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Variations in Cone Properties, Seed Yield and Seed Weight in Western White Pine When Pollination is Controlled

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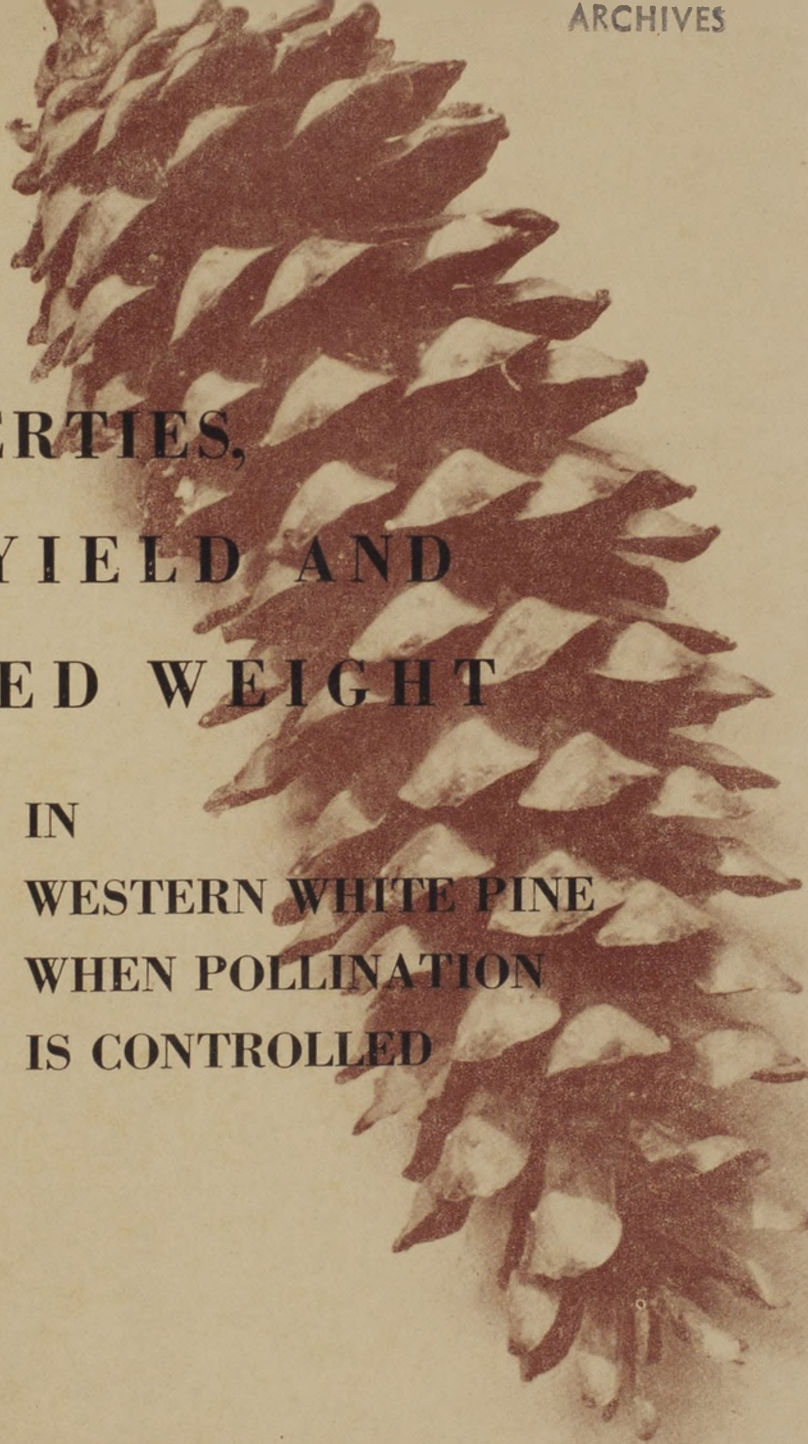

Variations In

CONE PROPERTIES, SEED YIELD AND SEED WEIGHT

IN WESTERN WHITE PINE WHEN POLLINATION IS CONTROLLED

By A. E. Squillace

SCHOOL of FORESTRY
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ERRATA SHEET

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Variations in Cone Properties......

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Variation in seed yield and seed weight in conifers has interested foresters for a number of years. Nurserymen and silviculturists especially have studied such variation in connection with regeneration work. Forest geneticists have become interested in the subject mainly because of its implications in studies of racial variation, progeny tests, and other breeding investigations. Seed yield, being the end product of controlled pollination, is obviously of direct importance to these latter workers. On the other hand, they are concerned with seed weight mainly because this factor often tends to mask inherent growth rate and other traits in seedling progenies.

In controlled breeding experiments differences in average cone size, sound seed yield, and seed weight are often found when different pollens are used on the same mother tree. The cause of these differences has often been speculated upon (especially for cone size and seed weight). Are they due to the use of different pollens, or to environmental factors, or both? The present study was designed mainly to gain some insight into this question, using data from controlled pollinations made on western white pine (*Pinus monticola Dougl.*) trees (figure 1). It encompassed the following points:

1. Within-tree variations in cone length and its relation to location of cone on tree, fruitfulness of cone-bearing shoot, and pollen source.
2. Variation in average cone-scale size among cones from the same tree and its relation to cone length and pollen source; relation of average scale width-scale length ratio to pollen source.
3. Variation in sound seed yield in different portions of cones; variation in sound seed yield among cones from the same tree and its relation to cone length, and pollen source.
4. Within-cone variation in seed weight and its relation to location of seed in cone; variation in average seed weight among cones from the same tree and its relation to location of cone on tree; fruitfulness of cone-bearing shoot, cone length, cone-scale size, sound seed yield per unit of cone length, and pollen source.

[1]Slightly revised thesis, presented in partial fulfillment of the requirements for the degree of Master of Science at Montana State University, 1955.

[2]Forester, Intermountain Forest and Range Experiment Station, Forest Service, Spokane, Washington.

Variations in Cone Properties, Seed Yield and Seed Weight in Western White Pine When Pollination is Controlled[1]

by

A. E. Squillace[2]

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4. Within-cone variation in seed weight and its relation to location of seed in cone; variation in average seed weight among cones from the same tree and its relation to location of cone on tree; fruitfulness of cone-bearing shoot, cone length, cone-scale size, sound seed yield per unit of cone length, and pollen source.

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Fig. 1. Controlled pollination on selection number 58.

REVIEW OF LITERATURE

Cone Size

Relatively few investigators have studied the nature of variation in cone size and its relation to other factors. Perry and Coover (19) noted that pitch pine (*P. rigida* Mill.) cones varied in size from tree to tree with little variation within trees and found no association of cone size with vertical position of cone in tree. Stone (25) likewise reported no relation of cone size with location on tree in Virginia pine (*P. virginiana* Mill.). Willis and Hoffmann (29) observed that in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) the size of the cone is directly dependent upon the vigor of the cone-bearing shoot.

Allen (2) noted that unpollinated and self-pollinated Douglas-fir cones grew just as rapidly and reached the same size at maturity as wind-pollinated controls, thus implying no effect of pollen source upon cone size. However, Gothe (11) found large differences in cone size following inter-and intraspecies crossing and self-pollination in various species of larch (*Larix* spp.) and noted that the differences may have been due to the different pollen parents used. Similarly, Forshell (10) found that Scotch pine (*Pinus sylvestris* L.) cones resulting from wind pollination were smaller on the average than cones produced from self and cross pollination. Metaxenia (effect of pollen parent on maternal tissue of the fruit) has been observed in oaks (*Quercus* spp.) by Schreiner and Duffield (22). They found that (a) many acorns produced through interspecies crossing matured later than acorns produced through wind pollination on the same tree, closely approximating the time of maturity of natural acorns on the pollen parent tree, and (b) acorns resulting from interspecies crossing were larger than those produced from controlled intraspecific pollination. Philp and Sherry (20) reported that self-pollinated pods were shorter than natural pods in green wattle (*Acacia decurrens* Willd.). Swingle (26) showed that metaxenia occurred in the date palm as an effect on time of ripening of fruit, which is of great practical importance. Several workers found it in apples. Among them, Nebel (18) also summarized the literature of earlier investigators and pointed out the possibility of improving the keeping quality of apples in orchard practice.

Seed Yield

Past investigations have shown that in most species larger cones usually yield more sound seed. This relationship was reported by Zon (31) in western white pine; Eliason and Heit (9), Kockarj (13), and Simak (23) in Scotch pine; Stone (25) in Virginia pine; Vincent (27) in Scotch pine and Norway spruce (*Picea abies* (L.) Karst); and Krstic (14) in Serbian spruce (P. *omorika* Panc.). McIntyre (15), on the other hand, found no correlation of seed yield with length or weight of cone in mountain pine (*Pinus pungens* Lamb.).

Some authors reported differences in yield of seed in different portions of cones, but results are not always consistent, neither within nor among different species. McIntyre (15) found that most seeds occurred in the upper (distal) third portion of cones in mountain pine with none in the lower (proximal) third. Munns (17), working with Jeffrey pine (P. *jeffreyi* Grev. and Balf.), found the greatest percentage of seed in the upper third of small cones and in the middle third of large- and medium-sized cones. Stone (25) found differences in yield in varying portions of cones, but results did not agree in cones collected in two different seasons. Vincent (27) reported that seeds in the middle third of cones were more numerous than at either end, in Scotch pine and Norway spruce. Perry and Coover (19) reported that seeds from the upper crowns of shortleaf pine (*P. echinata* Mill.) and pitch pine were more viable.

Numerous investigators have verified that pollen source may affect seed yield. As notable examples reduced yields are often encountered in hybridization and inbreeding. Variation in yield resulting from intraspecies crossing among individual trees has received less attention but there is little doubt that it occurs.

Seed Weight

Baldwin (3) summarized literature dealing with environmental influence on germinative behavior and size of seed. A number of workers have found that larger cones generally yield larger seeds. This association was reported by Buchholz and Stiemert (6) in ponderosa pine (*P. ponderosa* Laws.); Perry and Coover (19) in pitch pine; Vincent (27) in Scotch pine and Norway spruce; Willis (28) and Willis and Hofmann (29) in Douglas fir; Wright (30) in eastern white pine (*P. strobus* L) Eliason and Heit (9), Forshell (10), Kockarj (13), and Simak (23) in Scotch pine; Aldrich-Blake (1) in Corsican pine (*P. nigra v. poiretiana* (Ant.) Aschers and Graebn.); and Krstic (14) in Serbian spruce. As several authors point out, however, the relationship does not always hold among cones from different trees of the same species. Further, it apparently does not hold for all species because Perry and Coover (19) did not find the relationship in shortleaf pine. They state that "Many small and medium-size cones contained more and better seeds than the larger ones."

Vincent (27) found that seeds were heaviest in the middle third of Scotch pine and Norway spruce cones. Krstic (14) found the same tendency in Serbian spruce. On the other hand, Wright (30) reported that those in the basal third were heaviest in eastern white pine. Simak (23) working with Scotch pine, found that among cones of a given size, seed size varied inversely with number of seeds per cone.

Righter (21) pointed out that the heredity of the embryo of a developing pine seed probably cannot have more than a negligible effect upon seed weight. He arrived at this conclusion by noting first that the seed coat and endosperm together comprise most of the total seed weight, secondly, that the seed coat attains its full size before fertilization takes place, and thirdly, that much of the total seed weight variation is associated with cone size.

Righter's observations do not preclude the possibility that the pollen tube may affect seed size through differential stimulation of ovule development. This possibility was discussed by Buchholz (5). In pines, the pollen grain germinates and grows into the nucellus of the ovule long before the seed is mature, and thus could conceivably affect total seed size. Jamblinne (12), working with Austrian pine (*P. nigra Arnold*) and Scotch pine, found that seed from interspecific crossing were heavier than those from intraspecific crossing. Burlingame (7), however, reported that ovule development in *Araucaria* seemed to occur independently of pollen effect.

Xenia (effect of pollen parent upon tissues of the fruit evolved from both parents) has been observed in angiosperms. Clapper (8) and McKay and Crane (16) demonstrated the existence of it in chestnut (*Castanea* spp.), noting that use of different pollens in hybridization resulted in nuts of different sizes.

METHOD

The present study involved two tests conducted during the years 1952-1954. The earlier test was designed mainly as a preliminary investigation into the association of cone size, seed yield, and seed weight with environmental factors. The latter test, on the other hand, was designed specifically to determine whether or not different pollens applied in intraspecies crossing have an effect upon cone characteristics, seed yield, or seed weight, and to evaluate such effects, if any, in comparison with those of environmental factors. Both tests involved intraspecific pollinations made between individual western white pnie trees growing in northern Idaho. These trees had been selected on the basis of apparent resistance to blister rust (*Cronartium ribicola* Fischer.) for use in a project designed to breed superior western white pine trees, as reported by Bingham, Squillace, and Duffield (4) and Squillace and Bingham (24). Further details of the two tests, distinguished by the year in which the controlled pollinations were made, follow.

1952 Test

The 1952 test involved three trees (selections number 19, 59, and 62) on which routine controlled pollination had been made in the spring of 1952. From two to five different pollens had been used on the three seed trees (female parents). The controlled pollinations, being made in the customary manner, involved no purposive selection of immature female cones for use with each pollen source. In routine pollination work, the breeder usually applies pollen of a given source to female cones most easily within reach at the time he is using that particular pollen. After applying the pollen to a roughly predetermined number of cones he continues with the next pollen to be used. In doing so, he often has to move his position in the tree in order to be within reach of more cones. Thus, by this method, there tends to be a clustering of cones used for each pollen within different portions of the crown. As will be shown later, this tendency for clustering can have an important bearing on the average cone length, seed yield, and seed weight attendant with each pollen parent. Mature cones were collected in the fall of 1953 and at that time the location of each cone was recorded as follows:

1. Vertical position in cone-bearing portion of crown, recorded as "upper," "mid-

dle," and 'lower." (In western white pine trees most cones are usually borne in the upper one-half to one-third of the crown and it is this portion of the crown that is referred to as "cone-bearing.")

2. Horizontal position of cone in crown, recorded as "outer" or "inner."
3. Side of tree, recorded as "north," "east," "south," or "west."

Following cone collection, the total length of each cone was measured and then the seeds were extracted separately from each cone. Empty seeds were winnowed out by hand methods, and both the number of empty and full seeds were recorded for each cone. Finally, the sound seeds were weighed to obtain an average seed weight for each cone.

1953 Test

In the 1953 test two pollen sources were used on each of five seed trees (selections number 19, 30, 39, 58, and 64). The two pollen sources used on each were not the same in each case. Controlled pollinations were made in the spring of 1953 and the mature cones were collected in the fall of 1954. In contrast to the earlier test, the female cone-bearing shoots here were purposely selected. On each seed tree from 5 to 7 pairs of shoots bearing immature cones were selected on the basis of similarity in (a) location of shoot in crown, (b) number of cones on the shoot, and (c) stage of development of the cones. Then the pollen source to be used on each shoot of a pair was chosen in a random manner. The two pollen sources for each tree were applied on the same day in order to eliminate time of pollination as a possible variable. Also, all shoots received the same treatment in respect to bagging for isolation of the immature female cones prior to pollination, subsequent removal of pollination bags, and cone bagging in the following spring.

Following cone collection, the measurement of cone lengths, extraction of seeds, recording of numbers of sound and empty seeds, and the weighing of seeds were done essentially as in the earlier test. However, the following additional types of data were obtained in this test:

1. Three cone scales occurring at the approximate midpoint of each cone were selected in a systematic manner around the periphery of the cone. The total length and the width, measured across the widest portion of the apophysis of each scale, were obtained. These values were then averaged for each cone and the average scale length was multiplied by average scale width to obtain a measure of "scale size." Scale size as used here was not an accurate measure of the exact surface area of the scale because the scales were not rectangular. However, the values were considered suitable for comparative purposes.
2. Thirteen cones from tree number 30 were selected for a special study of individual seed weight variation occurring within cones and for a determination of possible association of weight with position of seed in cone. Cones from tree number 30 only were selected for this purpose because cones from other trees opened before or too soon after collection to make such a study possible. The seeds from the thirteen cones were extracted separately from the basal, middle, and upper thirds of each cone. These seeds were winnowed, counted, and weighed separately (in the same manner as was done with seed from whole cones) for each position on the cone.

ANALYSIS OF DATA

Analysis of variance methods were used in interpreting differences associated with environmental factors and pollen source. Correlation and regression methods were applied in evaluating relationships between various factors and in adjusting seed weight for its association with other factors.

RESULTS

Variation in Cone Length

Cone length varied greatly within trees and much of this variation was found to be ascribable to environmental factors. In the 1953 test, where pairs of similar female cone-bearing shoots were purposively selected for testing pollen-source effects, it was found that "shoot-pairs" accounted for much of the variation, in most of the seed trees studied (Table 1). Thus, cones within pairs of shoots tended to be more similar in length than cones from different shoot-pairs. Since the shoots had been paired on the basis of similarity in respect to position in crown, stage of immature cone development, and fruitfulness, it can be concluded from the test that cone length was associated with one or more of these factors.

In the same test differences associated with pollen source, on the other hand, were usually small (Tables 1 and 2). On seed tree number 30, the female flowers pollinated with pollen from tree number 16 developed into mature cones which differed significantly (5-percent level) in length from those produced from cones on which pollen of tree 37 was applied. On the other hand, differences associated with pollen source in the remaining four trees were nonsignificant. Therefore, there is some question as to whether or not the mean difference found in tree 30 was really due to the pollen parents or to sampling error. However, it is logical to assume that if a real metaxenial effect occurs the expression of such effects could vary, depending upon the particular pairs of pollens being tested. If so, one pair may show a difference, with no noticeable difference appearing in another pair. At any rate, the results indicate that further investigation would be necessary to prove the existence of pollen effect upon cone length and that if a real effect occurs it probably is small in comparison to environmental effects.

In the 1952 test where shoots were not paired but merely taken "as they came" in applying the different pollens, the average lengths of the mature cones produced in each cross varied greatly in one of the seed trees (Table 3). On this particular tree, number 19, cones resulting from cross 19x59 averaged considerably longer than cones from other crosses on the same tree. However, it was very likely that a large part of this variation was due to environmental effects but it was not possible to determine whether or not pollen had any effect. The differences are merely pointed out here to show what can occur when controlled pollinations are made in the ordinary manner and where the number of cones in each cross are few.

Although data from the 1952 test could not be used in searching for pollen parent effects they could be used, with caution, in an attempt to pinpoint environmental relationships more closely. As will be recalled the exact location of each shoot used in the test was recorded. It was felt that if cone length is strongly related to position in crown, the relationship would be apparent in spite of the possibility that pollen source effects might tend to obscure it. The data are summarized in Table 4. Although there appears to be some tendency toward longer cones in the upper and outer crown and on south and west sides, the differences are not statistically significant. Therefore, cone length apparently is not strongly related to position of cone in crown, although it is likely that a more sensitive test with a larger sample might have revealed significant trends.

In both tests, mature cones borne on the more fruitful shoots, as expressed by the number of immature or mature female cones on each shoot, were usually longer than those borne on less fruitful shoots. Correlation indices showing this relationship are summarized in Table 5. Note that statistically significant trends were found in over half of the trees studied and that the pooled, within group correlation indices, are highly significant, though not strong. The relationship was somewhat stronger when the number of immature cones was used as a measure of fruitfulness than when mature cones were used. A logical explanation of the correlation is that female cone-bearing shoots may differ in their reproductive vigor and that such vigor is not only expressed in the number of cones produced but also in their length.

The average numbers of cones per shoot, classified by position in the crown, are shown in Table 4. The meagerness of these data prevented sound statistical tests, but there appears to be some tendency for larger numbers of cones per shoot in the upper crown, with decreasing numbers toward the lower crown. Horizontal position and side-of-tree appeared to show little or no relationship.

Variation in Scale Size and Scale Width - Scale Length Ratio

Average scale size was strongly related to cone length, longer cones usually having larger scales (Table 6). Since cone length was shown to be largely related to environmental factors, it can probably be said that scale size is also influenced by environmental factors. Thus one would not expect much relationship of scale size as such with pollen source, and this was found to be the case (Table 2). Note in this table that although differences appeared to be large in most trees, the 5-percent level of significance was not reached in any case.

On the other hand, relative scale size (ratio of scale size to cone length) appeared to be associated with pollen source in some trees (Table 2). A statistically significant difference (5-percent level) was found in one of the seed trees, number 19. Significance was approached in tree 39 (less than 10-percent probability) while trees 30, 58, and 64 showed no significance. This relationship means that among cones of the same length on a given seed tree, scale size differed by pollen source. However, as with cone length, further confirmation would be needed to establish the existence of a metaxenial effect upon scale size.

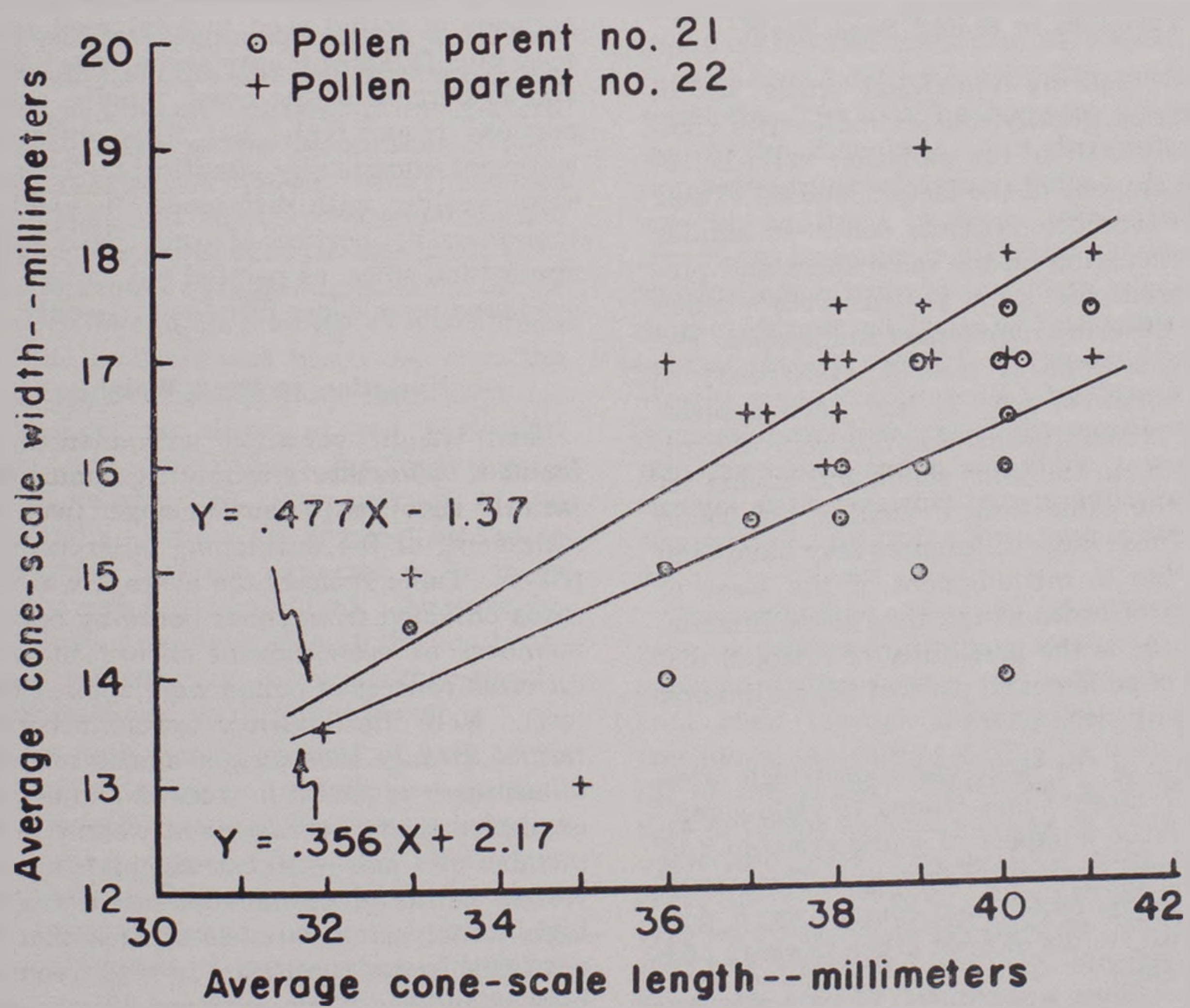

Fig. 2. Average cone-scale width plotted over average cone-scale length for each cone produced on seed tree number 58 (1953 test), showing apparent pollen parent effect upon scale width in relation to length. Regression lines are drawn through the data for each of the two pollen parents.

In contrast to the somewhat questionable metaxenial effect upon scale size related to cone length, a definite effect was noted upon the average cone-scale width versus average cone-scale length ratio (Tables 2 and 7). A highly significant difference was found in seed tree number 58 and a significant difference (closely approaching the 1-percent level) in tree 39. Average scale width is plotted over average scale length for seed tree number 58 in Figure 2 to show the same relationship. Note that the use of pollen parent number 22 apparently caused scales to be rather consistently wider, in relation to their length, than did pollen parent number 21. Differences in the ratios for remaining three seed trees of the 1953 test were not significant. However, in view of the rather strong effects found in two of the trees, this exemplification of metaxenia is considered real.

Variation in Sound Seed Yield

Sound seed by individual cones within trees varied greatly, but in most cases comparatively little of the variation could be related to any one of the factors studied (Table 1). For obscure reasons, cones of similar length occurring on the same shoot and produced from the same pollen often yielded greatly differing numbers of sound seed. For example, a cone of tree 58 (1953 test) to which pollen of tree 21 had been applied, yielded 12 sound seeds. Another cone of similar length, on the same shoot, and having received the same pollen, yielded 184 sound seeds. These large differences may have been partly due to misjudgment of the stage of maturity of cones at the time of pollination. Also, there is the possibility of unequal dispersion of pollen in all parts of the pollination bag having some effect.

In spite of the large variation which often occurred, larger cones tended to yield significantly large numbers of sound seeds in 3 of the 8 trees studied (Table 6). This result agrees, to the extent that comparison is possible, with results of most other workers previously cited.

Among the five trees which could be studied for pollen source effect (1953 test) sound seed yield was strongly affected by pollen source in one tree (Table 2). Differences by pollen source in the remaining four trees were not significant. In testing for association with pollen source, relative yield rather than actual yield was used. Relative yield was the ratio of seed yield to cone length or the number of seeds per unit of cone length. This procedure largely eliminated cone length as a factor affecting yield making the test of pollen source more sensitive.

Study of the 13 cones in which seeds were extracted separately from the three portions of each cone showed that the basal and middle portions yielded significantly more sound seeds than the upper portion. Average yields were 37.5, 39.4, and 23.2 seeds in the basal, middle, and top portions respectively. Lesser yield in the upper portions may have been related to the fact that scales in that portion were narrower and frequently appeared to bear only one seed rather than two. Proportions of sound seed to total seed (sound seed plus full-size empty seeds) were 81, 91, and 90 percent in the basal, middle, and top portions respectively, but these differences were not statistically significant. These results, dealing with differences in yield and soundness by portion of cone, have limited application since, as pointed out earlier, they are based upon cones from one tree only.

Variation in Seed Weight

Seed weight variation within trees was found to be rather strongly associated with factors that are environmental from the standpoint of the developing embryo or the pollen. Table 1 shows the average weight of seeds obtained from cones borne by opposite members of each pair of shoots, in which different sources of pollen were applied (1953 test). Note the tendency toward a correlation of average seed weight among members of each pair of shoots in trees 58 and 64. For example, where average seed weight in one member of a pair of shoots was high, average weight in the other member often was also high. Analysis of variance showed that this relationship was significant in seed tree numbers 58 and 64. Thus, seed weight was often affected to a large extent by the particular shoot on which seeds were borne, which must be considered an environmental factor.

Differences in average seed weight by pollen source (1953 test), on the other hand, were relatively small (Tables 1 and 2). Significant differences were not found in any of the seed trees tested, although significance was approached in tree 64. Sizable differences were also noted in trees 19 and 30 but they likewise could have been a result of random error. In view of the putative metaxenial effects upon cone length, scale size, and the scale width-scale length ratio in some trees, one would expect real differences in seed weight. (As will be shown later seed weight is related to those factors.) However, it can only be said thus far that if a real metaxenial effect upon seed weight occurs it is likely small and possibly easily obscured by the influence of environmental factors. The subject will be discussed further, after pointing out other relationships.

Further evidence of the association of seed weight with environmental factors was available in data from the 1952 test, in which it was possible to pinpoint certain of the factors. Relation of seed weight to position of cone in crown is shown in Table 4. Note that cones in the upper and outer crowns and on the south and west sides bore heavier seeds than those from cones in opposing portions of the crown. Although the number of cones upon which the analysis was based are few, the differences were statistically significant (1-percent level for direction and horizontal position and 5-percent level for vertical position). Note also that those portions of the crown tending to bear the heaviest seed were usually those that are expected to be more favorably exposed to sunlight. Apparently, availability of sunlight, then, has some bearing upon the variation in the average weight of seeds produced on different shoots.

Among most female parents of both tests, there was a tendency (usually not strong) toward the occurrence of heavier seeds in the more fruitful shoots (Table 5). The relationship was slightly stronger when the number of immature cones occurring on shoots was used instead of the number of mature cones.

Among cones from a given tree, the larger cones usually bore heavier seeds, and this relationship was moderately strong in most of the trees studied (Table 6). Since larger cones usually had larger scales, seed weight was also related to average cone-scale size. However, it was found that the relationship of seed weight to scale size was partly independent of cone length. In other words, among cones of the same length, usually those having larger scales bore heavier seeds.

Another factor found to be associated with average seed weight differences among cones from the same tree was the relative number of sound seeds per cone. Other factors being equal, cones having more sound seeds per unit of cone length tended to bear lighter seeds (Table 6). The relationship was not significant in all seed trees, being strong in some and weak in others. The trend was brought out more clearly in some trees by first adjusting average seed weight for the effects of cone length and scale size. Using unadjusted seed weight the pooled, within group correlation index was .24, whereas with the adjusted data it was .41. (The pooled correlation indices must be interpreted with caution in this case, because of the great variation among the individual indices. It should not be construed to mean that significant trends can be found in all trees. The value is shown here merely to provide a comparison of the average strength of this relationship against that of others.) These results agree closely with those reported by Simak (23). A possible explanation of the relationship is that there is more food available to seeds occurring in cones that have relatively few sound seeds and hence they tend to be heavier.

The association of relative seed weight with relative seed yield can have important implications. Pollen source can influence sound seed yield through incompatibility, partial sterility in the case of selfing, of poor viability of the pollen. Therefore, it is possible that different pollens, varying in their effect upon seed yield, may in turn cause differences in seed weight. An example of this type of influence is apparent in data of the 1952 test where the use of pollen from tree 64 on seed tree 19 resulted in a small relative seed yield (Table 3). Note that seeds resulting from that cross were heavier on the average than seeds from other crosses on the same seed parent even though cones were relatively small. This type of pollen parent effect upon seed weight cannot properly be termed metaxenia where developing maternal tissues are directly influenced through some sort of stimulus from the pollen or embryo. The genetic mechanisms involved in the present type of influence may be entirely different from those occurring in true metaxenia, or the process may be mainly physiological.

In view of the relation between seed weight and relative seed yield, one may suspect that the differences in average seed weight by pollen source in the 1953 test were partly caused by differences in yield. In order to test this possibility, the original seed weight averages were adjusted for relative yield. The results (Table 8) show that the original differences in seed weight between pollen sources changed only slightly after adjustment for relative yield. On the other hand, further adjustment for cone length and scale size largely eliminated the differences, as is also shown.

Individual sound seeds within cones varied considerably, the average (pooled) standard deviation being 1.29 milligrams for seeds from the 13 cones studied in detail. A large part of this variation was found to be associated with the position of seeds in the cone. Seeds from the middle portions were heaviest, averaging 22.82 milligrams, while seeds from the basal and top portions averaged 21.65 and 21.08 milligrams, respectively. These results agree with those of Vincent (27) for Scotch pine and Norway spruce and those of Krstic (14) for Serbian spruce.

PRACTICAL APPLICATION OF RESULTS

It is doubtful that the relationships of seed yield and weight with position of cone in crown would justify intensive selection of cones when collecting seed for large-scale operations. When cones are collected directly from trees for such purposes, the extra effort and cost involved in climbing may prohibit culling of cones to any large degree. However, if there is a substantial premium on large seeds, it may pay to select the larger cones from the more fruitful shoots occurring on the south and west sides of the outer and upper crowns.

The likelihood that some fruiting shoots may be more vigorous reproductively than others suggests a possible application in flower stimulation work. Experiments in top-grafting of scions into crowns of trees of fruiting age to stimulate flower production in the scions have been and are being conducted. Results of the present test indicate that it may be wise to concentrate such grafting work on heavily fruiting shoots occurring in the outer and upper portions and on the south and west sides of the crown. If, as suggested by the results, those shoots are more vigorous reproductively, selection may result in large numbers of cones and longer cones, with heavier seed. More important, however, is the possibility that scions grafted on such shoots may flower earlier (that is, earlier in terms of the number of years following grafting). The technique at least seems worthy of investigation.

In critical breeding experiments, where it is desirable to minimize variation in seed weight, such variation can be reduced by careful selecton of shoots. For each replication of treatments (or pollen source) shoots should be selected on the basis of similarity in respect to position in crown, fruitfulness, and stage of flower development. Selection for other factors not included in the present test, such as branch size, may also help to reduce variation. The design can be similar to ordinary randomized blocks with several "blocks" in each tree, and each treatment or pollen source assigned randomly to one shoot in each block.

The apparent effects of pollen source upon the cone scale width-length ratio in some cases seems to warrant further investigation. If corroborating evidence is found the relationship could have considerable practical value in certain breeding investigations such as selective fertilization studies.

SUMMARY

Two tests were conducted to study factors associated with within-tree variation in cone characteristics, seed yield, and seed weight in western pine, during the pericd 1952-1954. In these tests 149 cones were produced

through specially designed, intraspecific controlled pollinations on 8 trees growing in North Idaho. In one test pollinations were made in the ordinary manner but the position of each cone in the crown was recorded. In the other, the pollinations were designed to provide experimental control over certain environmental factors believed to affect cone length and seed weight and to explore the possibility of metaxenial effects. Cones were measured for length, and average widths and lengths of their scales were obtained. Seeds were extracted separately by cones, winnowed to remove empty seeds, counted, and weighed. Special data were taken on 13 cones from one tree to study variation in seed yield and seed weight in different portions of cones. The data were subjected to rigorous statistical analyses.

Within-tree variations in cone length and average seed weight by cones, was found to be associated with factors peculiar to the particular shoots on which the cones are borne. Seeds borne on shoots in the upper and outer crown and on the south and west sides tended to be heavier than those in opposing portions of the crown. A similar tendency is believed to exist with cone length but this could be demonstrated statistically, possibly because of meagerness of the data. Cones borne on the more fruitful shoots tended to be longer and contained heavier seeds than those on the less fruitful shoots.

Metaxenial effects upon the ratio of cone-scale width to scale length were rather definitely shown. Similar effects were also noted upon cone length, ratio of average scale size to cone length, and seed weight, but they did not occur in a sufficient number of cases, or the evidences were not strong enough, to establish conclusively such effects. The putative metaxenial effects were usually small and often easily obscured by environmental influences.

Sound seed yield was often directly correlated with cone length. Average seed weight by cones was directly correlated with cone length and average scale size and inversely correlated with relative sound seed yield (ratio of sound seed yield to cone length).

It was shown that pollen source can affect seed yield. Thus pollen can also affect seed weight indirectly through its influence upon seed yield.

In a test of cones from one tree only, sound seed yield was found to be greatest in the middle third of cones, and least in the top third. Similarly, seeds were heaviest in the middle, next heaviest in the basal third, and lightest in the upper third.

Practical applications of the results were discussed.

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TABLE 1. AVERAGE CONE LENGTH, RELATIVE SCALE SIZE,[1] RELATIVE SEED YIELD,[2] AND SEED WEIGHT, BY SHOOTS, 1953 TEST.[3]

Shoot number	Cone length	Relative scale size	Relative seed yield	Average seed weight	Basis, cones	Shoot number	Cone length	Relative scale size	Relative seed yield	Average seed weight	Basis, cones
	Cm.	Ratio	Ratio	Mg.	Number		Cm.	Ratio	Ratio	Mg.	Number
Seed Parent No. 19											
	POLLEN PARENT NO. 16						POLLEN PARENT NO. 21				
2168	20.4	29.8	4.07	20.40	1	2167	12.5	30.2	4.56	20.00	1
2169	14.3	28.2	1.12	16.40	1	2170	14.0	28.8	3.14	22.00	1
2171	16.2	30.6	2.58	20.85	2	2182	18.9	34.1	4.56	22.50	3
Av.[4]	16.8	29.8	2.59	19.62	—	Av.[4]	16.6	32.3	4.28	21.90	—
Seed Parent No. 30											
	POLLEN PARENT NO. 16						POLLEN PARENT NO. 37				
1126	18.6	32.0	5.86	23.90	1	1082	17.4	32.8	4.71	21.20	1
1127	17.5	30.8	6.36	19.45	2	1083	18.7	27.7	5.05	23.25	2
1128	14.0	33.2	8.43	18.10	1	1084	16.4	31.1	5.79	22.50	1
1129	20.1	21.8	1.67	26.05	2	1085	20.9	25.3	2.81	22.65	2
1130	12.5	35.4	8.80	15.00	1	1086	14.6	31.8	5.14	19.60	1
1131	16.1[5]	30.0	7.11	19.77	3	1087	19.3	31.9	6.37	23.50	3
Av.[4]	16.9	29.5	6.05	20.73	—	Av.[4]	18.6	29.7	5.05	22.56	—
Seed Parent No. 39											
	POLLEN PARENT NO. 17						POLLEN PARENT NO. 37				
1362	19.8	29.6	1.72	23.10	2	1363	22.2	31.6	4.05	24.70	1
1364	23.2	27.1	5.60	23.20	1	1365	18.3	27.9	2.40	22.20	1
1368	15.5	32.0	3.29	21.60	1	1369	16.2	37.5	4.32	21.60	1
1372	21.2	25.0	2.84	23.25	2	1373	18.7	33.0	4.33	23.45	2
Av.[4]	20.1	28.0	3.00	22.92	—	Av.[4]	18.8	32.6	3.89	23.08	—
Seed Parent No. 58											
	POLLEN PARENT NO. 21						POLLEN PARENT NO. 22				
2200	21.0	30.3	9.53	20.38	4	2199	20.3	32.4	6.48	21.22	4
2151	19.7	28.3	4.65	21.02	5	2152	21.3	33.5	8.53	22.06	5
2154	15.7	38.2	8.30	20.60	2	2161	14.9	34.8	5.05	18.73	3
2179	15.5	34.8	9.74	17.00	1	2193	14.3	30.2	6.71	15.30	1
2178	19.5	35.4	10.87	19.30	4	2186	17.8	35.7	9.16	18.92	5
Av.[4]	19.2	32.2	8.20	20.12	—	Av.[4]	18.6	33.9	7.57	20.07	—
Seed Parent No. 64											
	POLLEN PARENT NO. 22						POLLEN PARENT NO. 39				
2400	23.8	28.0	3.48	21.80	2	2399	22.6	33.4	3.64	22.85	2
2398	17.7	25.3	0.11	18.50	1	2397	18.9	31.3	6.51	18.90	1
2396	18.3	28.0	3.24	20.35	2	2395	22.1	25.2	2.14	21.65	2
2394	23.5	27.5	2.68	23.50	1	2393	18.3	33.4	1.20	23.60	1
2390	19.8	27.7	4.38	21.40	2	2389	25.3	26.6	2.96	22.20	2
2388	16.4	32.1	5.91	17.90	1	2387	13.7	32.7	5.33	17.20	1
Av.[4]	20.2	28.0	3.43	20.78	—	Av.[4]	21.2	29.8	3.39	21.46	—

[1]The ratio of average scale size to cone length.

[2]The ratio of sound seed yield to cone length.

[3]Shoots occurring in each row are members of a selected pair. Mortality of developing conelets resulted in unequal number of cones in some shoot pairs. Where all cones of a member of a pair died, the data from the opposite member were omitted in tests of pollen parent effects and are not shown in the table.

[4]Weighted by number of cones.

[5]Based upon only two cones rather than three because average scale size was inadvertently not obtained for one of the cones.

TABLE 2. AVERAGE CONE LENGTH, SCALE SIZE, RELATIVE SCALE SIZE,[1] RATIO OF SCALE WIDTH TO SCALE LENGTH, SOUND SEED YIELD, RELATIVE SOUND SEED YIELD,[2] AND SEED WEIGHT BY POLLEN PARENTS, 1953 TEST.

Cross[3]	Cone length	Scale size	Relative scale size	Scale width vs. length	Sound seeds per cone	Relative seed yield	Seed weight	Basis, cones
	Cm.	Sq. mm.	Ratio	Ratio	Number	Ratio	Mg.	Number
19x16	16.8	501	29.8*	.437	46	2.59*	19.62	4
19x21	16.6	543	32.3*	.432	72	4.28*	21.90	5
30x16	16.9*	[4] 496	29.5	.435	98	6.05	20.73	10
30x37	18.6*	[4] 549	29.7	.441	93	5.05	22.56	10
39x17	20.1	560	[4] 28.0	.495*	62	3.00	22.92	6
39x37	18.8	612	[4] 32.6	.441*	74	3.89	23.08	5
58x21	19.2	613	32.2	.412**	158	8.20	20.12	16
58x22	18.6	629	33.9	.440**	143	7.57	20.07	18
64x22	20.2	562	28.0	.461	69	3.43	[4] 20.78	9
64x39	21.2	624	29.8	.450	69	3.39	[4] 21.46	9

[1]The ratio of average scale size to cone length.

[2]The ratio of sound seed yield to cone length.

[3]The first number of each cross is the seed tree number and the latter is the pollen parent tree number.

[4]The differences between these pairs of values are considered as approaching significance, statistical tests revealing less than 10 - percent level of probability.

*Significant at the 5-percent level.

**Significant at the 1-percent level.

TABLE 3. AVERAGE CONE LENGTH, SOUND SEED YIELD PER CONE, RELATIVE SOUND SEED YIELD,[1] AND SEED WEIGHT, BY POLLEN PARENTS, 1952 TEST.

Cross[2]	Cone length	Sound seeds per cone	Relative sound seed yield	Seed weight	Basis, cones
	Cm.	Number	Ratio	Mg.	Number
19x11	18.6	64	3.45	25.20	4
19x59	20.9	69	3.29	27.60	11
19x62	19.0	57	3.03	22.90	3
19x64	18.3	15	0.82	29.50	5
19x67	13.9	21	1.52	22.80	2
59x58	18.8	128	6.78	17.02	6
59x64	19.6	117	6.01	18.40	3
62x16	15.2	62	4.00	22.60	3
62x19	15.2	67	4.29	22.40	8
62x25	15.5	72	4.47	23.60	4

[1]The ratio of sound seed yield to cone length.

[2]The first number of each cross is the seed tree number and the latter is the pollen parent tree number.

TABLE 4. RELATION OF AVERAGE CONE LENGTH, SEED WEIGHT, AND NUMBER OF CONES PER SHOOT TO LOCATION OF SHOOT IN CROWN. DATA FROM CONES PRODUCED ON 3 TREES,[1] 1952 TEST.

Vertical position in crown	Horizontal position in crown	Side of tree[2]	Cone length	Seed weight	Cones per shoot	Basis cones	Basis shoots
			Cm.	Mg.	Number	Number	Number
Upper	Outer	S&W	17.7	23.77	1.65	10	6
		N&E	—	—	—	0	0
	Inner	S&W	18.7	22.53	1.85	9	4
		N&E	—	—	—	0	0
Middle	Outer	S&W	19.0	23.41	1.42	8	6
		N&E	17.7	21.72	1.46	11	7
	Inner	S&W	18.3	23.10	1.00	1	1
		N&E	15.4	18.35	0.90	2	2
Lower	Outer	S&W	17.7	25.50	1.00	1	1
		N&E	16.3	21.28	1.40	5	4
	Inner	S&W	17.2	17.15	1.60	2	1
		N&E	—	—	—	0	0

[1]Data adjusted for mean differences between trees.

[2]S&W refer to the south and west sides of the trees, while N&E refer to the north and east sides.

TABLE 5. RELATION OF CONE LENGTH AND SEED WEIGHT TO NUMBER OF IMMATURE AND MATURE CONES ON SHOOT.

Seed tree number	Cone length related to: Immature cones on shoot	Cone length related to: Mature cones on shoot	Seed weight related to: Immature cones on shoot	Seed weight related to: Mature cones on shoot	Basis, cones
	Correlation indices				Number
1952 TEST					
19	—[1]	.58**	—[1]	.24	25
59	—[1]	.27	—[1]	-.28	9
62	—[1]	.02	—[1]	.15	15
1953 TEST					
19	.40	.52	.29	.24	13
30	.54*	.32	.42	.22	20
39	.11	.07	.34	.06	14
58	.60**	.62**	.50**	.51**	34
64	.47*	.49*	.36	.40	19
All trees[2]	.48**	.45**	.40**	.28**	—[3]

[1]Numbers of immature cones on shoots were not determined in the 1952 test.

[2]Pooled, within group correlation indices.

[3]The pooled, within group correlation indices involving immature cones on shoot were based upon 100 cones, while those involving mature cones on shoot were based upon 149 cones.

*Significant at the 5-percent level.

**Significant at the 1-percent level.

TABLE 6. CORRELATION INDICES BETWEEN (1) TOTAL SOUND SEED YIELD AND CONE LENGTH, (2) AVERAGE SEED WEIGHT AND CONE LENGTH, (3) AVERAGE SEED WEIGHT AND AVERAGE SCALE SIZE, (4) AVERAGE SEED WEIGHT AND RELATIVE SOUND SEED YIELD,[1] AND (5) AVERAGE SCALE SIZE AND CONE LENGTH.

Seed tree number	Sound seed yield related to cone length	Seed weight related to: Cone length	Seed weight related to: Scale size	Seed weight related to: Relative sound seed yield	Scale size related to cone length	Basis, cones
	Correlation Indices					Number
1952 TEST						
19	.61**	.30	—[2]	-.42*	—[2]	25
59	.33	.52	—[2]	-.76*	—[2]	9
62	.66**	.36	—[2]	-.72**	—[2]	15
1953 TEST						
19	.50	.32	.58*	-.12	.84**	13
30	-.12	.82**	.32	-.31	.48*	20
39	.21	.68**	.63*	.03	.41	14
58	.47**	.63**	.56**	-.34*	.67**	34
64	.08	.76**	.72**	-.41	.69**	19
All trees[3]	.32**	.53**	.52**	-.41**	.64**	—[4]

[1]Correlations of average seed weight with relative sound seed yield were determined after adjusting seed weight for relation to cone length and scale size in the 1953 test, and after adjustment for cone length in the 1952 test.

[2]Scale size was not measured in the 1953 test.

[3]Pooled, within group correlation indices.

[4]The pooled, within group correlation indices involving scale size were based upon 100 cones, while others were based upon 149 cones.

*Significant at the 5-percent level.

**Significant at the 1-percent level.

TABLE 7. AVERAGE CONE-SCALE LENGTH, CONE-SCALE WIDTH, AND WIDTH-LENGTH RATIO, BY POLLEN SOURCE. SEED TREES 58 AND 39, 1953 TEST.

Cone number	Cone-scale length	Cone-scale width	Width vs. length	Cone number	Cone-scale length	Cone-scale width	Width vs. length
	Mm.	Mm.	Ratio		Mm.	Mm.	Ratio
Seed Parent No. 58							
POLLEN PARENT NO. 21				**POLLEN PARENT NO. 22**			
2200a	38	16.0	.421	2199a	37	16.5	.446
b	40	16.5	.412	b	39	17.0	.436
c	39	16.0	.410	c	38	16.5	.434
d	40	16.0	.400	d	41	17.0	.415
2151a	37	15.5	.419	2152a	39	19.0	.487
b	40	14.0	.350	b	39	17.5	.449
c	36	14.0	.389	c	40	17.0	.425
d	40	17.0	.425	d	41	18.0	.439
e	33	14.5	.439	e	40	18.0	.450
2154a	38	15.5	.408	2161a	36	17.0	.472
b	39	15.0	.385	b	35	13.0	.371
c	—[1]	—[1]	—[1]	c	33	15.0	.454
2179a	36	15.0	.417	2193a	32	13.5	.422
2178a	41	17.5	.427	2186a	38	16.0	.421
b	40	17.0	.425	b	38	17.5	.460
c	40	17.5	.438	c	38	17.0	.447
d	39	17.0	.436	d	38	17.0	.447
e	—[1]	—[1]	—[1]	e	37	16.5	.446
Av.	38.5	15.9	.412	Av.	37.7	16.6	.440
Seed Parent No. 39							
POLLEN PARENT NO. 17				**POLLEN PARENT NO. 37**			
1362a	34	16.5	.485	1363a	39	18.0	.462
b	36	17.0	.472	b	—[1]	—[1]	—[1]
1364a	37	17.0	.459	1365a	34	15.0	.441
1368a	31	16.0	.516	1369a	38	16.0	.421
1372a	35	17.0	.486	1373a	39	17.0	.436
b	29	16.0	.552	b	36	16.0	.444
Av	33.7	16.6	.495	Av.	37.2	16.4	.441

[1]Dead or missing.

TABLE 8. AVERAGE SEED WEIGHTS, BEFORE AND AFTER ADJUSTMENT FOR ASSOCIATED FACTORS, BY POLLEN SOURCE, 1953 TEST.

Cross[1]	Average Seed Weight: Unadjusted	Adjusted for relative yield	Adjusted for relative yield cone length, and scale size	Basis, cones
	Mg.	Mg.	Mg.	Number
19x16	19.62	19.50	20.12	4
19x21	21.90	22.02	21.70	5
30x16	20.73	20.84	21.50	10
30x37	22.56	22.44	21.76	10
39x17	22.92	22.92	22.85	6
39x37	23.08	23.08	22.92	5
58x21	20.12	20.17	20.14	16
58x22	20.07	20.01	20.04	18
64x22	20.78	20.80	21.19	9
64x39	21.46	21.49	21.11	9

[1]The first number of each cross is the seed tree number, and the latter is the pollen parent tree number.