DEVELOPMENT OF SEEDS AND EMBRYOS IN *PINUS PONDEROSA*, WITH SPECIAL REFERENCE TO SEED SIZE

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INTRODUCTION

This investigation was begun in the summer of 1942 while the senior author was a visiting investigator at the Placerville Laboratory of the Institute of Forest Genetics. The material discussed in the first part, concerning seed size and cone size, was all obtained and tabulated at Placerville, California. Toward this part of the investigation the Institute furnished considerable help at the time of collection, in the climbing of trees and opening of the cones, including the time of a number of persons during several days. The dissections and measurements on the embryos of three of the trees (15-43, 3-14, 3-57) were also completed at that time. The data for tree 3-56 were obtained in part. The junior author has completed additional dissections and measurements on the seeds of tree 3-56 and all of the data on embryos of trees 3-40 and 3-52, work which was carried out at the University of Illinois on the seeds preserved in 1942. It is therefore appropriate to express thanks to the Institute for the facilities of their laboratories and for the cooperation of Mr. W. C. Cumming and many others employed at the Institute, which made this investigation possible on a scale that included more than 100 seed cones.

The western yellow pine, *Pinus ponderosa*, Lam., is an important timber tree occurring throughout the western part of the United States, from the Black Hills, Great Plains, and Rocky Mountains to the Pacific Coast. The Californian form of this tree is typical of this species and is more robust than the variety *scopulorum* Engelm. which occurs in the Rocky Mountains east of the Sierras. This latter variety is very similar to the typical form of the species, but somewhat smaller in all of its parts. The variety *scopulorum* may therefore be expected to have seeds that would average somewhat smaller.

In California, where this investigation applies, the ponderosa pine has a wide distribution. On the west slope of the Sierra Nevada, the species is noted for its wide altitudinal range. The Institute of Forest Genetics has experimental plots near Sacramento at altitudes of 185 and 350 feet with many other plots distributed between these and the station at Placerville which is at 2740 feet. Eastward, the trees occur at elevations up to 6,900 feet near Lake Tahoe. There are not many species of plants that occupy a larger area of distribution both geographic and altitudinal.

Within the area of a single site,

trees may be found that possess cones more than 5 inches long whereas in other trees the cones may be less than three inches in length. There has been an impression, supported by a few records in the literature, that large cones usually possess large seeds and that small cones usually have small seeds, but there seemed to be no records based upon individual cones. By the methods usually employed in harvesting the seed crop, the cones of all sizes from the same tree are massed together. There are many records at the Institute showing that large, medium, or small seeds have been obtained from individual trees, but it was not possible to know how much correlation may be found among seeds from cones of various sizes coming from a single tree. In connection with an effort to obtain embryos in developing stages from large vs. small seeds it happened that a large number of cones were harvested and measured during the early part of August 1942. The seeds of these contained embryos that were only about half developed, but the cones and their seeds had grown to their ultimate size more than a month earlier. The seeds possessed stony seed coats and could be handled in the same manner as fully ripe seeds, except that at this stage the cones had to be cut open by hand, the seeds carefully removed, sorted for size and kept from drying out.

Pine seeds, like those of most gymnosperms, are full grown at the time of fertilization. Fertilization occurs in nearly all pines 13-14 months after pollination. They are considered biennial, since two growing seasons are required to mature a seed crop. The only known exceptions to this are a few triennial species, for example *Pinus pinea* L. from northern Italy and *Pinus leiophylla* Schlecht. and Cham. from southern Mexico, which are not closely related taxonomically. These require about 25-26 months between pollination and fertilization.

The cones of biennial pines enlarge only slightly after pollination during the first season and remain small throughout the ensuing winter. With the opening of the buds in the following spring these year-old conelets experience their grand period of growth, enlarging rapidly to their full size within a period of less than six weeks. Hence the cones are full grown, though still somewhat succulent at the time of fertilization about the end of June or early in July; a month later the cones have become hard and woody, and they may remain green for weeks after the seeds are fully matured.

After fertilization there is no appreciable increase in the size of the ovules or seeds so that a seed in which fertilization has failed to take place remains as a full sized empty seed, in which the stony seed coat may be as fully developed as in a sound seed. Morphologists who have prepared pine ovules for microscopic examinations know that the seed coats begin to become so stony a few days after fertilization that it is very difficult, sometimes impossible to cut sections without first removing the seed coat in preparation for killing and fixing material that is to be sectioned.

The present study is concerned with seeds about a month or six weeks after fertilization, when the embryos, now about half developed, are beginning to differentiate stem tips and cotyledons. Since the seed coats had become fully thickened and hardened the seeds could be graded rapidly by passing them through screens of known gauge.

More than 25 years ago, the senior author (3) described the embryogeny of pine. This study was based upon the Jack pine and the Austrian pine. Since that time the embryology of more than 24 different species of pines, representing nearly all sections of the genus, has been examined. All of them agree in the essentials of embryological development. All pines have cleavage polyembryony (6). Eight embryos may result from each egg that is fertilized. The numerous embryos remain small for about 3-4 weeks. They compete in their development until one of them gains supremacy, shown by its larger size and forward position. This selected embryo enlarges to form the embryo with stem tip and cotyledons, which remains in the seed at maturity, while the great majority of the other similar embryonic units grow more slowly and finally cease to grow altogether, seldom reaching the stage in which these organs appear.

The stages of the embryos desired for the present investigation were these later ones, near the time when the root, stem tips, and cotyledons are forming, or have become fully differentiated. At this time the surviving embryos are growing rapidly. These stages were made the subject of a special study described in the later portion of this paper. The results of the first part of this study deal chiefly with the relation of seed size to the size of the cone and with records as to the proportion of sound seeds and empty ones that could be detected at this time.

From the standpoint of seed size there is little difference whether the seeds are collected in August or in October when the seeds are ripe. It is likely that dry ripe seeds would tend to be slightly smaller due to loss of imbibitional water. Certainly they would not be larger. The endosperm which surrounds the embryo throughout its period of development would be filled with food reserves so they may be heavier at ripeness.

The trees used were marked seed trees, most of them situated near the site of Sportsman's Hall, eleven miles east of Placerville along U. S. Highway 50 at an elevation of 3700 feet. The seeds from several other trees were included, one from the grounds of the Institute of Forest Genetics at an elevation of 2740 feet, also a few trees from another site 32 miles east of Placerville at an elevation of 4100 feet. Some of these seed trees were so tall that cones could be reached only by climbing with rope; others were small enough so that the most of the cones could be reached with little climbing or from the ground. Records of the Institute had indicated that large, medium or small sized seeds had been obtained from these particular trees that had been selected and marked with numbers, in investigations several years earlier involving certain progeny tests carried out at the Institute.

In general the seeds were found to belong to the size groups that had been recorded previously from the trees. Pollination of the trees in the previous season had been fairly successful. There were a few cones that showed some insect damage. This was only a fair cone year in ponderosa pine; it was not one of the best cone years. The cones of 1942 were much better than in the year 1944, when many of them were heavily infested with seed chalcids—*Megastigmus albifrons* Walk. The seeds of open wind-pollinated cones of tree 4B-56 were so badly infested with this insect in 1944 that no healthy seeds with embryos were found; only a few in the cones covered by bags.

The screens used in separating the seeds mechanically were standard screens employed as interchangeable parts in a small separator of the kind used for cleaning seeds at experiment stations. These screens consisted of framed metal sheets with round openings of various sizes ranging from No. 7 to 20, in which the number indicates the diameter of the openings in steps of 64th of an inch. Thus the openings of No. 14 screen are 14/64ths of an inch in diameter, a No. 14 seed is one that will pass through this opening but not through the smaller No. 13 screen with 13/64th inch openings.

The sizes of these openings, converted into metric units are as follows: No. 10 openings are 3.97 mm. in diameter; No. 11 = 4.37 mm.; No. 12 = 4.76 mm.; No. 13 = 5.16 mm.; No. 14 = 5.56 mm.; No. 15 = 5.95 mm.; No. 16 = 6.35 mm.; No. 17 = 6.75 mm.; No. 18 = 7.14 mm.

I. Relation Between Cone Size and Size of Seed

The following tables give the results of this study tabulated according to cone length. Defective seeds that were discarded (some of them only partially enlarged, others full sized, but obviously defective) were recorded in the columns to the right. The partially enlarged ovules became aborted before fertilization. There were still many ovules that had not begun to enlarge, which are disregarded. As is well known, the maximum potential output of 2 seeds per scale is not attained. Other obviously defective or insect damaged seeds even if they were full grown, were discarded and appear only in the column at the right, not among the seed output of the cones.

Each size of seed from the same tree was placed in preservative for future study. This preserving solution (FAA) contained about 50 percent alcohol. In this lower specific gravity the sound seeds sank whereas many defective empty seeds usually floated and could be separated easily, with a cutting test applied whenever in doubt, so that there would be no error in unintentionally discarding seeds with embryos. However among the heavier seeds there were still many that were found to be defective upon dissection in later studies. The discarded floating seeds, not separated individually by cones are shown as without embryos below, in the column showing individual seeds sizes. Where seeds were actually dissected later, this corrected entry of seeds without embryos was made for the total seeds of some of these trees. The embryos of the seeds of some of these trees still remain to be dissected. The first number of the tree is the plot number, the second the individual tree number. Thus 3-14 is tree No. 14 in plot 3.

In connection with the dissections of the embryos from the seeds, a number of these seeds were measured individually with micrometer calipers for length. It was found that each size class included seeds of the same length as others in the nearest size class, but the mean lengths were distinct. Measurements on 20 No. 10 seeds from tree 15-43 gave a mean length of 5.21 mm.; 14 No. 11 seeds gave a mean length of 5.75 mm.; 37 No. 12 seeds gave a mean length of 6.18 mm.; 42 No. 13 seeds gave a mean length of 6.64 mm.; 26 No. 14 seeds gave a mean length of 6.97 mm.; 15 No. 15 seeds gave a mean length of 7.01 mm. The last group of No. 15 seeds is probably not representative of this size class since this group, near the upper limit, did not include many of the largest seeds that would pass through No. 15 openings.

Another set of seed samples was measured from tree 3-38. These seeds were somewhat longer, especially in the larges sizes. Measurements of 20 No. 12 seeds gave a mean length of 6.89 mm.; 32 No. 13 seeds gave a mean length of 7.41 mm.; 34 No. 14 seeds gave a mean length of 8.31 mm., 40 No. 15 seeds gave a mean length of 8.74 mm.; 34 No. 16 seeds gave a mean length of 9.16 mm.; 30 No. 17 seeds gave a mean length of 9.30 mm.; 20 No. 18 seeds gave a mean length of 9.67 mm. The standard deviation of each size class might seem of interest, yet this calculation throughout the series does not seem justified. This value would be relatively large and nearly the same for all seed sizes. The standard deviation of length for No. 15 seeds of tree 3-38 is 0.37 mm.

It has been the belief of many that seed size is an indication of vigor in the plant that results from the seed. Records, such as those of Eliason and Heit (8) indicate this, but the differences are not significant by statistical standards. There can be no question about a large seed giving the seedling a better start than a small seed, others things being equal.

A larger seed contains a larger embryo as well as more endosperm with stored food. Large seeds usually germinate more rapidly and the seedlings grow faster in the first months. However other things, such as the inherent vigor of the embryo contained in the seed, are usually not equal. Righter (12) has shown, for example, that the seedlings possessing greater inherent vigor due to their hybrid genetic constitution will soon outgrow the non-hybrid seedlings even if they originate from a smaller seed.

It may be pointed out here that while the seeds of some angiosperms may actually become larger when they contain a more vigorous embryo than other seeds with less vigorous embryos, the situation is different in gymnosperms. In pines for example the seeds are full grown before fertilization takes place. They have hardened stony seed coats long before the embryo is visible to the naked eye and cannot yield to the growth pressure or other stimulus of a more vigorous embryo. As pointed out in the opening paragraphs, the abortive seeds in which fertilization has not taken place may be fully as large as those which are healthy seeds.

Most of these collections of cones were made at random—trees 3-6, 3-8, 3-10, 3-14, 3-38, 3-52, 3-55, and 3-56. The trees themselves were selected because they had been used in previous investigations and records of the size of the seeds were available, but the cones selected from these trees were taken by chance.

The large cones of trees 3-38 ($m = 5.36$ inches) and 3-40 ($m = 4.62$ in.) yielded large seeds; those of trees 3-7 ($m = 3.87$ in.) 3-52 ($m = 4.08$ in.) and 3-55 ($m = 4.08$ in.) yielded small seeds. However tree 3-8 with large cones ($m = 5.25$ in.) had medium sized seeds, very comparable to tree 4B-53 in which cones were only 3.37 inches long. To the extent that this limited survey shows anything, there are indications that seed size and cone size are not very closely correlated and that individual trees differ. Some of the largest seeds were taken from tree 3-14 having a mean cone length of only 4.34 inches. This was a tree that had been classified as large seeded in previous years. Unless the mean length of cones changes gradually with the age of the tree, one may expect this tree to have cones of medium length with large seeds in future years, and that the large cones of tree 3-38 will continue to be large and have large seeds. No doubt in certain years, the cones of all trees, probably also the seeds, would fall below their respective means or go higher, since seasonal conditions may affect all trees adversely or favorably.

Some of the trees such as 3-3 and 3-55 failed to show any correlation of seed size with cone size. Tree 3-40 appears to show a trend in the opposite direction, with a larger proportion of the larger seeds in the smallest cones. However tree 3-14 shows a definite trend in having more large seeds in the largest cones that were measured. The majority of the trees showed a similar trend.

From the literature on the subject there are a number of records that show the same general condition. Eliason and Heit (8), Munns (11) and several other investigators cited by Baldwin (2) indicate that large cones tend to have larger seeds than small cones, in pines and other conifers. In comparing the results of these records, one would come to believe that the tendency to find large seeds in large cones is less marked in *Pinus ponderosa* than in other species.

The records of Aldrich-Blake (1) give the weight distribution of the seeds from the cones of the Corsican pine—a variety under *Pinus nigra* Arn. In the examples from Aldrich-Blake, especially those tabulated by Righter (12), cones 3.5-4 cm. long have seeds ranging in weight from 6-7 milligrams to 16-17 mg., while the cones (from the same tree) that were 7-7.5 cm. long had seeds weighing between 11-12 and 28-29 mg. The mode of the seed weight in the small cones was 10-11 mg.; that of the large cones 22-23 mg. This is probably the most accurate record available for comparison.

One may gain an approximate basis of comparison by calculating the relative weights of the seeds on the basis of their volume. A pine seed is a flattened ovoidellipsoid. It is known from solid geometry that the volume of a series of similar bodies is proportional to the cube of any of the homologous dimensions, such as the length, width or thickness. Hence, the volumes of seeds of similar shape in a series of sizes may be compared. If the volume of No. 10 seed is taken as unity, that of No. 12 is 1.7 times the volume of a No. 10 seed, that of No. 16 is 4.14 times and a No. 18 seed is 5.85 times that of a No. 10 seed. Aldrich-Blake's largest seeds are slightly more than four times as heavy as his smallest seeds. The range of sizes included in the weight classes which he gives are therefore equivalent to the range between No. 10 and No. 16 seeds; they are slightly below the range between No. 11 and No. 18 seeds shown by tree 3-38.

These comparisons are all relative. The actual sizes of the seeds of *Pinus nigra* ranged between No. 8 and No. 11 on trees which we have had occasion to measure with screens, and it is likely that the precise variety of this species differed. However the seeds of *P. nigra* have a slightly different shape from those of *P. pondersosa;* they are somewhat longer in proportion to the width.

The corresponding differences in sizes of the cones of all of the series *Pinus ponderosa* is less than that shown for the Corsican pine. This comparison seems to show that our seeds include a range of seed sizes from single trees with about the same spread as the data of Aldrich-Blake, about two of whose lowest weight classes would be equivalent to the steps between No. 10 and 11 seeds while about 8-10 or more of his higher weight classes would be included in the size range between Nos. 15, 16, and 17 seeds.

McIntyre (9) has described the sizes of the cones matured in 1927 in *Pinus pungens* on trees of various ages, including some of the first cones, matured on a tree 7 years old; others from trees having ages at intervals of several years up to 18. His tabulation shows, aside from the number of seeds per cone scale, their distribution within the cone and the number of abortive seeds. The length of the cones varies from tree to tree in this particular year and the number of viable seeds appears to be closely correlated. Although McIntyre gives nothing concerning the sizes of the individual seeds from the different cones with which our data on seed size may be compared, his record includes the data on the total number of viable seeds from an uninterrupted series of the serotinous cones of this species produced over a 9 year period. This record seems to bear out the thesis that over a period of years the size of the cone and seed yield on a given tree remains about the same in spite of wide fluctuations in certain years which might be recorded in other species as good or bad cone years.

The cones of any given tree appear to show some correlation between cone size and seed size. The range in sizes of cones from individual trees in the first set of random collections were not great enough to provide desirable extremes for studies of cone and seed sizes in individual trees, though they show definite trends as indicated above. Consequently another collection was made a few days later, at a higher altitude, so that the embryos would also be found in the desired stages for study. These are shown in trees 15-43 and 15-78 from trees at 4100 feet. Here an effort was made to include the widest possible range in the sizes of the cones. From tree 15-43 there were cones 2.6-5 inches long; from tree 15-78 they were 5-6 inches long. Here several small cones less than 4 inches long had a large increase in seeds of the smallest sizes, a very large proportion of which were without embryos. However the largest cones from tree 15-78 did not contain seeds that were as much larger than the average as their large size would suggest.

The small amount of definite data shown here would seem to justify the conclusion that on a given tree the large cones would probably have larger seeds than the small cones. Between different trees of *Pinus ponderosa*, the largest seeds may be found in large cones or cones of about average size, seldom in the smallest, while the smallest seeds may be found in cones of average size or in the smallest cones, but usually not in the largest.

Complete records similar to those of McIntyre, Aldrich-Blake and those we are presenting in our tables serve to show the extreme complexity of the problems of seed production in pines. Pollination must be fairly good or the conelets will drop off in the first year, but even if they are retained and enlarge in the second season many of the ovules may fail to enlarge to form seeds. Presumably, these were not pollinated, but this early abortion of half grown ovules may include some that received pollen which failed in germination. If the ovules become full grown fertilization may still fail in many of them. These remain as full sized empty seeds. If fertilization actually takes place there are many embryos that compete with each other for about a month. Finally those that form cotyledons in the embryos about a month or 6 weeks old may develop fully as embryos of seeds. Then and then only does the viable seed arrive, provided that the season is not too short, as in very high altitudes, so that the embryos may reach sufficient maturity within the seeds to germinate. Throughout the period of development of the embryos there may be other losses through death of the embryos.

TABLE 1.—SIZES OF SEEDS OF PINUS PONDEROSA
Tree 3-56, collected Aug. 5, 8 and 12. Elevation 3700 ft.

Cone length (in.)	Seed sizes by screen openings[1]									Half grown and defective
	10	11	12	13	14	15	16	17	Total	
m = 3.28										
3	....	3	16	14	....	....	....	....	33	10
3	....	53	10	2	....	....	....	....	65	5
3	....	11	18	2	....	....	....	....	31	17
3	5	30	22	3	....	....	....	....	60	4
3.12	....	12	18	5	....	....	....	....	35	26
3.25	....	45	28	....	....	....	....	....	73	0
3.25	....	8	29	9	....	....	....	....	46	4
3.25	....	14	20	4	....	....	....	....	38	13
3.25	5	11	27	14	4	....	....	....	61	11
3.25	....	4	27	19	....	....	....	....	50	13
3.37	....	2	9	22	9	....	....	....	42	16
3.37	....	35	51	....	....	....	....	....	86	6
3.50	....	8	41	27	....	....	....	....	76	10
3.50	....	5	23	34	2	....	....	....	64	12
3.63	4	15	48	40	....	....	....	....	107	0
3.75	....	6	40	34	2	....	....	....	82	20
Not. measured	....	9	30	11	....	....	....	....	50	0
Total	14	271	457	240	17	....	....	....	999	
No embryos (less)	9	112	198	88	7	....	....	....	405	40%
Net good seeds	5	159	259	152	10				494	60%
Embs. dissected	5	94	144	62	0	(Not all dissected)				

[1] Screen sizes in millimeters:
No. 10 = 3.97; 11 = 4.37; No. 12 = 4.76; 13 = 5.16; No. 14 = 5.56; 15 = 5.95; No. 16 = 6.35; 17 = 6.75; 18 = 7.14

Tree 3-52, collected Aug. 5, 1942. Elevation 3700 ft.

Cone length (in.)	10	11	12	13	14	15	16	17	Total	Half grown and defective
m = 4.62										
4.0	18	22	....	....	....	....	....	....	40	31
4.5	5	21	31	....	....	....	....	....	57	12
4.62	2	9	8	....	....	....	....	....	19	22
4.75	14	22	3	....	....	....	....	....	39	74
4.87	3	14	72	6	....	....	....	....	95	5
5.0	2	12	15	2	....	....	....	....	31	34
Total	44	100	129	8	....	....	....	....	281	
No embryos	38	78	89	7	....	....	....	....	212	75%
Good seeds	6	22	40	1	....	....	....	....	69	25%

TABLE 1.—SIZES OF SEEDS OF PINUS PONDEROSA—Continued

Tree 3-10, collected Aug. 5, 1942. Elevation 3700 ft.

Cone length (in.)	Seed sizes by screen openings[1]										Half grown and defective
	10	11	12	13	14	15	16	17	18	Total	
m = 4.57											
3.87	....	....	....	30	21	5	....	....	....	56	16
4.0	....	....	1	23	23	9	....	....	....	56	4
4.5	....	....	....	32	57	16	....	....	....	105	12
4.75	....	....	....	8	37	48	1	....	....	94	6
5.0	....	....	....	7	43	32	....	....	....	82	6
5.25	....	....	....	13	46	35	....	....	....	94	0
Total	....	....	1	113	227	145	1	....	....	487	
No embryos	....	....	....	9	33	20	....	....	....	62	13%
Presumed good seeds	....	....	1	104	194	125	1	....	....	425	87%

Tree 15-43, collected Aug. 15, 1942. Elevation 4100 ft.

m = 3.94											
Small, not measured	....	4	25	36	8	....	....	....	....	73	0
2.62	53	10	3	....	....	....	....	....	....	66	11
3.0	11	21	20	3	....	....	....	....	....	55	12
4.0	....	....	4	10	13	7	....	....	....	34	29
4.5	....	....	1	22	23	5	....	....	....	51	25
4.5	....	....	....	21	22	6	....	....	....	49	16
5.0	....	....	3	38	27	11	....	....	....	79	31
Total	64	35	56	130	93	29	....	....	....	407	
No embryos	52	23	29	46	46	15	....	....	....	211	51%
Good seeds	12	12	27	84	47	14	....	....	....	196	49%

Tree 15-78, collected Aug. 15, 1942. Elevation 4100 ft.

m = 5.56											
5.0	....	2	0	9	3	....	....	....	....	14	56
5.0	....	1	7	23	1	1	....	....	....	33	52
5.62	....	2	0	16	12	2	....	....	....	32	10
5.75	....	2	15	18	3	....	....	....	....	38	10
6.0	....	1	5	11	5	....	....	....	....	22	55
6.0	....	3	5	21	1	....	....	....	....	30	67
6.1	....	....	2	12	12	7	....	....	....	33	?
Total	....	11	34	110	37	10	....	....	....	202	
No embryos	....	8	16	52	19	6	....	....	....	101	50%
Presumed good seeds	....	3	18	58	18	4	....	....	....	101	50%

TABLE 1.—SIZES OF SEEDS OF PINUS PONDEROSA—Continued

Tree 3-38, collected Aug. 5, 8, and 12, 1942. Elevation 3700 ft.

Cone length (in.)	Seed sizes by screen openings[1]										Half grown and defective
	10	11	12	13	14	15	16	17	18	Total	
m = 5.36											
5.0	....	....	3	19	48	27	7	4	....	108	31
5.0	....	....	....	....	5	12	35	23	....	75	41
5.12	....	....	1	4	6	30	53	3	....	97	13
5.25	....	....	....	1	7	15	34	28	2	87	?
5.25	....	....	3	12	24	37	29	4	....	109	16
5.25	....	1	5	19	26	49	24	4	....	128	14
5.25	....	2	0	9	24	55	29	7	....	126	16
5.25	....	2	2	12	33	35	24	3	....	111	11
5.37	....	....	3	3	13	36	34	18	....	107	31
5.37	....	....	4	8	23	31	24	9	....	99	17
5.37	....	....	1	1	11	35	39	6	7	100	30
5.50	....	....	....	....	7	25	38	26	....	96	16
5.75	....	....	....	....	2	19	23	26	18	88	17
Total	....	5	22	88	229	406	393	161	27	1331	
No embryos	....	1	7	70	32	47	34	6	....	197	15%
Presumed good seeds	....	4	14	18	197	359	359	155	27	1134	85%

Tree 4B-53, collected July 11, 1942. Elevation 2740 ft. Stages I and II

m = 3.37											
3.25	....	....	3	9	16	11	....	....	....	39	14
3.50	....	2	17	25	10	5	1	....	....	60	15
Total	....	2	20	34	26	16	1	....	....	99	
No embryos	....	1	2	3	1	1	....	....	....	8	8%
Good seeds	....	1	18	31	25	15	1	....	....	91	92%

Tree 3-7, collected Aug. 5, 1942. Elevation 3700 ft.

Cone length (in.)	Seed sizes by screen openings[1]									Half grown and defective
	10	11	12	13	14	15	16	17	Total	
m = 3.87										
3.5	....	4	19	13	....	....	....	....	36	6
3.75	....	4	20	21	....	....	....	....	45	33
3.75	....	6	13	3	....	....	....	....	22	5
3.75	....	....	6	24	1	....	....	....	31	28
4.0	....	1	16	19	....	....	....	....	36	11
4.5	....	3	5	31	10	....	....	....	49	21
Total	....	18	79	111	11	....	....	....	219	
No embryos	....	2	22	16	1	....	....	....	41	19%
Good seeds	....	16	57	95	9	....	....	....	178	81%

TABLE 1.—SIZES OF SEEDS OF PINUS PONDEROSA—Continued

Tree 3-40, collected Aug. 5, 1942. Elevation 3700 ft.

Cone length (in.)	Seed sizes by screen openings[1]									Half grown and defective
	10	11	12	13	14	15	16	17	Total	
m = 4.63										
4	....	....	2	6	4	10	6	1	29	10
4.5	....	2	5	15	15	9	2	....	48	19
4.5	....	....	....	3	18	29	21	....	53	33
4.5	....	....	....	5	30	23	1	....	59	6
4.63	....	....	....	6	9	23	21	....	59	28
4.75	....	3	7	9	33	7	....	....	59	11
5.0	....	....	1	18	25	10	2	....	56	15
5.25	....	1	0	7	25	25	17	....	75	30
Total	....	6	15	69	159	136	52	1	438	
No embryos	....	6	9	24	80	59	22	1	201	41%
Good seeds	....	0	6	45	79	77	30	0	237	59%

Tree 3-14, collected Aug. 1 and 5, 1942. Elevation 3700 ft.

Cone length (in.)	Seed sizes by screen openings[1]										Half grown and defective
	10	11	12	13	14	15	16	17	18	Total	
m = 4.37											
3.5	....	....	....	7	10	9	....	....	....	26	14
3.75	....	....	....	....	20	25	10	5	....	60	9
4.5	....	....	4	12	22	12	14	....	....	64	?
4.75	....	....	....	1	12	19	16	12	....	60	15
5.37	....	....	....	....	5	34	33	17	6	95	49
Not measured	....	....	1	1	6	8	4	2	....	22	35
Not measured	....	....	....	....	3	24	17	5	....	49	31
Total	....	....	5	21	78	131	94	41	6	376	
No embryos	....	....	3	7	33	63	38	13	1	158	42%
Good seeds	....	....	2	14	45	68	56	28	5	218	58%

Tree 3-3, collected Aug. 12, 1942. Elevation 3700 ft.

m = 5.3											
5.0	....	....	2	22	33	22	2	....	....	81	7
5.25	....	....	5	23	43	6	....	....	....	77	22
6.25	....	....	....	48	22	10	1	....	....	81	3
Total	....	....	7	93	98	38	3	....	....	239	

TABLE 1.—SIZES OF SEEDS OF PINUS PONDEROSA—Concluded

Tree 3-55, collected Aug. 5, 1942. Elevation 3700 ft.

Cone length (in.)	Seed sizes by screen openings[1]										Half grown and defective
	10	11	12	13	14	15	16	17	18	Total	
m = 4.08											
3.62	....	6	1	4	3	....	....	....	....	14	3
4.0	....	6	22	13	....	....	....	....	....	41	23
4.0	....	1	1	3	2	....	....	....	....	7	15
4.12	....	9	20	21	....	....	....	....	....	50	20
4.37	....	3	5	28	....	....	....	....	....	36	21
4.37	....	8	11	40	3	....	....	....	....	62	25
Total	....	33	60	109	8	....	....	....	....	210	
No embryos	....	25	29	87	7	....	....	....	....	148	70%
Presumed good seeds	....	8	31	22	1	....	....	....	....	62	30%

Tree 3-6, collected Aug. 5 and 8, 1942. Elevation 3700 ft.

Cone length (in.)	10	11	12	13	14	15	16	17	18	Total	Half grown and defective
m = 4.8											
4.0	....	3	5	5	2	1	....	....	....	16	44
4.0	....	1	2	9	5	2	....	....	....	19	14
4.37	....	4	3	6	11	5	....	....	....	29	39
4.5	....	....	1	5	18	15	3	....	....	42	18
4.5	....	1	14	12	5	....	....	....	....	32	19
4.5	....	....	....	10	15	10	2	....	....	37	30
4.75	....	3	7	9	3	....	....	....	....	22	76
4.75	....	....	....	2	5	5	2	....	....	14	50
4.75	....	....	....	8	15	3	....	....	....	26	56
4.87	....	....	1	3	10	10	1	....	....	25	18
4.87	....	....	1	11	12	8	....	....	....	32	29
5.0	....	....	2	14	12	8	2	....	....	38	45
5.25	....	....	4	6	11	18	10	2	....	51	24
5.25	....	....	2	15	8	6	2	2	....	35	34
5.37	....	....	1	5	7	8	2	....	....	23	59
5.37	....	....	....	7	11	8	1	....	....	27	41
5.5	....	....	1	1	9	13	2	1	....	27	47
Total	....	12	44	128	159	120	27	5	....	495	
No embryos (less)	....	8	27	61	77	69	17	3	....	262	53%
Presumed good seeds	....	4	17	67	82	51	10	2	....	233	47%

Tree 3-8, collected Aug. 5, 1942. Elevation 3700 ft.

Cone length (in.)	10	11	12	13	14	15	16	17	18	Total	Half grown and defective
m = 5.25											
4.87	1	....	5	79	6	....	....	....	....	91	2
5.37	....	1	5	55	32	5	....	....	....	98	4
5.50	....	....	8	43	54	9	....	....	....	114	7
Total	1	1	18	177	92	14	....	....	....	303	
No embryos	....	....	10	67	18	3	....	....	....	98	32%
Presumed good seeds	1	1	8	110	74	11	....	....	....	205	68%

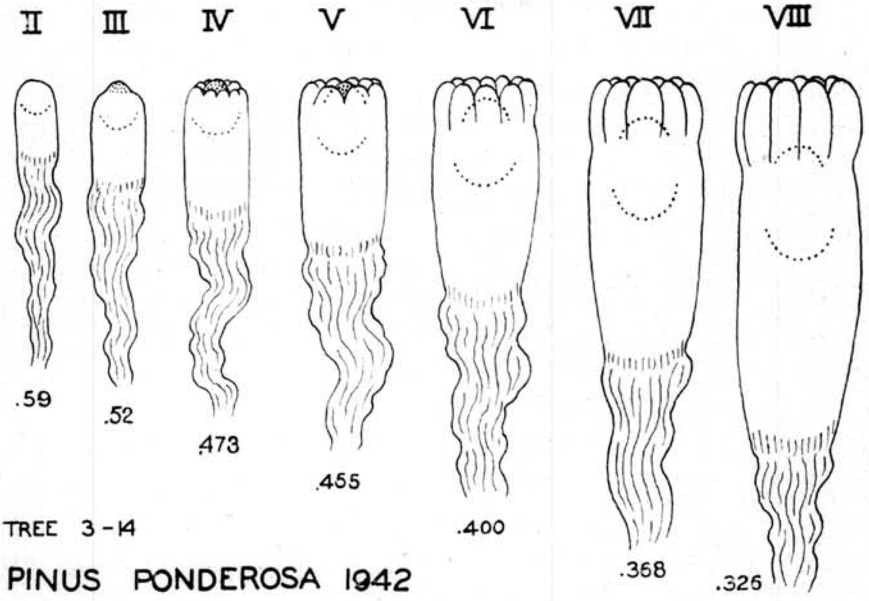

FIG. 1.—Embryos and parts of suspensors in various stages (X 12).

II. THE RELATION BETWEEN THE SIZE OF THE EMBRYO AT DIFFERENTIATION AND THE SIZE OF THE SEED.

Previous investigations on the embryos of the pine (3, 6) have been concerned very largely with the early stages of the embryogeny, the period during which embryonic selection (5) occurs. The later development of the embryo was described only in its broad outline. Some of the stages concerned here have been known for many years. They were illustrated or briefly described long ago by Strasburger (15-16) and others. Stages III and IV as defined in this paper, were illustrated by rather crude woodcuts in Schleiden's textbook more than a century ago. In the second edition of Schleiden (13) the illustrations of the embryo of a fir appears on page 373 of Part 2; his fig. 225A is an embryo in stage III, B an embryo in stage IV. Buchholz (3) in reviewing Schleiden's and other early contributions pointed out that at an earlier stage than these stages the plerome of the root tip becomes recognizable internally, shown in sections of the embryo. The order of appearance of these organs is: 1, root tip and root cap; 2, stem tip; 3, cotyledons.

Figure 1 shows a series of embryos of the pine in successive stages of development, drawn closely to the same scale, with the stages designated by the Roman numerals II-VIII. During stages I and II the embryo is composed of a cylindrical mass of dividing cells, rounded at the apex. At the base of the embryo successive layers of cells elongate to form a long suspensor of greatly elongated cells and the massive root cap that continues to give rise to additions to the suspensor. Only the spherical area above the dotted line contributes to the embryo seen in a young seedling.

Stage III is reached when the stem tip primordium becomes visible as a special bulge at the end of the larger dome that terminates the upper end. This is the first change in the cylindrical embryo that is recognizable externally. As may be seen in the tables of measurements of embryos which follow, the actual dimension when this stage is reached differs considerably, depending upon the size of the seed. Under a binocular dissecting microscope this stem tip primordium has a striking appearance, due to a greater transluscency at this point.

Schopf (13) in his detailed histological study of the embryo of Larix has designated the stages as pro-stage, meta-stage etc. Stage I would be included in the meta-stage. The greater part of stage II belongs to his ana-stage, but it is not certain how closely the end point of stage I would correspond to the end of meta-stage or how much of the ana-stage would be included in stage II. Stage III begins in the later portion of the ana-stage while the remaining stages III-VIII all belong to the telo-stage. These externally recognizable stages therefore appear to parallel some of Schopf's stages based upon internal anatomy, and the two systems are entirely consistent. Our stages represent subdivisions of his stages, mostly of his telo-stage. It was found necessary in dissecting large numbers of embryos from seeds of different sizes, to define a progressive system of morphological growth stages that could be recognized quickly by means of critera visible externally during dissection.

Stage IV is reached when the circle of cotyledonary primordia may be observed surrounding the stem tip on the shoulder of the embryo. The number of these primordia may usually be counted by tilting and rotating the embryo. As long as the cotyledons are small so that the stem tip protrudes beyond the length of the cotyledons the embryo is classified as belonging to stage IV.

Stage V includes embryos in which the cotyledons and stem tip are equal in length. This condition is easily recognized under the dissecting microscope, and may require some exercise of judgment only if the embryo is slightly asymmetrical.

Stage VI has cotyledons that are definitely longer than the stem tip, but less than twice as long. Usually the stem tip is still observable by tilting the embryo under the dissecting microscope even though this apical point is now overtopped on all sides by the cotyledons.

Stage VII is a stage older and larger than Stage VI in which the cotyledons are long enough to hide the stem tip completely from view. The upper dotted lines in these stages of figure 1 show the position of the stem tip. Stage VIII differs from stage VII only in the size of the embryo and in the relative length of the cotyledons. These last two stages are therefore somewhat arbitrarily separated from each other as size classes. The mean dimensions of stages VII and VIII might vary considerably in collections made from the same tree on different dates with a week between. In seeds that are fully ripe all embryos would be expected to be in stage VIII. Hence as ripeness is approached the mean dimensions for this stage would increase. On the other hand in seeds from cones that have a majority of their embryos in stages IV-VI the most mature embryos in some seeds belonging to stage VIII would fall far short of the dimensions observed later in the ripe seeds. For this reason the embryos of stage VIII in some of the tables have been designated VIIIa.

Not all trees were found to have the embryos in their seeds in the same stages of development on August 5, the first date on which many cones were collected. The seeds of several of the trees were already too mature to include many of the cotyledon-forming stages. Some of these were sampled but the series was not dissected. The tables show that a few of the trees from which all embryos were dissected, were found to include too many embryos in the older stages. Other trees gave a very satisfactory distribution of stages in a single collection of cones obtained on the same or successive days. From several trees, in which sampling indicated that the embryos were mostly still in the earlier stages, a second collection was made 5-6 days later.

The advantages offered by the possibility of recognizing morphological growth stages without resort to sections are apparent, not only in the possibility of comparing steps of maturity in large seeds vs. small seeds, but also in comparing the embryos of different species or related genera of conifers.

The embryos of the seeds of all sizes coming from six of the trees concerned in the first part of this paper were dissected out. These were classified as to their stage of development and measured under low magnification with an ocular micrometer. Two measurements were taken: diameter (d) of the embryonic cylinder near the widest part of its upper end (near the plerome apex in smaller embryos; across the cotyledons in the later stages); length (l) from the stem tip or tip of the cotyledons, whichever is the longer, to the place where the suspensor begins. The suspensor consists of elongated cells while the adjacent root cap has small cells more nearly isodiametric.

There were very many embryos that belonged to the same size of seed and to the same stage of development, of which the mean diameter and the mean length only was entered in the tables. The number of embryos belonging to each of these classes is indicated in the column showing frequency (f). Measurements were all converted to microns and may be considered accurate only to about 8 micron units where the frequency is only one.

It was believed that the ratio of diameter to length (d/l) would be useful in these comparisons. These are shown in all of the tables and are interesting insofar as they reveal general tendencies in all of the embryos of certain trees to be more slender or more stout at any and all stages of development. The d/l ratio is relatively high for the earlier stages and diminishes rapidly in early stages, more gradually as the embryos approach the condition of ripe seeds. Aside from the fact that differences in the d/l ratio exist in the embryos of different trees, no other particular significance may be attached to this item at the present time.

The embryos of stages in which the cotyledons have begun to form included counts of the cotyledons primordia or cotyledons. A few of the earliest sets of measurements did not include counts of the cotyledons; hence the frequency of the cotyledon counts is below the frequency of the set of measurements of embryos in two of the trees. In all cases the cotyledon counts were extensive enough to provide a satisfactory random sample, and are complete for the embryos of most of the trees.

Before this investigation was undertaken, it had been assumed, speculatively that an embryo might be expected to differentiate its stem tip and cotyledons when the embryonic cell mass reached a certain size or volume. This idea would suppose that conditions within the embryo determine the point at which differentiation would begin.

The results of these tabulations have shown that this idea was erroneous. They show clearly that even in these earliest stages of differentiation the embryo is very definitely influenced by the size of the seed.

It is remarkable to find that the increase in size of the embryos follows the increase in the size of the seeds so closely. There are some variations and irregularities as may be expected in all limited samples of biological material. The greatest digressions appear where individual embryos or small numbers of them are averaged as indicated by the frequency (f) for the class.

There can be no doubt that the size of the female gametophyte enters into the size relationship of the embryo at the time of differentiation. The female gametophyte is formed long before the embryo and surrounds the latter at all times, serving as endosperm in the matured seed. However efforts to measure and evaluate the endosperm have failed thus far. No satisfactory method has been divised by which the differences and irregularities found may be shown. The difficulty is primarily one of measurement and a lack of knowledge of the precise history of this member in its growth and maturity within the seed, throughout the period of development. We must content ourselves with the knowledge that the gametophyte or endosperm must also be limited by the size of the seed; realizing that seed size must serve as the nearest indirect measure of the endosperm.

When the embryos of stages III-VI are compared in the largest vs. smallest seeds, the volumes of the embryos are probably the important measure of differences. A few comparisons have been made by calculating the relative volumes of the embryos, which are from 2-4 times as large in the largest seeds as in the smallest. Estimates could be made of the relative volumes of the corresponding seeds, but their volumes appear to be from 3-5 times as large in the large seeds as in the small ones. There is enough agreement between these values to indicate that a very high correlation may be expected, but not a perfect one, between the volumes of the embryos dissected from large vs. small seeds and the volumes of the seeds themselves. The entire series of data on the sizes of embryos in relation to seed size point to the conclusion that the size of the partially developed embryo during which its organs become differentiated is conditioned by the size of the seed. The larger the seed, the larger the embryo becomes before its stem tip and cotyledons appear.

The question of the cause of variation in the number of cotyledons in pine embryos has always been one of interest to morphologists. A recent survey by Butts and Buchholz (7) shows how these are known to vary throughout conifers. At one time the senior author (4) was concerned with this problem in the Jack Pine, the Black Spruce in Larix, Cedrus and a few other conifers. The conclusions reached, following the more formal morphology, indicated that in the ontogeny of some embryos, the cotyledon number is reduced through fusion of small cotyledonary primordia and sometimes through the abortion of some of these primordia. This was considered a sort of recapitulation in the embryogeny which was interpreted as indicating that phylogenetically the number of cotyledons was reduced from the large number shown in some pines to the smaller number shown in others.

Many of these embryos showed similar evidence of fusion of cotyledons in stages V and VI. However, when it became apparent that another factor, seed size, has a much more profound influence on the size of the embryo at the time when the cotyledonary primordia first appear, this phase of the investigation was not pursued further. At best the observed evidence of fusions could not account for a reduction in the number of cotyledons by as much as one seed leaf per embryo, while the differences due to seed size bring about differences in the number of cotyledons of about five per embryo. In any repetition of this type of investigation, one would need to take into account the size of the embryo and seed.

The largest number of cotyledons observed in any embryos was 14, the smallest 6. The mean of the largest embryos in the largest seeds was 12.2, and in the smallest embryos found in the smallest seeds it was 7.3 —a difference of 5 cotyledons.

The number of cotyledons is definitely related to the sizes of the seeds, as shown in the tabulations of the embryos dissected from the 6 trees studied. This condition is shown throughout the series. The mean number of cotyledons per embryo found in seeds of the same size in different trees is not precisely the same, but on any one tree the results are consistent when they are based on the means of more than a few embryos.

The results actually show that the embryos which are the smallest at the time of differentiation have the smallest number of cotyledons, and these are found in the smallest seeds. The largest embryos have the largest number of cotyledons, and are found in the largest seeds. There is a variability throughout that is a well known characteristic of cotyledon numbers.

A small embryo at the time of differentiation of these organs would have a smaller circumference on the shoulder of the embryo surrounding the stem tip, so that a smaller number of primordia could be formed. It is only in the largest seeds that the circle of this cotyledonary shoulder is large enough to accommodate the 5 or more additional primordia found in these.

It follows from this that the stem tip primordium must be largest in the embryos which happen to develop within large seeds. This larger stem primordium would have more volume and be composed of a larger number of cells, when surrounded by a larger number of cotyledons. No doubt the more rapid initial growth in the seedlings coming from large seeds is due to a larger, more robust embryo as well as to a larger reserve food supply in the endosperm. That this difference is only of temporary advantage was shown by the work of Righter (12) in his comparison of the seedlings of hybrid origin with the seedlings originating from the wind pollination with both classes coming from seeds of equal weight.

A practical question which would occur to foresters is whether or not any of the seeds collected for this series of observations would actually germinate. No experiments were carried out that would answer this question, which would probably depend upon the condition of the endosperm as well as the stage of the embryo. However our tabulations of embryo maturity on certain dates may be compared with those of Maki (10), who made a series of records of seed germination in cones that were harvested prematurely in Idaho. None of the cones harvested in July contained seeds that would germinate. The cones from which he extracted seeds that would germinate were collected on August 6. These gave about 5 percent germination. His seeds of August 16, gave about 50 percent germination while his later collections were somewhat better. There is good reason to suppose that seeds with embryos in stage VIII might grow, possibly some of those in stage VII. Our table showing the embryos of tree 3-40, collected August 5, which had 158 embryos in stage VIII might be expected to give 36 percent germination, but tree 3-52 collected on the same day, with only 3 embryos in this stage might be expected to show only about 1 percent germination, about 11 percent if stage VII is included in the count of viable seeds.

Our work shows therefore that among different trees growing on a given site there are differences in the degree of maturity of the embryos, when cones are harvested prematurely. Of course the altitude of the site would affect this, and in a comparison of seeds in Idaho and California would involve an allowance for latitude.

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TABLE 2.—EMBRYOS DISSECTED FROM SEEDS OF VARIOUS SIZES OF PINUS PONDEROSA
Tree 3-14, collected Aug. 1, 5, 1942. Elevation 3700 ft.

Seed sizes	Stage II				Stage III				Stage IV					Stage V				
	f	d	l	d/l	f	d	l	d/l	f	d	i	d/l	Cots.	f	d	l	d/l	Cots.
12	0	...	...	...	0	...	...	...	1	630	1303	.48	8	0	...	...	...	...
13	2	422	716	.59	0	...	...	...	4	564	1401	.40	9	0	...	...	...	...
14	6	413	727	.57	4	531	977	.54	8	662	1313	.50	9.8	7	793	1726	.46	9.7
15	5	489	879	.56	7	576	1259	.46	17	695	1497	.46	10.5	13	858	1867	.46	9.9
16	5	564	771	.74	9	727	1205	.60	6	737	1564	.47	10.4	10	847	1965	.43	10.5
17	4	499	902	.55	4	662	1541	.43	4	766	1466	.52	11.0	4	890	1998	.45	10.9
18	0	...	...	...	0	...	...	...	0	...	...	...	...	3	1031	1993	.52	11.3
Total	22	476	802	.59	24	640	1233	.52	40	687	1453	.47		37	860	1892	.45	

Seed sizes	Stage VI					Stage VII					Stage VIIIa					Cotyledons	
	f	d	l	d/l	Cots.	f	d	l	d/l	Cots.	f	d	l	d/l	Cots.	f	Summary by seed sizes
12	1	727	2117	.34	9	0	...	...	...	...	0	...	...	...	...	2	8.50
13	2	814	1849	.44	10	1	956	2605	.37	12	0	...	...	...	...	7	9.57
14	15	879	2476	.36	10.3	3	1042	2952	.35	11.7	2	1096	3018	.36	12	32	10.37
15	13	956	2150	.44	10.1	8	1107	3050	.36	11.1	5	1215	3865	.31	10.8	43	10.42
16	7	998	2410	.41	10.9	11	1150	3061	.37	11.3	8	1292	4082	.32	10.1	37	10.67
17	5	1064	2649	.40	12.0	4	1227	3387	.36	11.8	3	1336	3778	.35	12.3	20	11.50
18	1	1248	2660	.47	13.0	1	1411	3582	.39	14.0	0	...	...	...	...	5	12.20
Total	44	944	2356	.42		28	1140	3095	.37		18	1257	3853	.33			

In this and the following tables the symbols are: f=frequency, d=diameter of embryo; l=length of embryonic cylinder, exclusive of suspensor; d/l=ratio of diameter divided by lengths; Cots.=cotyledons. For seed sizes and stages of embryos see text and Fig. 1. Measurements are given in microns, by conversion from larger units.

TABLE 2.—EMBRYOS DISSECTED FROM SEEDS OF VARIOUS SIZES OF PINUS PONDEROSA—Continued

Tree 3-57, collected Aug. 1, 2, 1942. Elevation 3700 ft.

Seed sizes	Stage II				Stage III				Stage IV					Stage V				
	f	d	l	d/l	f	d	l	d/l	f	d	l	d/l	Cots.	f	d	l	d/l	Cots.
12	0	...	...	...	0	...	...	...	0	...	...	...	...	2	739	2313	.32	9.5
13	2	261	434	.60	1	662	1737	.38	10	651	1726	.38	...	18	727	1933	.38	10.2
14	1	359	706	.51	0	...	...	...	3	673	1802	.37	...	6	859	2301	.37	11.0
Total	3	294	524	.56	1	662	1737	.38	13	658	1745	.38		26	753	2047	.37	

Seed sizes	Stage VI					Stage VII					Stage VIIIa					Cotyledons	
	f	d	l	d/l	Cots.	f	d	l	d/l	Cots.	f	d	l	d/l	Cots.	f	Summary by seed sizes
12	0	...	...	...	...	8	923	2788	.33	8.8	0	...	...	...	...	10	9.00
13	18	825	2336	.35	9.3	33	902	2768	.32	9.6	11	1042	3463	.30	9.7	25	9.72
14	7	847	2388	.35	10.8	10	933	2692	.35	10.2	5	1086	3376	.32	11.5	19	10.89
Total	25	832	2346	.35		51	910	2738	.33		16	1054	3436	.31			

Tree 15-43, collected Aug. 14, 1942. Elevation 4100 ft.

Seed sizes	Stage II				Stage III				Stage IV					Stage V				
	f	d	l	d/l	f	d	l	d/l	f	d	l	d/l	Cots.	f	d	l	d/l	Cots.
10	1	207	260	.79	5	406	701	.58	4	472	1067	.45	7	3	568	1375	.41	6.3
11	0	...	...	...	0	...	...	...	1	520	1324	.39	8	5	641	1499	.43	7.6
12	2	266	363	.73	2	445	933	.48	5	602	1182	.51	9	7	674	1607	.42	8.6
13	3	307	505	.61	1	489	977	.50	6	641	1278	.50	9	20	730	1604	.46	9.4
14	1	413	597	.69	0	...	...	...	3	604	1287	.47	10	4	765	1639	.47	9.1
15	0	...	...	...	0	...	...	...	0	...	...	...	...	1	781	1704	.46	10.0
Total	7	296	445	.66	8	426	794	.54	19	583	1234	.47		40	702	1580	.44	

Seed sizes	Stage VI					Stage VII					Stage VIIIa					Cotyledons	
	f	d	l	d/l	Cots.	f	d	l	d/l	Cots.	f	d	l	d/l	Cots.	f	Summary by seed sizes
10	1	706	2171	.33	7	0	...	...	...	...	0	...	...	...	...	8	6.77
11	6	741	1788	.41	7.7	0	...	...	...	...	0	...	...	...	...	12	7.83
12	7	807	2112	.38	8.6	6	903	2551	.35	9.2	0	...	...	...	...	25	8.40
13	18	833	2142	.39	9.3	28	946	2904	.33	9.1	6	1126	3827	.29	9.2	79	9.23
14	13	868	2138	.41	9.2	29	998	2904	.34	9.4	7	1143	3810	.30	9.6	55	9.34
15	3	958	2204	.43	9.3	8	1066	2877	.37	10.1	2	1080	3772	.29	10.0	14	9.94
Total	48	884	2072	.43		71	977	2862	.34		15	1128	3811	.30			

TABLE 2.—EMBRYOS DISSECTED FROM SEEDS OF VARIOUS SIZES OF PINUS PONDEROSA—Continued

Tree 3-56, collected Aug. 5, 8, 12, 1942. Elevation 3700 ft.

Seed sizes	Stage II				Stage III				Stage IV					Stage V				
	f	d	l	d/l	f	d	l	d/l	f	d	l	d/l	Cots.	f	d	l	d/l	Cots.
10	0	...	...	...	0	...	...	...	...	...	...	...	...	3	608	1646	.37	7.6
11	1	217	282	.77	1	326	597	.55	5	439	1051	.42	7.8	13	630	1624	.39	8.5
12	2	299	461	.65	1	510	1140	.45	4	608	1520	.40	9.3	6	701	1677	.40	9.3
13	0	...	...	...	0	...	...	...	0	...	...	...	...	2	743	1764	.42	9.5
Total	3	271	401	.68	2	418	868	.48	9	514	1259	.41		24	655	1652	.40	

Seed sizes	Stage VI					Stage VII					Stage VIII					Cotyledons	
	f	d	l	d/l	Cots.	f	d	l	d/l	Cots.	f	d	l	d/l	Cots.	f	Summary by seed sizes
10	2	614	1529	.40	8	...	...	...	...	...	...	...	...	...	...	5	7.80
11	24	629	1765	.36	7.9	35	748	2539	.29	8.7	15	886	3461	.26	9.1	92	8.49
12	10	800	2189	.37	9.1	39	906	2899	.31	9.3	82	1127	3968	.28	10.	140	9.7
13	2	868	2334	.37	10.5	10	896	3066	.29	8.9	48	1279	4424	.29	10.3	62	10.06
Total	38	671	1894	.35		84	839	2771	.30		145	1152	4066	.28			

Tree 3-40, collected Aug. 5, 1942. Elevation 3700 ft.

Seed sizes	Stage II				Stage III				Stage IV					Stage V				
	f	d	l	d/l	f	d	l	d/l	f	d	l	d/l	Cots.	f	d	l	d/l	Cots.
12	2	389	608	.64	...	...	...	...	...	...	...	...	...	1	608	1628	.37	8.0
13	...	...	...	...	...	...	...	...	...	...	...	...	...	2	608	1378	.44	8.0
14	...	...	...	...	...	...	...	...	...	...	...	...	...	1	825	1716	.48	10.0
15	3	513	1005	.51	...	...	...	...	3	781	1324	.59	11	2	825	1683	.49	9.0
16	1	455	673	.68	...	...	...	...	...	...	...	...	...	2	868	2008	.43	10.5
Total	6	466	818	.57	...	...	...	...	3	781	1324	.59		8	754	1686	.45	

Seed sizes	Stage VI					Stage VII					Stage VIII					Cotyledons	
	f	d	l	d/l	Cots.	f	d	l	d/l	Cots.	f	d	l	d/l	Cots.	f	Summary by seed sizes
12	...	...	...	...	...	...	...	...	...	...	4	1146	3705	.31	7.5	5	7.80
13	1	825	1716	.48	10	13	1005	3148	.32	9.2	29	1299	4742	.27	9.5	45	9.82
14	...	...	...	...	...	24	1075	3105	.35	10.3	54	1278	4630	.28	9.9	79	10.04
15	4	912	2177	.42	10	9	1054	3158	.33	10.0	55	1310	4589	.29	10.2	73	10.14
16	...	...	...	...	...	11	1042	3311	.31	10.5	16	1371	4961	.28	10.1	29	10.31
Total	5	894	2084	.43		57	1045	3214	.33		158	1299	4646	.28			

TABLE 2.—EMBRYOS DISSECTED FROM SEEDS OF VARIOUS SIZES OF PINUS PONDEROSA—Concluded

Tree 3-52, collected Aug. 5, 1942. Elevation 3700 ft.

Seed sizes	Stage II				Stage III				Stage IV					Stage V				
	f	d	l	d/l	f	d	l	d/l	f	d	l	d/l	Cots.	f	d	l	d/l	Cots.
11	0	....	....	....	1	413	651	.63	1	564	1107	.51	9	1	608	1086	.56	9
12	0	....	....	....	2	434	802	.54	1	586	1151	.51	8	4	628	1309	.48	9
13	0	....	....	....	0	....	....	....	0	....	....	....	....	2	630	1476	.43	10
14	0	....	....	....	0	....	....	....	0	....	....	....	....	0	....	....	....	....
Total	....	....	....	....	3	427	753	.57	2	576	1129	.51		7	625	1324	.47	

Seed sizes	Stage VI					Stage VII					Stage VIII					Cotyledons	
	f	d	l	d/l	Cots.	f	d	l	d/l	Cots.	f	d	l	d/l	Cots.	f	Summary by seed sizes
11	1	737	2084	.35	9	1	868	2410	.36	9	....	....	....	....	....	4	9.
12	6	779	2008	.39	9	8	896	2685	.33	9.25	1	977	3626	.27	9	20	9.10
13	19	797	2150	.37	9.3	18	886	2859	.31	9.06	2	1096	3691	.30	10.5	41	9.2
14	0	....	....	....	....	1	956	2779	.34	8.0	0	....	....	....	....	1	8.00
Total	26	791	2117	.37		28	890	2791	.32		3	1056	3671	.29			