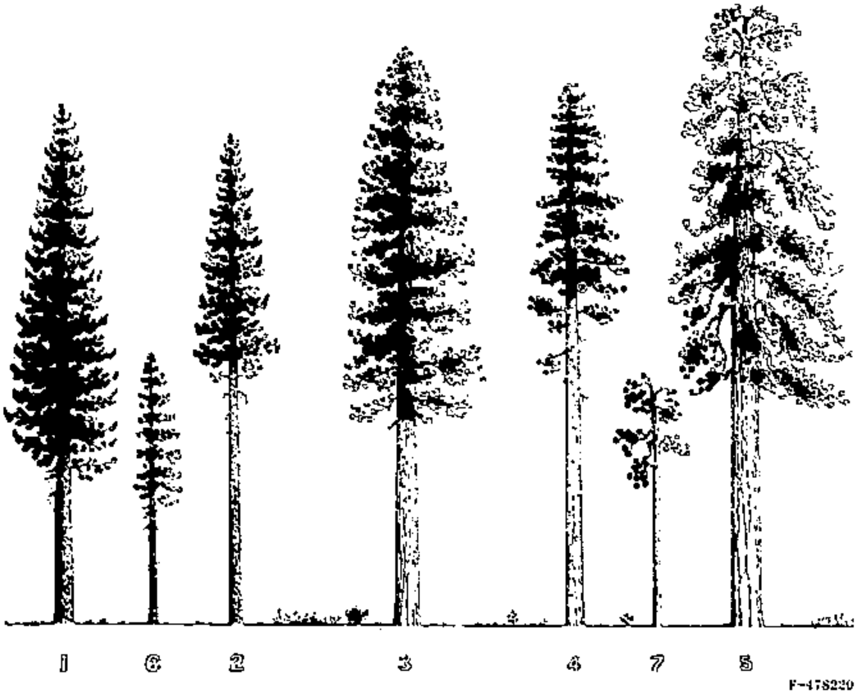

FIGURE 8.—Dunning tree classes, selection stands, ponderosa pine (*6*).

TABLE 4.—*Description of Dunning tree classes* [1]

Tree class	Age class	Position	Crown length	Crown width	Form of top	Vigor
1	Young or thrifty mature.	Isolated or dominant; rarely codominant.	At least 65 percent of total height.	Average or wider.	Pointed	Good.
2	do	Usually codominant; rarely isolated or dominant.	Less than 65 percent of total height.	Average or narrower.	do	Good or moderate.
3	Mature	Isolated or dominant; rarely codominant.	At least 65 percent of total height.	Average or wider.	Round	Moderate.
4	do	Usually codominant; rarely isolated or dominant.	Less than 65 percent of total height.	Average or narrower.	do	Moderate or poor.
5	Overmature	Isolated or dominant; rarely codominant.	Any size	Any size	Flat	Poor
6	Young or thrifty mature.	Intermediate or suppressed.	Any size but usually small.	Any size but usually small.	Round or pointed.	Moderate or poor.
7	Mature or overmature.	do	do	do	Flat	Poor.

[1] Source: DUNNING, DUNCAN. A TREE CLASSIFICATION FOR THE SELECTION FORESTS OF THE SIERRA NEVADA. Jour. Agr. Res. 36: 755–771, illus. 1928.

TABLE 5.—*Trees bearing 1 or more cones in 16 years, by species and Dunning tree classes, Stanislaus National Forest plots*

Dunning tree class	Ponderosa pine			Sugar pine			White fir		
	All	Bearing		All	Bearing		All	Bearing	
	Number	*Number*	*Percent*	*Number*	*Number*	*Percent*	*Number*	*Number*	*Percent*
1	75	43	57	194	89	46	776	489	63
2	31	10	32	182	22	12	621	214	34
3	25	25	100	39	39	100	66	66	100
4	1	1	100	6	5	83	33	29	88
5	15	15	100	16	16	100	75	72	96
6	44	6	14	298	2	1	934	33	4
7	3	0	0	4	1	25	11	4	36
Total or average	194	100	52	739	174	24	2,516	907	36

of the cones (table 6). Almost all of the remaining ponderosa and sugar pine cones were on class 1 and 5 trees. By contrast, 68 percent of the total cone production of white fir was on class 1 trees, which made up 54 percent of the cone-bearing white firs. About 10 percent of the fir cones were on the 24 percent of the white fir trees in class 2. Most of the remaining fir cones (about 20 percent) were on class 3 and 5 trees.

Because the various tree classes were not equally represented in the study area, their relative production does not indicate the cone-bearing capacity of individual trees. When cone production was averaged for individual trees, the class 3 trees were found to be the most prolific cone bearers among both ponderosa pine and white fir (table 6). For the white fir stand as a whole, the class 1 trees produced more cones partly because more trees existed in this class. But taken as individuals, the class 3 trees were more prolific and the class 1 trees ranked second. Among the sugar pines, class 5 trees were best.

Dominant trees were by far the most prolific of the crown classes. Practically all of the cones on ponderosa and sugar pines were produced on dominant trees, a fact of extreme silvicultural significance. Codominants produced only 1 to 1.5 percent of the pine cones; intermediate and suppressed crown classes, only a small fraction of 1 percent (table 7). Almost 88 percent of the fir cones were produced on dominant trees, and about 12 percent on codominants. As in the pines, intermediate and suppressed firs contributed practically no cones.

The fact that most of the cones were found on the dominant trees should not be interpreted to mean that all dominant trees were good producers. Actually, dominant trees were not alike; they varied considerably in width and length of crown and in vigor of foliage. These criteria were thought to be objective enough that they could be used in selecting good seed trees. Vigor was judged chiefly by density, length, and needle complement of the foliage, but the judgement was also influenced by color of needles. Study trees were classified as to crown development and vigor in 1946. Although some changes in condition

TABLE 6.—*Distribution of cone-bearing trees and of cones, 16-year average, by Dunning tree class, Stanislaus National Forest plots*

Dunning tree class	Ponderosa pine			Sugar pine			White fir		
	Trees	Cones	Cones per tree	Trees	Cones	Cones per tree	Trees	Cones	Cones per tree
	Percent	*Percent*	*Number*	*Percent*	*Percent*	*Number*	*Percent*	*Percent*	*Number*
1	43	29.4	571	51	20.8	99	54	67.8	219
2	10	0.9	73	13	1.1	21	21	9.8	73
3	25	51.4	1,716	22	50.9	555	7	11.3	270
4	1	(1)	39	3	0.4	37	3	2.0	108
5	15	18.3	1,017	9	26.8	712	8	8.5	180
6	6	(1)	6	1	(1)	3	4	0.6	29
7	0			1	(1)	7	(2)	0.0	13
Total	100	100.0		100	100.0		100	100.0	
	Number	*Number*		*Number*	*Number*		*Number*	*Number*	
Basis	100	83,497		174	42,489		907	157,984	

[1] Less than 0.1 percent.
[2] Less than 1 percent.

TABLE 7.—*Cone production by crown class and species, 16-year record, Stanislaus National Forest plots*

Crown class	Ponderosa pine			Sugar pine			White fir		
	Total cones produced		Cones per tree	Total cones produced		Cones per tree	Total cones produced		Cones per tree
	Number	*Percent*	*Number*	*Number*	*Percent*	*Number*	*Number*	*Percent*	*Number*
Dominant	82,692	99.03	906	41,836	98.46	291	138,334	87.56	221
Codominant	767	0.92	70	640	1.51	24	18,655	11.81	77
Intermediate and suppressed	38	0.05	6	13	0.03	4	995	0.63	27
Total	83,497	100.00		42,489	100.00		157,984	100.00	

of the trees had occurred since the beginning of the study, most changes were small.

As a simple indicator of productivity, the bearing of 500 or more cones by a tree in 16 years was chosen as the standard. Although this is admittedly an arbitrary standard, it serves to segregate the better yielding from the poorer yielding trees.

The expected relationship between size and vigor of crown and productivity of cone bearing was not evident from the record of all dominant trees (table 8). Dominants with small crowns and poor foliage vigor seemed to produce as well as, or better than, the larger, more vigorous ones. But when the analysis was restricted to trees which had borne 500 or more cones, a relationship of cone production to crown size and vigor was found. In this restricted group, most of the heavy producing trees were of moderate or good vigor and possessed a crown of moderate or better length and width. For example, 89 percent of the ponderosa pines were of good or moderate vigor, 75 percent had a medium or wide crown, and 77 percent had a medium or long crown (table 9). Even more trees of the other two species were in the moderate or good classes.

Why was the relationship evident in this restricted group of dominant trees and not in all the dominant trees? The reason appears to be that "all dominants" (table 8) included a great many small trees of Dunning tree class 1 which bore few or no cones. Counting these small trees obscured the effect of crown size and vigor on productivity of those which did bear cones. When only the trees which bore 500 or more cones were considered (table 9), it was clearly demonstrated that the size of the crown and the vigor of the foliage affected cone production.

TABLE 8.—*Number of dominant trees and percent bearing 500 or more cones in 16 years, by species and by crown development and vigor, Stanislaus National Forest plots*

Crown development and vigor classes	Ponderosa pine		Sugar pine		White fir	
	Dominant trees	Bearing 500 or more cones	Dominant trees	Bearing 500 or more cones	Dominant trees	Bearing 500 or more cones
	Number	*Percent*	*Number*	*Percent*	*Number*	*Percent*
Total	115		244		893	
Vigor:						
Poor	11	55	9	11	109	6
Moderate	32	56	73	32	185	7
Good	72	40	162	2	599	9
Crown width:						
Narrow	26	50	27	0	140	5
Medium	65	49	157	8	514	10
Wide	24	33	60	27	239	7
Crown length:						
Short	19	63	30	17	72	3
Medium	45	51	84	18	258	9
Long	51	35	130	6	563	9

TABLE 9.—*Number and distribution of dominant trees producing 500 or more cones in 16 years, and distribution of cones, by crown development and foliage vigor, Stanislaus National Forest plots*

Crown development and vigor classes	Ponderosa pine			Sugar pine			White fir		
	Trees		Cones	Trees		Cones	Trees		Cones
	Number	*Percent*	*Percent*	*Number*	*Percent*	*Percent*	*Number*	*Percent*	*Percent*
Total	53	100	100	28	100	100	74	100	100
Foliage vigor:									
Poor	6	11	7	1	4	3	7	9	7
Moderate	18	34	32	23	82	82	13	18	18
Good	29	55	61	4	14	15	54	73	75
Crown width:									
Narrow	13	25	16	0	0	0	7	9	7
Medium	32	60	64	12	43	37	50	68	65
Wide	8	15	20	16	57	63	17	23	28
Crown length:									
Short	12	23	18	5	18	14	2	3	2
Medium	23	43	39	15	54	45	24	32	29
Long	18	34	43	8	28	41	48	65	69

SIZE AND FREQUENCY OF CONE CROPS

Even though trees of some diameters and classes produced a great number of cones, only a few bore cones regularly. To demonstrate the frequency of crops, the 16 years of cone count data were supplemented with cone counts from a single plot for an additional 7 years and with estimates of seed crops inferred from seedling records in the study plots on the Stanislaus forest. These supplemental data, of course, are not nearly as reliable as the main body of the record, but their use helps fill in information on cone production for several years when cones were not counted.

Annual Cone Production Per Acre

The number of cones produced each year is one way of showing the frequency of cone crops. Accordingly, the average annual cone production per acre was determined for 100 ponderosa pines, 174 sugar pines, and 907 white firs on the 46.8 acres of study area on the Stanislaus National Forest:

	Cones produced per acre		
Year: [1]	*Ponderosa pine (number)*	*Sugar pine (number)*	*White fir (number)*
1933	237	65	24
1934	203	90	685
1935	0	2	5
1936	338	158	67
1937	12	13	54
1938	18	52	38
1939	5	0	5
1940	72	2	296
1941	166	138	36
1942	7	1	38
1948	105	113	1,622
1949	154	4	33
1950	7	0	0
1951	0	0	466
1952	291	267	6
1953	169	4	0

[1] No data for 1943–47.

Ponderosa pine produced from 0 to 338 cones per acre per year. No ponderosa pine cones occurred in 1935 and 1951. The largest number was in 1936. Other good seed years were 1952, 1933, and 1934.

The best sugar pine cone crop occurred in 1952 with 267 cones per acre. Other good seed years were 1934, 1936, 1941, and 1948. Each of these good sugar pine seed years was followed by very poor seed years. A heavy buildup of the sugar pine cone beetle (*Conophthorus lambertianae* Hopk.) in years of good crops apparently prevented one good crop being followed by another. The beetles must have destroyed the succeeding crop.

White fir bore from 0 to 1,622 cones per acre per year. The poorest seed year was in 1950 when no cones were found on any of the trees. The best seed year for white fir was 1948 with 1,622 cones per acre.

Sometimes good seed crops of all three species coincided, as in 1934 and 1948. In several other years heavy seed crops of two of the species happened the same year. In general, good seed years coincided more often for the the two pines than for either of the pines and white fir. Since the pines each require 2 years for cone development after the flower buds have been formed but white fir requires only 1 year, some climatic or physiological factors might tend to favor coincidence of cone crops of the two pines but not of the pines and fir.

Sometimes poor seed crops of all three species coincided. In 1935, no cones occurred on ponderosa pine and only 2 and 5 cones per acre respectively for sugar pine and white fir. In 1939, there were only 5 ponderosa pine cones per acre, no sugar pine cones, and 5 white fir cones. Other poor seed years for all three species were 1942 and 1950.

Annual Cone Production by Individual Trees

The average number of cones borne annually by dominant trees provides another basis by which to compare yearly cone production and to show the frequency of various size cone crops. For this comparison, only the crops of dominant trees larger than 19.5 inches were tallied. Most of the cone production for the two pines was included, but an appreciable number of cones borne on the smaller dominant white firs and all the codominant fir trees was omitted.

The number of cones borne on dominant ponderosa pines varied a great deal during the study period. The maximum cone production was in 1926, with an average of 299 cones per dominant tree. The poorest seed year was in 1935 when no ponderosa pine cones were observed on the plots. This year of lowest cone production preceded the second best year, 1936, in which there was an average of 228 cones per dominant tree. Only 5 other years have an average of more than 100 cones per dominant tree (fig. 9).

Cone production on dominant sugar pines also showed considerable variation during the period. On dominant sugar pines larger than 19.5 inches in diameter, the highest average yield was 109 cones per tree in 1952. The second highest yield was 99 cones per tree in 1931. None of the sugar pines on the plots produced cones in 1939, 1950, and 1951.

The highest average number of cones per dominant white fir was 254 cones per tree in 1948. In 1928, 1934, 1943, and 1951, the average fell between 50 and 100 cones per tree and in all the remaining years except 1940 it was less than 10 cones per tree.

Frequency by Size of Crop

To summarize the frequency of cone crops in a more general way, a cone crop index was devised. Based on the average number of cones on dominant trees larger than 19.5 inches, which produced the bulk of the cones, this index contains 5 classes of crops:

	Cones per dominant tree larger than 19.5 inches d. b. h.	
	Ponderosa pine (number)	*Sugar pine or white fir (number)*
Cone crop rating:		
None	0	0
Light	1–20	1–10
Medium	21–80	11–40
Heavy	81–160	41–80
Very heavy	161 or more	81 or more

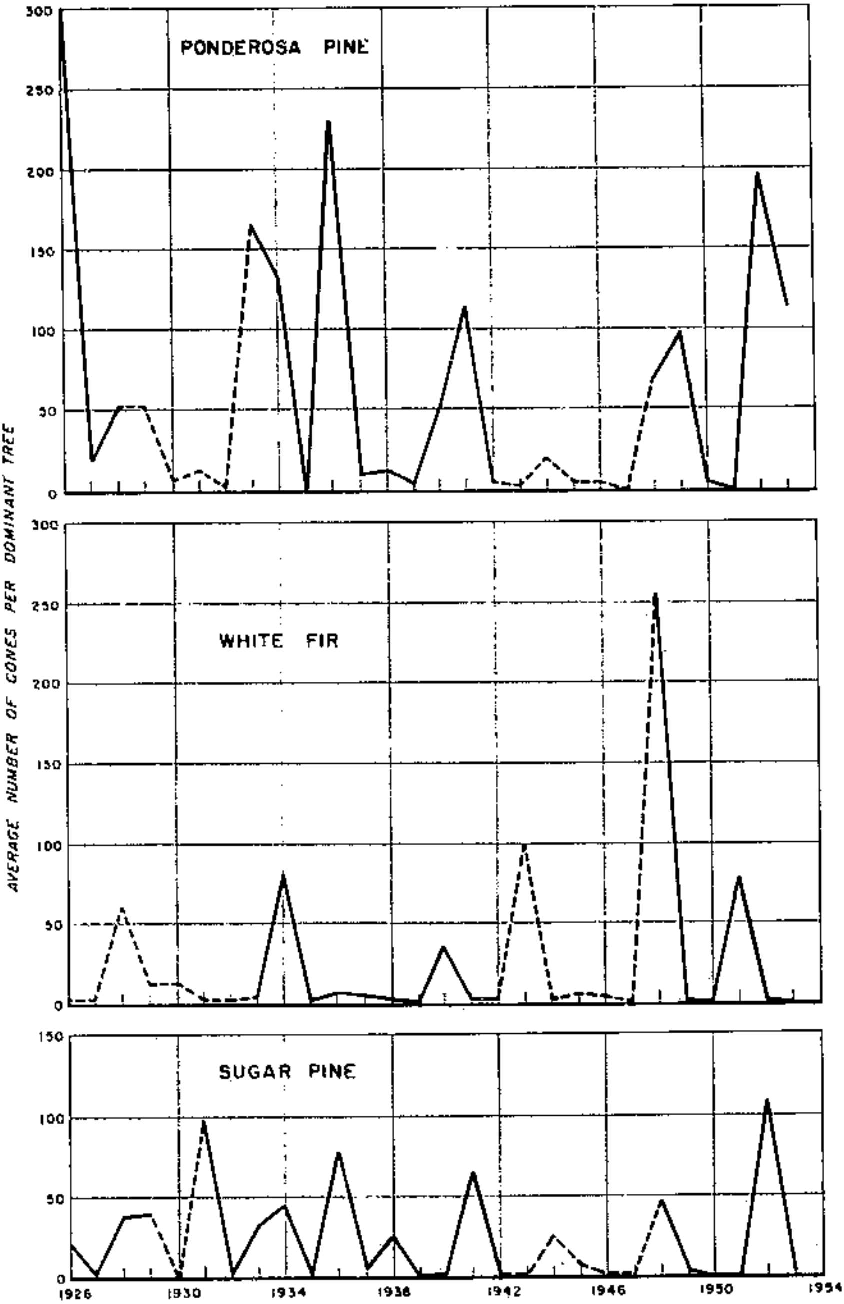

FIGURE 9.—Average number of cones per dominant ponderosa pine, sugar pine, and white fir tree larger than 19.5 inches d. b. h., Stanislaus National Forest 1926–1953. Points joined by dotted lines are based on supplemental data.

Having a quantitative basis, the index can supplant less specific designations such as "good," "poor," or "average." In the proposed index, the number of ponderosa pine cones required for each class was set at twice that for sugar pine or white fir because ponderosa pine cones have only about half as many fertile seed per cone.

When cone crops for 1926–53 on the Stanislaus National Forest study area were classified as follows by this index, 2 of the ponderosa pine and sugar pine crops and 1 of the white fir crops were rated as "none":

	Cone crops		
Size of cone crop:[1]	*Ponderosa pine (number)*	*Sugar pine (number)*	*White fir (number)*
None	2	2	1
Light	13	14	19
Medium	5	6	3
Heavy	4	4	2
Very heavy	4	2	3
Total	28	28	28

[1] Basis of crop size: number of cones per dominant tree larger than 19.5 inches d. b. h.

The majority of the crops of all 3 species—13 ponderosa pine, 14 sugar pine, and 19 white fir—were classified as "light." "Medium" or heavier crops occurred 13 times for ponderosa pine, 12 times for sugar pine, and only 8 times for white fir.

How often may we expect a good seed year for the two pines and white fir? The average and range for the Stanislaus plots, 1926–53, were as follows:

	Time between cone crops		
	Medium or heavier crop (years)	*Heavy or very heavy crop (years)*	*Very heavy crop (years)*
Ponderosa pine:			
Average	2	3	8
Range	1–7	1–8	3–16
Sugar pine:			
Average	2	4	21
Range	1–4	2–7	([1])
White fir:			
Average	3	5	7
Range	1–6	3–9	5–9

[1] Only two very heavy crops of sugar pine cones occurred during the observation period.

On the average, medium or heavier cone crops occurred every 2 years for the two pines and every 3 years for white fir. Very heavy crops occurred even less frequently. During the 28-year period only two very heavy sugar pine cone crops occurred. The first was in 1931 and the other in 1952—a period of 21 years between these two crops. A very good sugar pine cone crop was reported to have occurred in 1920. If this crop was the same as "very heavy," we might expect a crop of this size to occur every 16 years. Much more time than the 28 years of this study would be required to determine reliably the interval between very heavy seed crops for sugar pine. The average interval between very heavy cone crops for ponderosa pine was 8 years and for white fir 7 years. In the Southwest, Pearson

(20) reported exceptionally heavy ponderosa pine seed crops occurred in 1913, 1918, 1927, 1936, 1942, and 1945. If these cone crops were the same as "very heavy," the average interval would have been 6 years in the Southwest compared to the 8 years for the California pine region.

Incense-cedar cone crops on the Stanislaus National Forest plots also varied greatly during the period 1926–53 as indicated in the following tabulation:

Year:	*Estimated cone crop*	*Basis for estimate*
1926	None to light	Seedling count.
1927	do	Do.
1928	do	Do.
1929	Light	Do.
1930	Medium	Do.
1931	Heavy	Do.
1932	Medium	Do.
1933	do	Seed trap count.
1934	Very heavy	Do.
1935	Light	Do.
1936	Medium	Do.
1937	Very heavy	Do.
1938	Light	Do.
1939	Medium	Seedling count.
1940	Light	Seed trap count.
1941	Heavy	Do.
1942	Light	Seedling count.
1943	Medium	Do.
1944	Heavy	Do.
1945	Light	Do.
1946	Medium	Do.
1947	Light	Visual observation.
1948	do	Seed trap count.
1949	Heavy	Visual observation.
1950	Light	Do.
1951	do	Do.
1952	Medium	Seed trap count.
1953	Light	Visual observation.

The crops of this species were estimated only qualitatively because of the difficulty of counting the great numbers of the small cones. Relative abundance of the incense-cedar crops was noted when the cones of the other species were counted. These observations were supplemented with seed trap counts during a few years and with records of seedling incidence on permanent quadrats in other years. In the 28 years, 6 years had a heavy or very heavy crop, 8 a medium crop, and 14 a light or no crop of incense-cedar.

Crop Frequency by Diameter Classes

In general, the number of cone crops of one or more cones in 16 years was strongly correlated with diameter up to certain tree sizes. For ponderosa pine the limit was 32 inches. For trees larger than 32 inches, however, the relationship did not continue. Trees in the lower diameter classes had fewer crops than the larger trees. The average for dominant trees varied from one crop for the 7.6- to 11.5-inch class to 10.5 crops for the 27.6- to 31.5-inch class, with an average of approximately 10 crops for all trees larger than 24 inches (table 10).

Sugar pine exhibited the same general trend; however, the number of crops borne was fewer than in ponderosa pine. The average number

TABLE 10.—*Number of cone crops borne by individual dominant ponderosa pine trees, by diameter classes, 16-year period, Stanislaus National Forest plots*

Diameter class (inches)	Cone crops per tree in 16 years			Basis, trees [1]
	Average	Minimum	Maximum	
	Number	*Number*	*Number*	*Number*
7.6–11.5	1.0	1	1	2
11.6–15.5	3.3	1	9	9
15.6–19.5	6.8	3	9	8
19.6–23.5	8.2	4	11	11
23.6–27.5	9.6	5	12	9
27.6–31.5	10.5	8	12	11
31.6–35.5	10.0	4	13	9
35.6–39.5	10.0	7	13	10
39.6–43.5	9.7	7	12	7
43.6–47.5	9.8	7	12	4
47.6–51.5				0
51.6–55.5	9.5	9	10	2
55.6–59.5	10.0	10	10	1
All	8.5	1	13	83

[1] Includes only trees which survived during the entire study.

of cone crops for dominant sugar pine varied from one in the lowest diameter class to 8 in the highest, with an average of 7 crops for trees larger than 24 inches (table 11).

Very little to no correlation was evident between number of crops and diameter for the larger white fir trees; however, for trees less than 24 inches d.b.h., cone bearing was correlated with tree size. The average number of crops for all dominant trees bearing cones was 3.6 (table 12).

TABLE 11.—*Number of cone crops borne by individual dominant sugar pine trees, by diameter classes, 16-year period, Stanislaus National Forest plots*

Diameter class (inches)	Cone crops per tree in 16 years			Basis, trees [1]
	Average	Minimum	Maximum	
	Number	*Number*	*Number*	*Number*
7.6–11.5	1.0	1	1	1
11.6–15.5	1.5	1	2	11
15.6–19.5	3.3	1	7	25
19.6–23.5	5.0	1	12	20
23.6–27.5	5.6	1	11	10
27.6–31.5	7.2	5	10	13
31.6–35.5	7.6	4	10	11
35.6–39.5	7.5	4	12	11
39.6–43.5	6.2	5	9	6
43.6–47.5	7.4	6	11	7
47.6–51.5	7.4	6	10	7
51.6–55.5	7.8	6	8	3
55.6–59.5	8.0	8	8	4
All	5.5	1	12	129

[1] Includes only trees which survived during the entire study.

TABLE 12.—*Number of crops borne by individual dominant white fir trees, by diameter classes, 16-year period, Stanislaus National Forest plots*

Diameter class (inches)	Cone crops per tree in 16 years			Basis, trees [1]
	Average	Minimum	Maximum	
	Number	*Number*	*Number*	*Number*
3.6- 7.5	1.4	1	3	32
7.6-11.5	2.0	1	5	96
11.6-15.5	3.1	1	8	129
15.6-19.5	4.2	1	10	99
19.6-23.5	5.4	2	9	60
23.6-27.5	5.1	1	11	35
27.6-31.5	4.8	1	8	33
31.6-35.5	4.3	1	8	30
35.6-39.5	3.7	1	7	20
39.6-43.5	4.2	1	8	13
43.6-47.5	4.8	2	8	12
47.6-51.5	5.3	1	11	7
51.6-55.5	5.0	2	7	4
All	3.6	1	11	570

[1] Includes only trees which survived during the entire study.

Frequency of Cone Bearing by Individual Trees

No tree bore cones every year during the 16 years when all trees were carefully observed. In fact even among dominant trees larger than 19.5 inches in diameter, few bore cones as often as 12 years in 16, or three-fourths of the time. Practically no sugar pines or white firs bore cones that often, and only about 17 percent of the ponderosa pines did (fig. 10). Only about 10 percent of the white firs, 36 percent

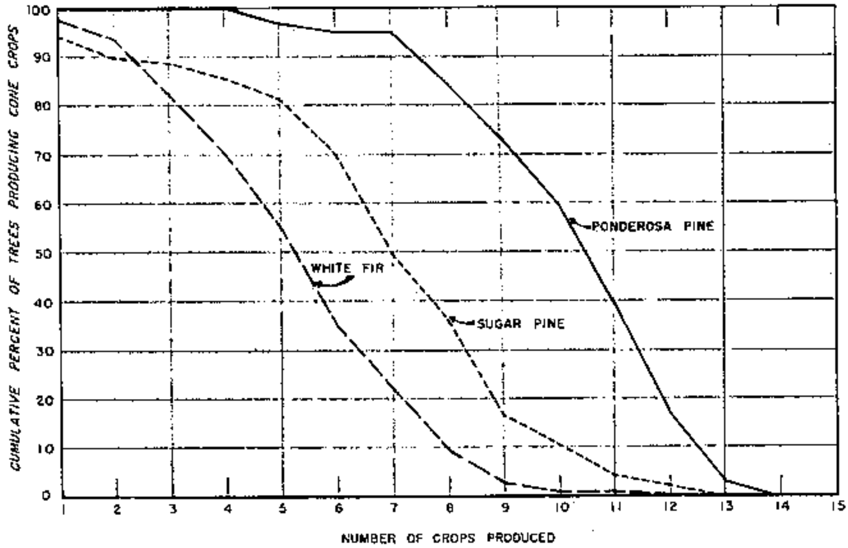

FIGURE 10.—Frequency of cone bearing of individual dominant trees larger than 19.5 inches d.b.h., Stanislaus National Forest.

of the sugar pines, but 84 percent of the ponderosa pines bore crops half the time during this period. Thus one of the key problems in securing natural regeneration in this region is that seed crops may be too infrequent to depend on.

CAUSES OF LOSS

Not enough is known about the causes of the frequency of cone crops to enable us to state definitely why bumper crops of cones occur in some years and no cones at all in other years. Many factors, singly and in combination, affect cone crops. Quite probably some tendencies for regular or irregular cone bearing are inherited. Certainly, changing environmental factors are of importance. One theory for periodicity of fruiting, advanced long ago by Hartig, according to Busgen and Munch (*1*) is that periodic bearing in forest trees, such as beech, is related to the period of time required by the tree to build up reserve materials that are depleted during the seed year. Such evidence as the effect of fertilizers in stimulating seed crops of forest trees (*8*) and the effect of release of seed trees on the subsequent crop (*34*) suggests that increased nutrition and light stimulate trees to bear seed. However, application of fertilizers has not always resulted in increased cone crops (*35*).

Weather

Weather obviously had important effects in the development of cone crops, but not all the relationships were clear. However, the study served to clarify certain points. One effect was that of low temperatures; developing conelets of white fir were killed by severe frosts during late May and early June. For example, on May 20, 1936, when the air temperature was 23° F. in the weather instrument shelter 5 feet above the ground level, the temperature was 26.5° in the crown of the white fir study trees, 100 feet above the ground. By June 8 many of the conelets had turned brown and the white fir seed crop was relatively small that year (fig. 9). Frost damage was noted again in 1939 after below-freezing temperatures occurred in late May and early June.

There was some additional circumstantial evidence that below-freezing temperatures reduced the size of the white fir cone crops. Temperatures 5 to 7 degrees below freezing in instrument shelters within the timber stand were observed in late May every year between 1933 and 1941 except in 1934 and 1940. In these two years the minimum air temperature during May was 30° F. On the basis of the relationship between temperatures in the shelter and in the crowns (*10*), below-freezing temperatures did not occur in the crowns of the trees during May in 1934 and 1940. White fir bore more seed in these two years than in those years with low May temperatures. However, the largest fir seed crop matured in 1948 when the minimum temperature in the shelter was 27° on May 22, and 28° on May 23. Again in 1951 many fir cones developed after a minimum temperature of 24° in the middle of May and 28° on June 2.

Since the minimum temperature in the crown may be several degrees higher than at the base of the tree, temperature at the level of cones might have been only a few degrees below freezing—not low enough to cause much damage. In 1950 and 1952 practically no cones matured after temperatures of 24° and 25° F. were reached in the first part of June. Thus the direct and indirect evidence gives support to the belief that the seed crops of white fir are influenced adversely by low temperatures during the flowering period. The critical temperature associated with frost damage naturally will vary with the stage of growth of the conelets and the duration of the freezing temperature.

There is less evidence for a relationship between climatic factors and cone production of the pines and incense-cedar, although it must be assumed that weather has some effect. Freezing temperatures probably had less effect on the pine cones because the floral period of the two pines is late in the growing season, when below-freezing temperatures usually do not occur. Fertilization, however, does not occur until the spring after floral development. It is conceivable that freezing temperatures might have harmful effects during the interval between pollination and fertilization. Schubert (*28*) recently has observed what appeared to be frost killing of year-old sugar pine cones, after a minimum temperature of 20° F. in early June. A study in Colorado revealed no frost damage to ponderosa pine flowers (*23*).

Weather may have been a factor in the coincidence of cone crops of the two pines. For example, the best crops of ponderosa pine occurred in 1926, 1933, 1934, 1936, and 1952, and good crops in 1941, 1948, 1949, and 1953. The best crops of sugar pine were in 1931, 1934, 1936, 1941, 1948, and 1952; a medium crop developed in 1933 and a potentially heavy crop in 1949 was destroyed by cone beetles. Moreover, there was coincidence in years of failures or near failures. By actual counts, both pines bore practically no cones in 1935, 1937, 1939, 1942, 1950, and 1951 and, by indirect evidence, in 1930, 1932, 1943, 1946, and 1947. Some climatic conditions probably are related to these coincidences of abundant crops and failures between the two pines. Both of the pines, of course, require 2 years for cone development.

Effect of Pests

Cone beetles (*Conophthorus* spp.) at times cause heavy damage to the pine cones. A quantitative measure of the extent of the damage is available only for sugar pine because cones of this species are large enough to count at the end of their first growing season. Of the cones set on 19 trees in 1940, 66 percent matured in the fall of 1941. Much of the loss was attributed to sugar pine cone beetles (*C. lambertianae* Hopk.). Only 38 percent of 2,171 cones counted on 28 trees in the fall of 1947 were found as mature cones in the fall of 1948. Again cone beetles damaged many of the cones. Many conelets were formed in 1948, but very few, if any, matured during 1949. It was assumed that the beetles increased in population in the 1948 crop to such an extent that they almost completely destroyed the 1949 crop. Many aborted cones riddled by the larvae of the beetle were found on the ground under the trees. That damage caused by the sugar pine cone beetle may be widespread was indicated by Miller (*19*), who reported 25 to 75 percent of the sugar pine cone crop destroyed over large areas.

Although quantitative data are not available to show the extent of damage by cone beetles to ponderosa pine cones, it is known that the beetles (*Conophthorus ponderosae* Hopk.) do cause losses (*17*). Occasionally most of the cones on a few trees were aborted, but seldom the cone crop in entire stands. Although in the aggregate the damage may be fairly serious, it is not as striking in ponderosa pine as in sugar pine.

Other insects may destroy the cones—the pine cone moths (*Laspeyresia piperana* Kearf., *Dioryctria abietella* (D. and S.), *D. xanthoenobares* Dyar, and *Eucosma bobana* Kearf.) and the fir cone moths (*Barbara colfaxiana* var. *siskiyouana* Kearf.) (*17*).

The amount of sound seed of ponderosa pine and white fir is often reduced by the seed chalcids (*Megastigmus* spp.). These wasps deposit their eggs within the immature seeds, and the developing larvae destroy the embryo and endosperm of the seed. Much of the poor quality of white fir seed is attributed to infestation of these insects.

Forest rodents, particularly the Douglas pine squirrel or chickaree (*Tamiasciurus douglassii* Backman), cut down many of the cones before they had matured and shed their seed, as indicated by the following proportion of cones cut by squirrels at the time cones were counted on the Stanislaus plots:

	Cones cut by squirrels		
Year:	Ponderosa pine (percent)	Sugar pine (percent)	White fir (percent)
1933	3. 3	0. 9	0. 3
1934	12. 7	33. 1	4. 2
1935	[1] 0. 0	[1] 50. 0	[1] 3. 8
1936	1. 5	0. 6	0. 0
1937	11. 8	[1] 2. 2	1. 3
1938	47. 1	56. 5	0. 0
1939	22. 8	[1] 0. 0	[1] 2. 1
1940	12. 1	[1] 6. 3	0. 3
1941	27. 4	1. 6	1. 2
1942	[1] 52. 3	[1] 4. 7	0. 1
1948	15. 3	0. 2	0. 1
1949	10. 5	3. 0	0. 0
1950	[1] 0. 0	[1] 0. 0	[1] 0. 0
1951	[1] 0. 0	[1] 0. 0	2. 0
1952	31. 7	1. 2	[1] 1. 1
1953	20. 9	[1] 1. 1	[1] 0. 0

[1] Relatively small crop of cones.

Squirrels often cut all but a few cones on the trees by the time seed was normally dispersed. For example, in 1938, 56.5 percent of the sugar pine crop had been cut at the time the counts were made. By mid-September, when the cones normally would start opening, only 3 were left of the original 547 on the trees in 31.2 acres of plots. Recently Tevis (*32*) reported on the fate of an estimated 1,656 healthy cones borne on 20 sugar pines. Of these cones, 54 percent were cut down by squirrels before the seed was shed. Further evidence is given in a report of 863 ponderosa pine cones cut from one tree, an estimated 93 percent of the crop (*27*). In the northern Rocky Mountain forests, 60 to 89 percent of the crop of individual ponderosa pine trees was cut down by squirrels during a 3-year period of observation (*30*). Red squirrels in the Lake States were probably responsible to a considerable degree for light cone crops and failures (*22*, *25*).

Additional data support the contention that squirrels in some years are extremely destructive to seed crops. For example, only 1,350 ponderosa pine seeds per acre were trapped on one plot in 1941, but earlier a count of 149 cones had indicated a possible seed fall of about 10,500 seed per acre. On another plot, 5,830 seed fell per acre in 1934 after 536 cones had been estimated per acre, a potential of about 37,500 seed per acre. Squirrels were actively cutting cones in those two years. There can be no doubt but that in some years the seed crops are almost wholly devoured by squirrels.

On the basis of the evidence presented in the tabulation, squirrels preferred the cones of ponderosa pine. However, this apparent preference for ponderosa cones does not mean that the squirrels do not turn to sugar pine or white fir before the ponderosa cones are exhausted. We observed large caches of white fir cones on the plots late in some years. And occasionally, when cones of the pines or white fir were not available, we found numbers of incense-cedar cones cut.

In some years, white-headed woodpeckers (*Dendrocopos albolarvatus* [Cassin]) completely riddle sugar pine cones (fig. 11). The birds tended to concentrate on certain trees rather than destroy some cones on all sugar pine trees. Furthermore, the woodpeckers did not attack the cones every year during the observation period. The white-headed woodpecker was observed by Tevis (*31*) to have destroyed 34 percent of the 1,656 sugar pine cones counted on 20 trees near Lake Almanor in Plumas County, Calif. At no time did we notice a similar type of damage on cones of the other species.

Seed depredation by birds is not limited to the white-headed woodpeckers. Other birds eat coniferous seeds; however, the quantities eaten are not known. The Clark's nutcracker (*Nucifrage columbiana* [Wilson]) has been observed to pick seeds from partly opened cones. Similarly, the Steller's jays (*Cyanocitta stelleri* [Gmelin]) have been observed by Tevis (*31*) to extract seeds from sugar pine cones after the cones began to open on the trees. White-breasted nuthatches (*Sitta carolinensis* Lath.), red-breasted nuthatches (*Sitta canadensis* Linn), and mountain chickadees (*Parus gambeli* Ridway) have been observed removing seeds from cones cut by squirrels after the cones opened on the ground (*31*).

Crown Decadence

Changes in the cone-bearing crown of the tree, as a result of mistletoe infection, attack by various beetles, or mechanical damage, such as wind and ice breakage, affected the regularity with which the trees bore cones and the number they bore. The effect of mistletoe infection, both the fir mistletoe and the dwarfmistletoe, was very noticeable. In the study area 94 percent of the firs larger than 27.5 inches d. b. h. were infected with one or both of these mistletoes, which in the advanced stages of infection are characterized by clumps of mistletoe, or witches' brooms, in the firs (fig. 12). Since fir cones are borne almost exclusively in the top of the crown, the effect of the infection

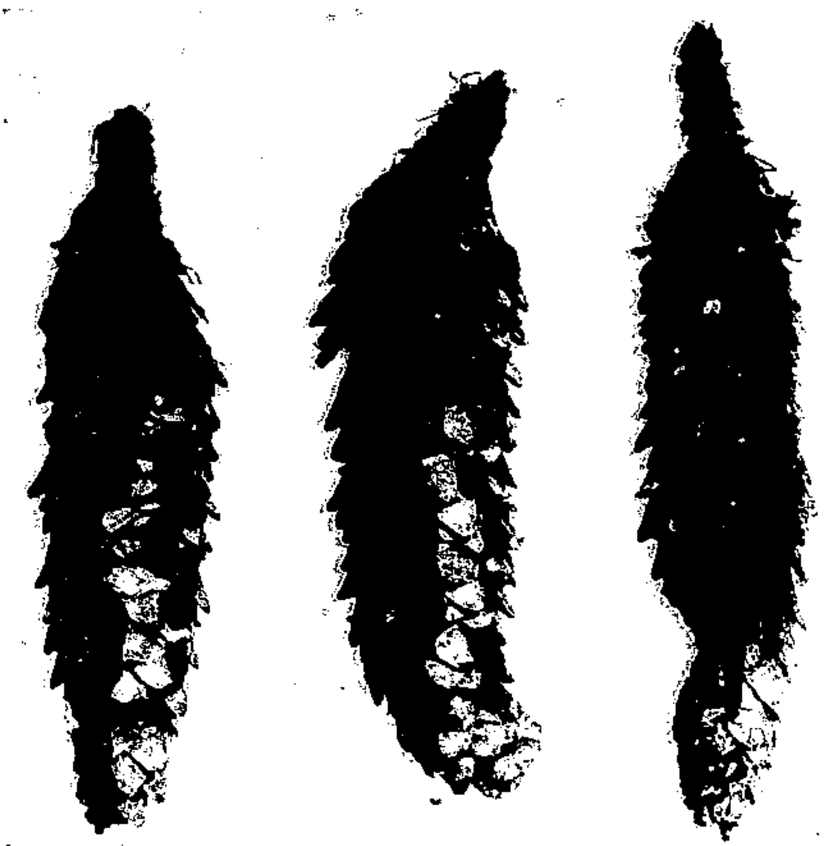

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FIGURE 11.—Sugar pine cones riddled by white-headed woodpeckers.

was to reduce the vigor of the crown and amount of crown that was capable of cone bearing. Approximately 19 percent of the mistletoe-infected trees were stag-headed or dead-topped. Some tops were killed by the mistletoe infection, others by attack by the fir engraver beetles (*Scolytus ventralis* Lec.).

Some of the firs which had lost their tops developed new terminals, and began to bear cones again. For example, a fir 52 inches in diameter bore few cones prior to 1948; the most cones recorded were 21 in 1934 and 24 in 1937. New vigorous terminals developed in the top of this overmature tree, and it bore 446 cones in 1948 and 134 in 1951.

In the pines, infection with dwarfmistletoe or the presence of stag or dead tops appeared to be less of a factor in the number of cones borne or the frequency of bearing. Mistletoe infection was not nearly as prevalent in the pines as in white fir. Moreover, the pines bear cones throughout most of the crown instead of at the very top, so that loss of the uppermost part was of less importance.

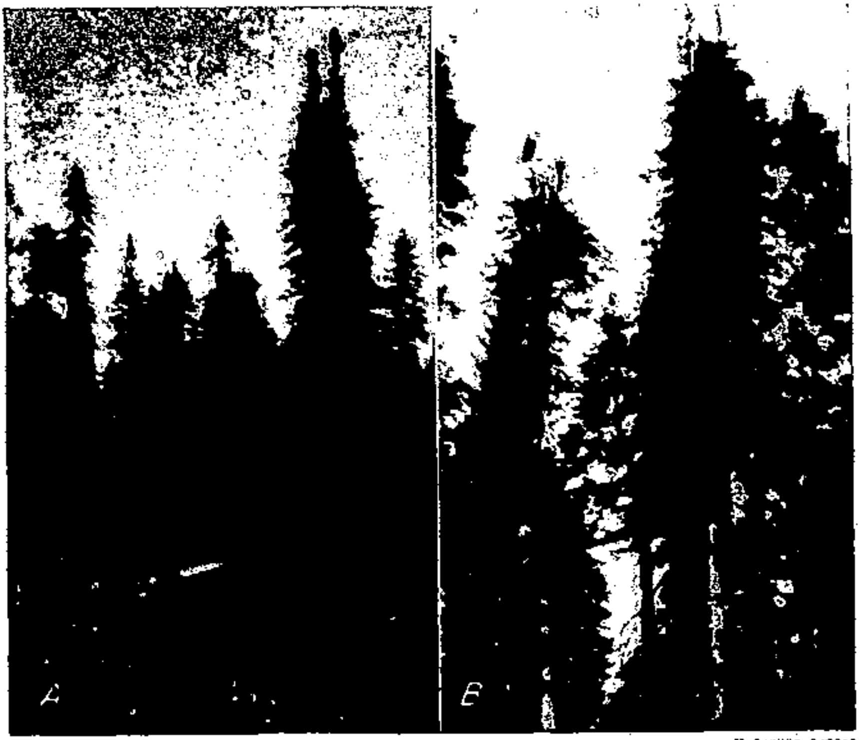

FIGURE 12.—*A*, Mature and overmature white firs infested with fir mistletoe. *B*, Multiple terminals on mature white fir following attack by fir engraver beetles. The affected tree also exhibits fir mistletoe and dwarfmistletoe witches' brooms.

DISSEMINATION OF SEED

Estimates of seed fall per acre from seed traps, measurements of seed flight, cutting tests of seed, and counts of seed fall at intervals during the period of dissemination provide information about the distribution and soundness of the seed.

Number of Seed Per Acre

In 1936, sugar pine seed fell on the 5 Stanislaus plots at the average rate of nearly 35,000 sound seed per acre (table 13), or 17.5 pounds of sound seed assuming 2,000 seed per pound. The fall of sugar pine seed on individual plots ranged from 1,500 to 134,400 sound seed per acre. The sugar pine cone crop of 1952 was even heavier than in 1936; however, no seed traps were set out on these plots in 1952. On a nearby Unit Area Control cutting plot, sound seed fell in 1952 at the rate of 180,330 per acre, or about 90 pounds. The plot had an average of 5.0 cone-bearing trees per acre which bore an estimated 167 cones

TABLE 13.—*Estimated number of seeds per acre on 5 Stanislaus plots, by species and years (total seed 1933–35, sound seed 1936–41)*

Year	Sugar pine	Ponderosa pine	White fir	Incense-cedar	Basis, traps
	Number	*Number*	*Number*	*Number*	*Number*
1933	8,180	15,560	4,940	11,770	107
1934	6,430	2,330	152,340	186,210	107
1935	0	40	2,160	310	107
1936	34,910	58,080	3,400	11,760	107
1937	290	10	970	54,040	659
1938	940	0	120	260	659
1939	(1)	(1)	(1)	(1)	(1)
1940	90	4,470	27,820	7,160	659
1941	21,780	830	240	60,810	659

[1] Not sampled, too few cones.

per tree. If the average number of seeds per cone is assumed to be 215, the potential yield was 179,500 per acre which agrees closely with the seed trap estimate of 180,330.

Ponderosa pine, white fir, and incense-cedar also produced great numbers of seeds per acre at times. In 1936 more than 58,000 good ponderosa pine seeds per acre fell on the 5 Stanislaus plots. Inclusion of data from 4 temporary plots raised the average seed fall to more than 110,000 good ponderosa seed per acre. On one plot of 12 acres, the catch was estimated to be about 230,000 seeds per acre. At Blacks Mountain Experimental Forest, 41,000 sound ponderosa and Jeffrey pine seeds per acre fell in 1942, and 88,500 fell in 1948. This estimate was based on 380 acres of plots containing 760 seed traps. The greatest number of seeds estimated on a single plot of 20 acres was 164,200 per acre.

In 1934 the estimated seed fall per acre of white fir was 152,340 and of incense-cedar 186,210. The maximums for individual plots during that year were 223,600 white fir seeds and 389,100 incense-cedar seeds. This was a total seed count, not just sound seeds. But even if only

TABLE 14.—*Standard errors for some of the estimates of seed fall at Stanislaus and Blacks Mountain plots*

Place and year	Species	Traps	Seed per acre	Standard error of mean
Stanislaus:		*Number*	*Number*	*Percent*
1940	White fir	624	36,100	5.6
1936	Sugar pine	72	4,195	29.1
1941	do	624	8,200	5.8
1948	do	390	29,000	4.0
1952	do	175	180,330	7.1
1936	Ponderosa pine	72	6,850	22.9
Blacks Mountain:				
1942	do	[1] 840	30,200	6.4
1945	do	[1] 320	4,200	12.8
1948	do	[1] 840	180,300	4.3

[1] Traps were set out in groups of five so that the number of observations is one-fifth the number of traps.

50 to 60 percent of the seed were sound, enormous amounts of sound seed were disseminated.

The question may well be asked: How accurate are the estimates of seed fall? Of course, the accuracy depends on the intensity of the sampling and on the variation of seed distribution. As a measure of the accuracy of the samples, standard errors were computed for a number of plots and groups of plots. And as might be expected, these errors varied considerably. During those years when few traps were used or when the seed crop was light and patchy, the errors were sometimes 20 percent or even 100 percent of the mean. For example, on one plot on which only 24 traps were exposed, the error was larger than the mean. However, when more traps were used or plots were grouped, estimates of seed fall were much more reliable. The standard errors for some estimates of seed fall were only of the order of 5 percent of the mean (table 14). The data are thus very reliable except when few seed fell or in those early years when few traps were used.

Distance of Spread

How far seed may be scattered from a tree is a question of much importance in the selection of seed trees for regeneration. Unfortunately only a few of the data collected in this study yield any answer to this question. Most of the data were collected in uncut or selectively cut stands with the result that there were no cutting edges from which to measure seed flight.

In a test of the distribution of sugar pine seed (*12*), 80 percent fell within 100 feet of the seed trees, although some seed was trapped 200 feet away. Traps were not placed at any greater distances and it is thus not possible to say that 200 feet was the limit of seed distribution. However, the estimated seed fall in the 3.2 acres sampled around each tree accounted for most of the seed borne on the trees. It is quite probable that very little seed was carried farther than 200 feet, even though winds reached gale proportions during the period of seed fall.

The findings of Siggins (*29*) give a basis for setting theoretical distances. He measured the rate of fall of various lots of seed of several species in still air. From these rates of fall and an assumed tree height, the flight of the seed for various wind velocities can be calculated. For example, sugar pine seed falls 8.7 feet per second in still air. Seed falling 100 feet with a uniform wind of 10 miles per hour would travel, on the average, about 168 feet horizontally (table 15). Under the same conditions ponderosa pine would travel about 294 feet and white fir 256 feet. The flight distance of incense-cedar seed is about the same as that of white fir, and that of Jeffrey pine is intermediate between ponderosa pine and sugar pine.

Theoretical flight distances, at assumed constant, horizontal wind velocities, do not account for some important factors in seed dissemination. For example, many seeds are probably shaken out by gusts of winds and lighter seeds may be carried considerable distances or dropped quickly. In mountainous terrain, updrafts and air turbulence may lift seeds to considerable heights and scatter them much farther than the distances calculated from assumed horizontal air movement. Under average conditions probably very little seed is scattered more than about 300 feet.

TABLE 15.—*Seed flight distances*[1] *for three species, for specified heights and wind velocities*

Species and height (feet)	Distance when average wind velocity, in miles per hour, is—			
	5	10	15	20
	Feet	*Feet*	*Feet*	*Feet*
Sugar pine:				
50	42	84	126	168
100	84	168	253	336
150	126	252	379	504
200	168	336	506	672
Ponderosa pine:				
50	74	147	220	294
100	147	294	441	588
150	220	441	661	882
200	294	588	881	1,176
White fir:				
50	64	128	193	257
100	128	256	385	513
150	193	385	578	770
200	256	512	770	1,010

[1] Based on original work by Siggins (29).

Proportion of Sound Seed

Soundness of the seed varied from species to species, but for each species the percentage of sound seed was highest in years of heavy crops. Generally a high proportion of sugar pine seed was sound—in 5 of the 6 years in which seed was tested by cutting, more than 80 percent was sound (table 16). The percent of sound ponderosa pine seed was also high in some years. The highest occurred in 1936 in the heaviest crop of ponderosa pine seed sampled on the Stanislaus plots. Jemison and Korstian (*16*) reported that in loblolly pine the best seed was produced during the years of abundant seed production and that the most viable seed fell during the peak of seed fall.

Even during good seed years, a relatively small proportion of the white fir seed was sound. In 1948, 57 percent of the white fir seed was sound, the highest proportion observed. Incense-cedar seed, on the average, had a higher proportion of sound seed than did white fir.

TABLE 16.—*Percent of sound seed, by species and years, in seed trap collections, Stanislaus National Forest plots*

Year	Sugar pine	Ponderosa pine	White fir	Incense-cedar	Basis, traps
	Percent	*Percent*	*Percent*	*Percent*	*Number*
1936	92	79	30	44	188
1937	28	4	9	60	740
1938	81	3	4	14	740
1940	(1)	32	27	23	740
1941	89	45	13	65	843
1948[2]	92	(1)	57	(1)	330
1952[2]	97	(1)	(1)	(1)	175

[1] Too few seed fell to supply a reliable average.

[2] Data for 1948 and 1952 are from a different series of plots than those of previous years.

At Blacks Mountain Experimental Forest in 1942, 72 percent of both ponderosa pine and Jeffrey pine seed found in 840 traps was sound. In 1945 only 27 percent of the pine seed were sound, on the basis of a sample of 320 traps. Again in 1948, 72 percent of the seed were sound in 800 seed traps. Much more seed fell in 1942 and 1948 than in 1945.

Time of Seed Fall

Opening of cones probably depends to a considerable extent on weather conditions in the autumn. However, this relationship was not clearly demonstrated except in 1941 when strong, dry winds in the first part of October caused most of the sugar pine cones to open and shed their seed. In general, no tendency was evident for the seed to fall in any given period during the autumn (table 17).

Not all the seeds were shed during the autumn months, however. Although the seed traps were generally picked up by the end of November before they filled with snow, they were left out over winter twice. At Blacks Mountain, when the 160 seed traps were rechecked in August 1949, the count showed that only 67 percent of the seed had fallen at the time the traps were examined the previous autumn. In 1952 at the Stanislaus forest, 84 percent of the sugar pine seed had fallen by November; the remaining 16 percent had fallen by July 1953 when the traps were checked again. White fir seed occasionally was seen in the snow in midwinter, suggesting that the cones were slow to break up or that the seed and scales lodged in the needles and branches and slowly sifted down.

TABLE 17.—*Percent of all seed and percent of sound seed caught in seed traps at different dates* [1]

Date	Sugar pine		Ponderosa pine		White fir		Incense-cedar	
	All seed	Sound seed	All seed	Sound seed	All seed	Sound seed	All seed	Sound seed
1937:	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*
October 8	58	90	32		34	22	11	3
October 27	3	10	49		33	36	30	37
November 11	39	0	19		33	42	53	60
1940:								
October 11			34	86	50	55	32	54
October 29			10	7	31	35	34	38
November 13			56	7	19	10	34	8
1941:								
October 9	76	79						
October 18	18	17						
October 29	6	4						

[1] The catches of seed reported here are not necessarily the total annual production. Some seed may be retained on the trees and be dispersed later.

Even though seed were disseminated at irregular intervals during the autumn, a large part of the sound seed of the pines fell in the early part of the season (table 17). This timing is no doubt related to the way pine cones open. The central scales open first and the tip and the basal scales last. Generally seed in the tip and the basal scales is less likely to be sound than the seed in the central portion of the cone.

Relation of Seed Fall to Cone Estimates

The number of seeds trapped per acre might be expected to be directly proportional to the cones counted. Several factors, however, tend to prevent such a simple relationship. For one thing, less of the seed was sound in years of light cone crops. And further, rodents destroyed a larger proportion of the cones in these years. Also, not all of the seed had fallen for every year at the time the traps were checked. The net result was that fewer seed per acre were indicated by the recovery from traps than might be expected on the basis of the cone estimate. On the other hand, in heavy seed years the cones occurred in dense bunches and the estimates of cone crops were low compared to the actual crops. Thus the estimate based on seed caught in seed traps exceeded the prediction based on the cone counts. Furthermore, it is quite probable that there were more seeds per cone in the heavy seed years. For these, and probably other reasons, the relation between the seed-fall sample and the cone estimate was curvilinear (fig. 13), and seed fall cannot always be estimated accurately by simply multiplying estimates of cones per acre by the number of seeds per cone.

PRODUCTION IN RELATION TO STAND VOLUME

Seed production was found to be related to the board-foot volume of certain components of the timber stand, but not to the total volume. The relationship, however, was not readily apparent. The number of seed per acre for the Blacks Mountain plots was analyzed in relation to the reserve volume, which varied from 3,600 to 20,000 board-feet per acre. They were not significantly correlated. The correlation coefficients for the 1942 and 1948 data were 0.06 and 0.19, respectively, neither significant. Nor could the data be fitted with a second degree curve to yield a significant regression coefficient.

The volume per acre in Dunning tree classes 1 and 3 was then related to seed fall per acre. The correlation coefficient for the 1942 data at Blacks Mountain was −0.37, a nonsignificant value. Omitting the uncut plots did not materially change the coefficient; it remained nonsignificant with a value of −0.39. The correlation coefficient for the 1948 data at Blacks Mountain was 0.53, a value statistically significant. When the uncut plots were omitted from the analysis of the 1948 data, the coefficient of correlation between seed fall and volume per acre in Dunning tree classes 1 and 3 was increased to 0.82. The data are well fitted by the regression line (fig. 14).

Previously we noted that the ponderosa pine class 5 trees were good cone producers, although no better than the class 3 trees (table 6). Inasmuch as no strong relationship was shown when the Class 5 trees were included in the above analysis, we can infer that these trees are not good seed producers on a board-foot basis. Simply put, the

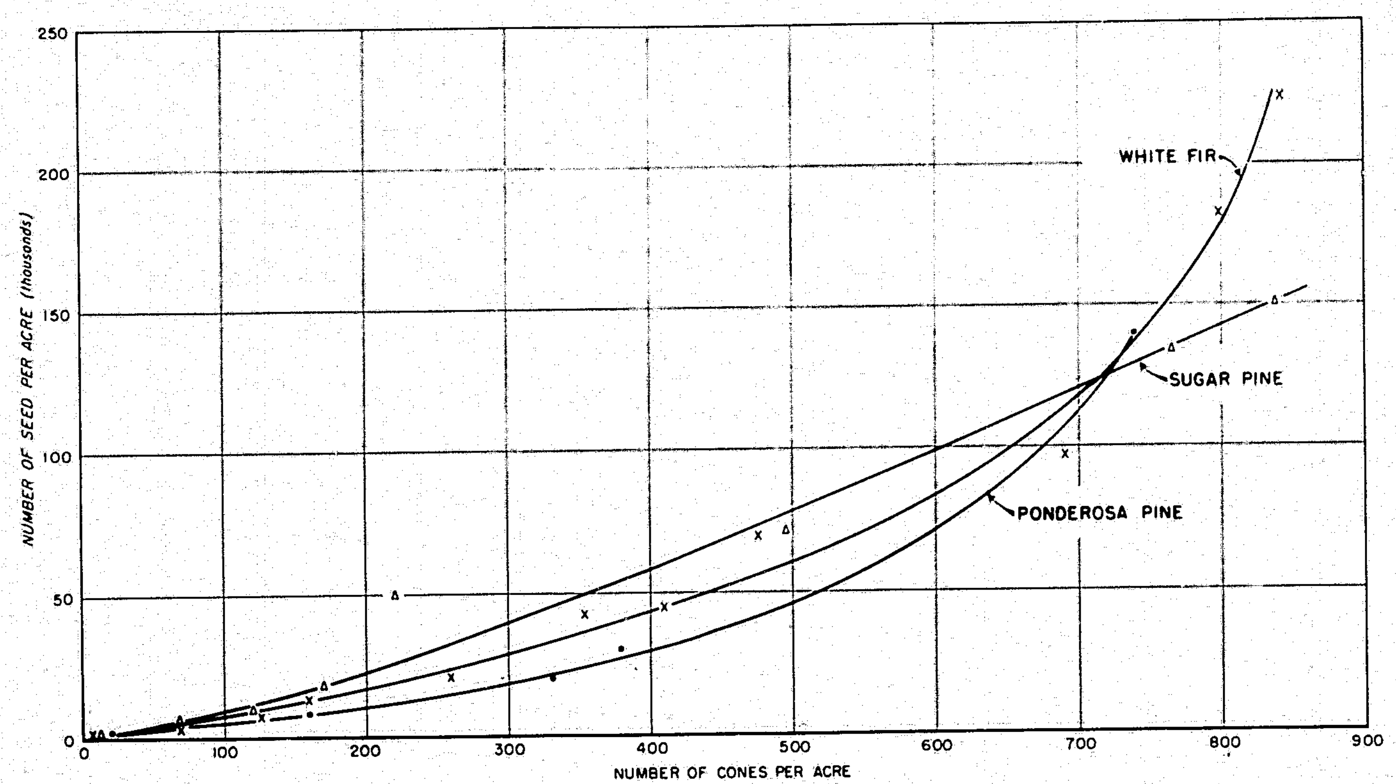

FIGURE 13.—The relation between number of seed per acre and number of cones per acre for sugar pine, ponderosa pine, and white fir, Stanislaus National Forest plots.

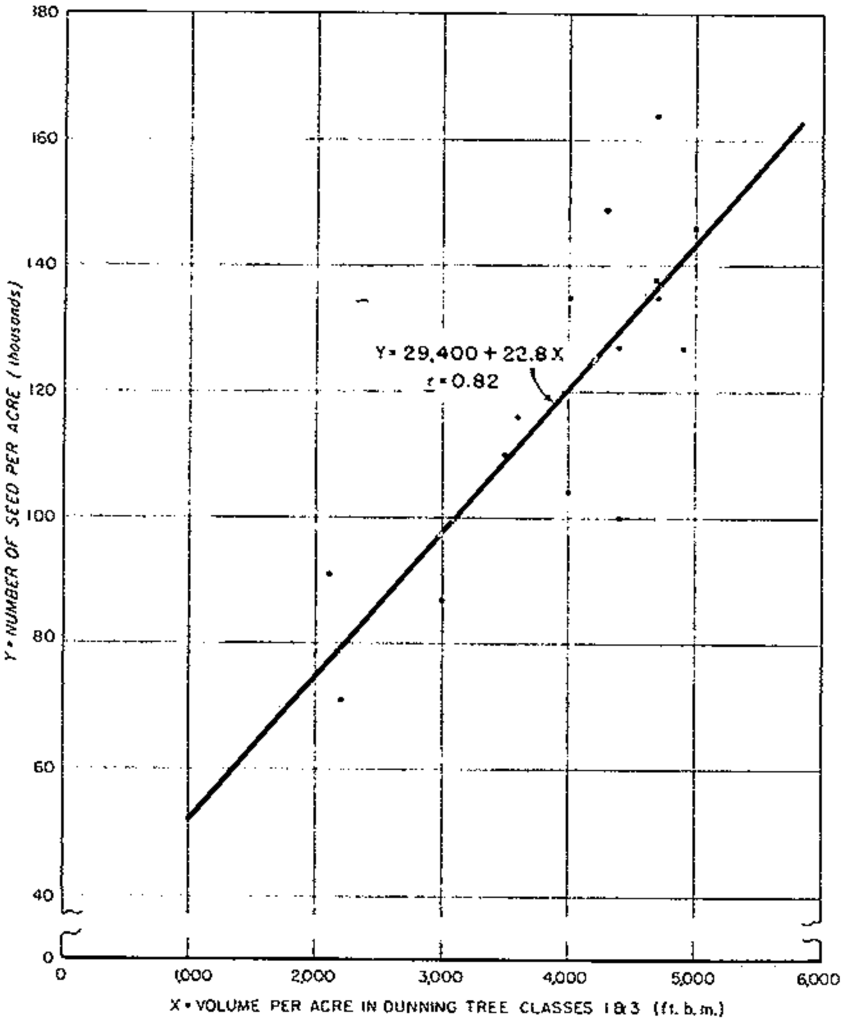

FIGURE 14.—The relation between number of seed per acre and the board-foot volume per acre of trees in Dunning classes 1 and 3, ponderosa and Jeffrey pine, 1948. Blacks Mountain Experimental Forest.

class 5 tree is a good seed tree when it is considered regardless of size. But it is not as good as some other tree classes on a tree volume basis.

The low correlations in light seed years between seed fall and total or partial stand possibly can be explained. During light seed years, as in 1942, only a few trees in each plot bore cones so that volume on the plot had little effect. In the heavy seed years, as in 1948, most of the vigorous trees bore cones so that volume of the stand was strongly related to the amount of seed produced. In 1948, stand volume of tree class 1 and 3 explained 65 percent of the variation in seed fall.

The relation between stand per acre and seed production in the Stanislaus plots was also poorly defined when total volume per acre was used as a variable. Because only 5 plots were available, the seed fall for each species was averaged for the 3 years of highest seed fall. This average was used as the measure of seed fall to be related to stand per acre. For tree classes 1 and 3, fairly good trends were defined by the data for sugar pine and ponderosa pine trees in the stand (fig. 15). But the white fir data showed a very poor trend. Volume per acre in tree class 1 alone, however, did show a definite trend with seed per acre.

A fair relation existed between seed fall of incense-cedar and the volume of trees in class 1 and 3, according to the following tabulation:

Plot:	*Volume per acre (board-feet)*	*Seed per acre (number)*
5	230	14, 070
11	260	68, 030
9	1, 200	171, 200
12 (uncut)	1, 230	12, 690
10	2, 220	237, 270

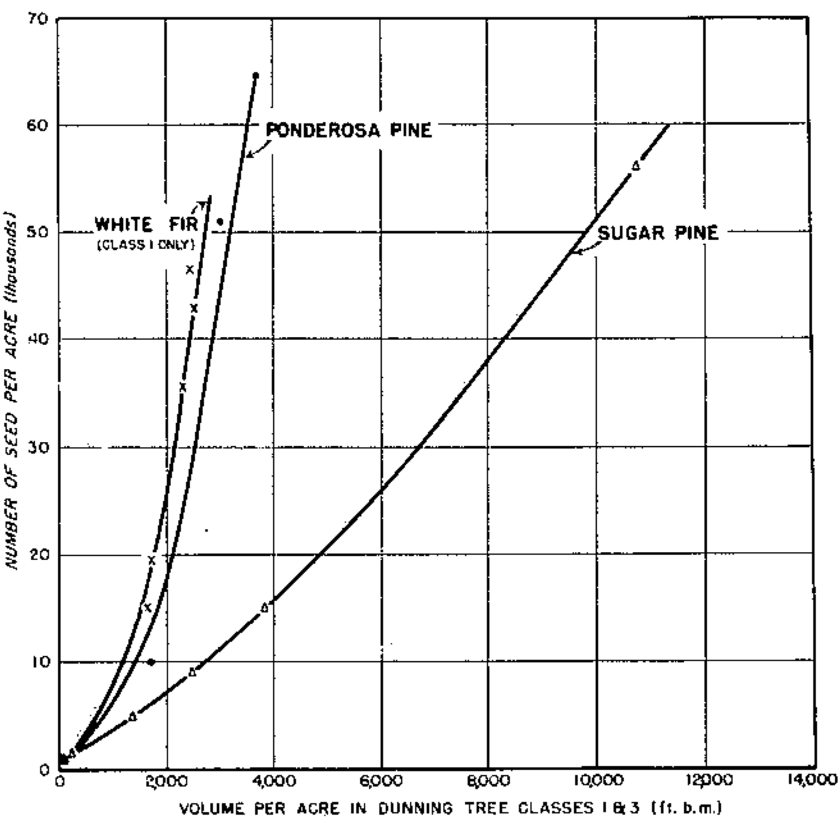

FIGURE 15.—The relation between number of seed per acre and the board-foot volume per acre of trees in Dunning classes 1 and 3, sugar pine, ponderosa pine, and white fir, Stanislaus National Forest plots.

And if the data for the uncut plot were omitted, this trend is quite pronounced, although defined by only 4 points.

The curves in figure 15 should not be interpreted to mean that seed production would continue to increase at the same rate with still heavier stands. At some stand volume per acre, competition will cause a leveling off in the amount of seed produced. Nor should the curves be interpreted to mean that only class 1 and 3 trees bear seed. For although the intercepts of the curves would lead to the conclusion that little, if any, seed was produced when the volume in class 1 and 3 trees approached zero, it should be remembered that some plots had little volume in tree classes other than 1 and 3. Moreover, when seed fall was very heavy much more seed per acre was produced than might be predicted by these curves. In the year of largest crop for each species (table 18), at least twice as many seeds per acre were disseminated as in the average of the three best years on the Stanislaus plots.

TABLE 18.—*Maximum seed fall per acre, number of trees, and volume in class 1 and 3 trees, by species and year of record* [1]

Species	Year	Seed	Cone-bearing trees	All trees more than 3.6 inches d. b. h.	Volume in class 1 and 3 trees
		Number	*Number*	*Number*	*Board-feet*
Ponderosa pine	1936	58,080	2.3	3.7	1,820
Sugar pine	1930	34,910	4.9	15.4	3,730
White fir	1934	[2] 152,340	10.6	53.8	6,810
Incense-cedar	1934	[2] 186,210		17.5	1,450

[1] Source of data: 5 plots, totaling 46 acres, on Stanislaus National Forest.
[2] Total seed per acre. Probably only about 50 or 60 percent of the seed was sound.

SILVICULTURAL IMPLICATIONS OF THE RESULTS

The many observations and enumerations of cone and seed crops are of most value if they can provide guides for silvicultural practices. These data do have important silvicultural implications. For example, certain types of trees are best for seed trees, and timber cutting must leave enough of them to provide adequate amounts of seed. Furthermore, the demonstration that heavy seed crops are irregular and uncertain should clarify the need for taking positive regeneration measures, not only to make the seed crop more effective, but also to protect what crop there is.

Type of Seed Trees to Select

The study showed clearly that certain kinds of trees are the best cone producers. Although the relative merits of various types or classes of trees have been pointed out before (*6*), the many observations in the long period of this study have provided overwhelming evidence that dominant trees are by far the best seed trees. Of the many thousands of cones counted, 99 percent of the ponderosa pine, 98 percent of the sugar pine, and 88 percent of the white fir cones were borne on dominant trees. Obviously, then, most of the cones were produced by trees of Dunning tree classes 1, 3, and 5, for these are the dominant trees of the stand.

Selection of seed trees within these classes should be governed not only by cone-producing ability but also by spacing, growth rates, investment value, and the risk of losing the reserved trees before they can be harvested at a later time. For ponderosa pine, the class 3 trees are probably the best class for seed trees. They produced more than 50 percent of the cones while making up only 13 percent in number of trees of the stand. The class 5 trees produced 18 percent of the cones and constituted 8 percent of the stand; class 1 trees produced 29 percent of the cones and made up 39 percent of the stand. In view of timber values and the possible risk in reserving class 5 trees, it is questionable whether they should be reserved as seed trees in preference to the class 1 and 3 trees unless salvage of older trees is an assured procedure. A point to be kept in mind is that the only strong relation between board-foot volume and seed production was obtained with the class 1 and 3 trees.

Half the cones of sugar pine occurred on class 3 trees, which accounted for only 5 percent of the number of trees in the stand. Class 1 trees made up 26 percent of the stand but produced only 21 percent of the cones, whereas class 5 trees, only 2 percent of the stand, produced 27 percent of the cones. The higher yield of cones on sugar pines greater than 28 inches in diameter was particularly striking (fig. 6). Trees of the smaller diameters, such as many of those in class 1, produced relatively few cones. Class 5 trees bore more cones per tree than the other classes and certainly should be considered as seed trees, together with the larger trees in classes 1 and 3.

Most of the white fir cones, 68 percent, were on the class 1 trees, which made up 31 percent of the stand. However, the class 3 trees bore more cones per tree than did the others. Maximum cone production was on trees from about 22 to 34 inches in diameter. If white fir seed trees are desired, then class 1 and class 3 trees in this range should be selected, with recognition of the possible mistletoe damage in the larger trees.

Little information is available concerning incense-cedar seed trees. The relationship between seed production and stand volume in class 1 and class 3 trees indicates, however, that relatively small volumes in cutover stands, as little as 500 board-feet, will produce approximately 100,000 seed per acre. It has been observed that full-crowned trees in the immature age class bear tremendous quantities of seed.

Species control, to obtain a preponderance of the pines may be a secondary but important objective of the regeneration cutting. Therefore, it might be well to consider the beneficial effect of removing small vigorous white fir and incense-cedar trees. These trees may be smaller than the usually accepted diameter cutting limit, yet they are often heavy seed producers. To favor pine reproduction, silviculturists may need to eliminate class 1 and 2 firs and incense-cedars.

Number of Seed Trees to Leave

A consideration of the adequacy of seed trees probably should be preceded by some definition of acceptable stocking and by a review of available information on the effectiveness of the seed crop. Although the definition of acceptable stocking is subject to some disagreement, 500 established seedlings per acre, well distributed, might be assumed to be acceptable. To obtain this number of seedlings would require varying amounts of seeds, depending on seedbed conditions, rodent control, and other factors that affect germination and survival. Several estimates of the effectiveness of seed under different conditions are available.

A seed-to-seedling ratio of 38 sugar pine seeds per seedling was found from reproduction counts on the Stanislaus Experimental Forest after logging in 1948. Sugar pine seed fell in the fall of 1948 at the rate of 29,200 good seeds per acre. The next summer an average of 770 seedlings was found on the same area. The ground surface had been scarified and the rodents poisoned. On this forest in 1952 the seed-seedling ratio was 345 to 1—180,330 sugar pine seeds produced 522 seedlings. However, there had been no fresh site preparation and no additional rodent control. Many of the seedlings, 408 per acre, occurred in rodent caches (fig. 16), that is, a group of seedlings resulting from burial of seeds by rodents. Some caches contained as many as 30 seedlings, but each cache was tallied as only 1 tree in the reproduction counts. A ratio of 70 to 1 was found in 1941 on plots which had been scarified but had no rodent control (*9*).

Ponderosa pine seed was very effective on the Blacks Mountain Experimental Forest in 1948. After scarification and rodent control, ponderosa pine seedlings appeared on bare areas at the rate of 33,000 per acre (*31*). Seed was not trapped on the treated areas, but on comparable plots nearby the seed fall amounted to about 130,000 good seeds per acre. Hence, the effectiveness ratio was apparently about 4 seeds to 1 seedling. On quadrats with medium or heavy cover of vegetation, litter, or logging debris, however, the seed was not nearly as effective; the ratio was about 40 to 1.

Estimates of seed effectiveness without seedbed or rodent-control measures are available from the records of four plots on the Stanislaus National Forest. Data averaged for a 9-year period show that the number of seed per seedling varied widely among plots (table 19). The greatest spread was found in the ratios for ponderosa pine. One plot had no ponderosa pine seedlings after more than 6,000 seeds had fallen, and the ratio, of course, was indeterminate. On the average only one seedling resulted from several hundred seeds.

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FIGURE 16.—Sugar pine seedlings produced from seed cached by rodents.

TABLE 19.—*Number of seeds per seedling, by species, Stanislaus plots, 1933–41* [1]

Plot	Ponderosa pine	Sugar pine	White fir	Incense-cedar
	Number	*Number*	*Number*	*Number*
5	1,746	244	400	178
9	3,234	483	158	20
10	266	233	377	110
11	(2)	343	181	355

[1] Total seed fall per acre divided by total seedlings found per acre on each plot. Seedling count did not represent total germination because some seedlings probably died before the quadrat examination.
[2] Indeterminate.

After germination, part of the resultant seedlings perish from various causes. Hence the number of seeds per established seedling is much larger than the number per seedling at the time of germination counts—most likely 4 to 5 times as large. Studies of seedling incidence and survival on the Stanislaus plots (*13*) showed that only 20 to 25 percent of the seedlings lived for 10 years. In the Blacks Mountain study (*31*), 33 percent of the seedlings lived for 4 years on bare soil. Further mortality can be expected.

To obtain 500 established seedlings per acre, or 2,000 seedlings after germination, would require, conservatively, about 60,000 seeds per acre. This requirement assumes that 1 seed in 30 germinates and that survival is 25 percent. A seed effectiveness ratio of this size—120 to 1—would ordinarily be obtained only if a mineral soil seedbed were prepared and rodents poisoned.

If the seed tree requirement is deduced from the relation between cone crop and seed fall per acre (fig. 13), an estimated crop of 500 to 600 ponderosa pine cones per acre will give 60,000 seed per acre. During average seed years 500 to 600 cones might be borne on 5 or 6 trees 26 inches in diameter, or on 8 or 9 trees 20 inches in diameter (fig. 6). During years of heavier seed crops about half as many trees would suffice. By the same approach, a crop of 400 to 450 sugar pine cones per acre will yield 60,000 seed per acre. In average years 4 trees, 50 inches in diameter, would probably be necessary to produce 450 sugar pine cones, but in heavier seed years 2 trees would be sufficient.

On the basis of the relation between stand volume per acre and seed dissemination during the heaviest seed years at Blacks Mountain Experimental Forest (fig. 14), a reserve volume of about 1,400 board-feet per acre in tree classes 1 and 3 of ponderosa pine would produce 60,000 good seed per acre; a reserve of 3,100 board-feet per acre would produce 100,000 seed per acre. The lower volume might consist of 3 or 4 trees 20 inches in diameter or 2 trees 24 to 26 inches in diameter (*8*). For the larger reserve volume, 7 or 8 trees 20 inches in diameter or 4 trees 26 inches in diameter would be necessary.

On the Stanislaus plots the relation between reserve volume of ponderosa pine and seed fall (fig. 15) shows that about 3,500 board-feet reserve volume per acre of ponderosa pine is required, or about 4 trees 26 inches in diameter. The much larger reserve required on the Stanislaus plots is due in part, at least, to the difference in site. For the same diameter, the Stanislaus trees contain more volume.

Other factors, such as inherently higher seed production or lower losses, may also account for the difference. The reserve volume requirement for sugar pine is about 11,000 board-feet per acre, equal to 2 trees 50 inches in diameter. Of course, in this mixed type the seed tree requirements should be considered for the two pines together and not independently.

Although the emphasis in the pine region has been directed at obtaining regeneration of the pines, under some circumstances and on certain sites white fir regeneration may be sought. The relation between cone crop and seed fall (fig. 13) shows that about 500 cones will yield 60,000 seed per acre. In average years this many cones might be borne by 8 to 10 trees 18 inches in diameter.

How Periodicity of Cone Crops Affects Regeneration Cuts

Even the best of the seed trees do not bear cones every year. On the average, only at intervals of about 3 or 4 years will the cone crops be heavy enough to enable effective regeneration cuts. Moreover, cone crops do not occur at regular intervals, like every third or fourth year, so scheduling cuts for natural regeneration in advance is difficult. The presence of developing pine cones gives a year's notice of the possibility of a good seed crop. However, this advance notice gives the manager only a partially satisfactory basis for planning regeneration because even these potentially heavy crops do not always mature. For example, in 1948 immature sugar pine cones indicated that a second heavy crop in 1949 would follow the heavy crop of 1948, but the 1949 crop failed because of the sugar pine cone beetles.

When cone crops fail or none is in prospect, the manager cannot rely on natural regeneration. He must decide whether to regenerate artificially or to wait for the next heavy cone crop. He may have to wait from 1 to 8 years in ponderosa pine and from 2 to 7 years in sugar pine, during which time the effects of any rodent-control or site-preparation measures probably will have been dissipated. Moreover, control of the ground may be lost to the less desirable trees, white fir and incense-cedar, or to shrubs. If shrubs gain control of the area, the opportunity for the pines to become established in a reasonable time diminishes greatly. Conversion of the forest to fir or incense-cedar certainly would be better than losing the land to brush but nonetheless would probably reduce the financial yield of the site. If the aim of the forester is to grow as much pine as the site will produce in the shortest time, then he should plant following logging when no seed crop is in sight.

Planning Seed Collection

The study findings have an important bearing in seed collection programs. The best seed is produced in years of heavier seed crops, and collecting costs are lower in these years. Good pine seed can be stored without serious loss of viability for periods at least as long as the observed intervals between good crops, 7 or 8 years at the maximum (*26*). Collecting and storing enough seed during good years for use in intervening years of poor crops would be prudent management.

As forest management practices become more intensive, specially selected and managed seed-production areas will become the source of increasing amounts of the seed used for artificial regeneration. Selection of the seed parent obviously, for the present, will be on the basis of desirable phenotypic characteristics.

It is hardly conceivable that trees other than vigorous dominants should be selected for seed production. But within this group as a whole there are those trees which are more consistent and more prolific seed producers. It is significant that among the trees we studied, about 85 percent of the dominant ponderosa pine trees and 35 percent of the dominant sugar pines bore cones half the time. It is also significant that during years of heavy seed crops, 30 to 70 percent of the dominant ponderosa pines and 15 to 40 percent of the dominant sugar pines bore more than 100 cones each. These are the trees which should be selected for seed production if they meet other phenotypic specifications.

How to select seed trees without a previous case history is somewhat of a problem. But as has been pointed out (*4, 21*), one of the best indications of a good seed producer is the accumulation of old cones under the trees. A disposition toward heavy seed production certainly should be a specification of trees selected in seed-production areas, provided that the trees also exhibit desirable timber growth characters.

Protecting Potential Seed Crops

Because good seed crops are infrequent, they should be protected. One of the serious causes of loss of cones was shown to be tree squirrels. In some years these rodents practically destroyed the cone crops, particularly of ponderosa pine. Although they were most serious in years of small or medium crops, they did reduce the crops even in years of abundance. To save a seed crop, control measures might be considered, but the control program had best be attempted in cooperation with the U. S. Fish and Wildlife Service and local game officers. Tree squirrels are usually protected or classed as game animals. Hence they cannot be eliminated without danger of public condemnation. To exclude squirrels from individual isolated trees, sheet metal bands around the tree (*30*) or barriers of hardware cloth at right angles to the trunk have been found effective.

Damage by cone insects possibly can be prevented by aerial spraying. In a preliminary test [5] to reduce the damage caused by the sugar pine cone beetle, an area of 80 acres was sprayed by helicopter with 2 pounds of DDT in 2 gallons of diesel oil per acre. In the year in which the trees were sprayed, 14 percent of the cones aborted on the sprayed trees compared to 56 percent on the check area. The following year 8 percent were destroyed on the sprayed area and 77 percent on the check. These results are insufficient to be regarded as conclusive evidence, but they are encouraging.

In a broad sense, protecting the seed means, for natural reproduction, making it most effective. When the establishment of natural reproduction is as difficult as it is in the pine region of California,

[5] HALL, RALPH C., and SCHUBERT, GILBERT H. THE CONTROL OF THE SUGAR PINE CONE BEETLE THROUGH AERIAL APPLICATION OF DDT. Manuscript report, Calif. Forest and Range Exp. Sta., Berkeley, Calif. January 4, 1955.

protection of seed crops is especially important. Measures which will assist in protecting seed crops include prevention of seed losses that are caused by tree squirrels, cone insects, and other seed destroyers and improvement of seedbeds by disturbance or scarification of the soil surface.

SUMMARY

Cone crops and seed dispersal were observed for a period of about 28 years in the pine region of California. The species studied mainly were ponderosa pine, sugar pine, and white fir.

Definite cone-bearing characteristics were observed among the several species. Nearly all cones were produced on dominant trees; trees of other crown classes bore so few cones that they can be ignored as seed trees. Within the dominant crown class, cone production on ponderosa pine increased with diameter up to about 38 inches and then leveled off or declined. But in sugar pine, cone production continued to rise with increased diameter. The larger white fir trees bore fewer cones than the intermediate sizes because of mistletoe infection and insect or mechanical injury in the crowns. Tree classes recommended as seed trees are: Ponderosa pine, Dunning classes 1 and 3; sugar pine, classes 3 and 5; and white fir, classes 1 and 3.

Cone crops occurred at irregular intervals. On the basis of a proposed cone-crop index, ponderosa pine produced heavy and very heavy crops only 8 times and sugar pine 6 times during the 28 years for which data are available. The interval between heavy crops of ponderosa pine varied between 1 and 8 years, and of sugar pine between 2 and 7 years. White fir produced heavily at intervals of 3 to 9 years. None of the trees on the plots bore cones every year, but 85 percent of the ponderosa pines, 35 percent of the sugar pines, and 9 percent of the white firs larger than 19.5 inches in diameter bore cones half of the time.

Tree squirrels, birds, and several cone insects reduced cone crops. In some years almost no cones matured because of damage by one or more of these agents.

In good seed years seed fall per acre was very high: As many as 180,000 sound sugar pine seeds, 164,000 sound ponderosa pine seeds, 223,000 white fir seeds, and 389,000 incense-cedar seeds. The proportion of sound seed of the pines was usually high in good seed years, ranging from about 70 percent upwards. The proportion of sound white fir and incense-cedar seed was lower but was also highest in good seed years.

A strong relationship was found on cutover areas between the volume per acre in Dunning tree classes 1 and 3 and amount of pine seed produced per acre. At Blacks Mountain Experimental Forest in heavy seed years a ponderosa pine reserve stand of 1,400 board-feet per acre in tree classes 1 and 3 produced adequate seed for regeneration. The criterion of adequacy was 2,000 seedlings per acre at germination, or 500 established seedlings after early mortality. About 3,500 board-feet of ponderosa pine on the Stanislaus National Forest produced enough seed. The necessary reserve volume of sugar pine was much larger, about 11,000 board-feet, because of the relatively few cones produced on small trees.

In terms of number and kind of trees per acre, 3 or 4 ponderosa pines 20 to 26 inches in diameter in tree class 1 or 3 should produce enough seed for adequate reproduction if rodent control and ground

preparation have prepared the way for regeneration. For adequate sugar pine regeneration, 2 class 3 or 5 trees about 50 inches in diameter would suffice or several more smaller trees, with a minimum seed tree size of 30 inches.

Because good seed crops are infrequent, steps should be taken to protect them and to make the most of them in seed collection programs and in planning for natural reproduction.

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