Pinus ponderosa

Height Growth of Wind-pollinated Progenies[1])

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Ponderosa pine (*Pinus ponderosa* Laws.) is the most important species of pine in the western United States. Efforts to improve this pine through phenotypic selection have been a principal part of the program of the Institute of Forest Genetics for more than 30 years. In 1929 a study of broad geographic variation in this pine was undertaken at Placerville. Early in this work geneticists found that seed from local sources produced the most vigorous progenies at Placerville.

To study this local variation more intensively, Mr. Lloyd Austin started in 1933 a study of heritable variation in the wind-pollinated progenies of 627[3]) ponderosa seed trees. This is perhaps the most comprehensive study of heritable variation of selected seed trees which has ever been undertaken for any conifer species.

The selected trees were scattered through the El Dorado transect of the Sierra Nevada Mountains. They represented a distribution of more than 7,000 feet in elevation and about 1° of latitude (figure 1).

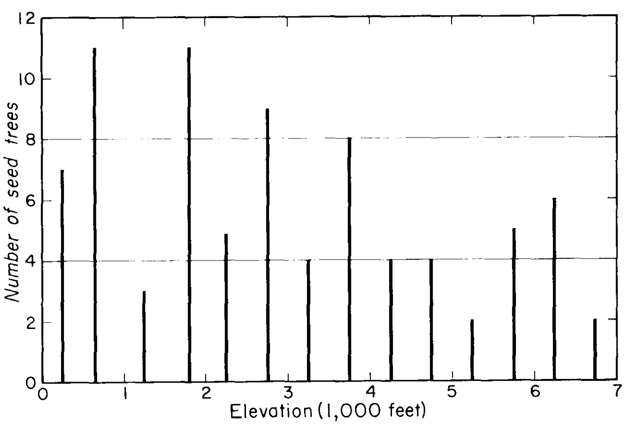

Figure 1. — Elevational distribution of the 81 Sierra Nevada seed trees included in the plantation phase of the 1937 progeny test, Institute of Forest Genetics. Placerville, California.

The two primary objectives of this study were put forth by Day and Austin (1939):

"(1) To determine the hereditary nature of the numerous local strains of ponderosa pine occurring in the various localities through El Dorado County, California, including probable casual relationships with elevation and other factors of the seed-trees' environment; (2) to discover which individual seed trees in each strain, or in each elevational belt, have the inherent ability to produce the most rapidly growing offspring, as determined by measurement of the height, diameter, and branching of the progenies."

Most of the information we obtained pertains to the first of these objectives. With respect to the detection of outstanding seed trees, a few trees whose progenies showed superior height growth were found in the plantation phase of this study. What is more important, a statistical relationship has been found for predicting the performance of progenies of seed trees. The bases of prediction are the second-year height growth of the progenies and the elevation of the seed tree. This finding satisfied one of the motives for conducting this study: the development of a method for detecting through nursery tests the seed trees which produce outstanding progenies.

An Outline of the Study

Before reading the description of this work, readers should remember In fairness to Austin and his associates that studies of this kind were in their infancy when this study was conceived. Information on effective pollination distances (Wright, 1953, 1955) was not available. Neither were methods of estimating genotypic variance as highly developed as they are today. Organized selection of outstanding phenotypes was just beginning.

The description of Austin's procedures is provided to enable the reader to evaluate the results of this study in their proper light. These results also exemplify some biological and statistical features of experimental design of which forest geneticists of today and tomorrow should be aware, so as not to fall into the same pitfalls.

The premise basic to the study was that pollination and fertilization in a stand occur completely at random. That is to say that a complete mixing of pollen from all trees occurs before pollination is accomplished. The many seeds in a cone represent the maternal parent as crossed with an average cross-section of the pollen produced in the stand. The paternal contribution to the variance within progenies is assumed to be the same for all progenies. Differences between progenies then must reflect average differences between seed trees. Thus, studies of open-pollinated progenies were justified in Austin's mind.

Austin realized the theoretical desirability of selecting only trees of outstanding form and growth rate for inclusion in this study. However, he did not consider such selection as practical, for one of the objects of the study was to achieve as broad a geographic base as possible. Furthermore, phenotypic selection in the area involved is difficult due to admixtures of several conifer species, uneven-aged conditions, irregular topography, and frequent changes in soil type. Therefore, the principal criterion by which trees were selected was that they were bearing at least 10 cones. Only infrequently, when the tree-locating crews found more cone-bearing trees than were needed in a collection area, did they give special emphasis to trees of superior form or vigor.

[1]) The third in a series of papers presenting the results of long-term investigations into the variation in this species being conducted at the Institute of Forest Genetics, Placerville, California. The first two papers in this series (Mirov *et al*, 1952; Callaham and Metcalf, 1959) showed the influence of elevation of seed source on subsequent growth.

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[3]) The number 646 given by Mirov *et al*, (1952) was the number of progenies included in the analysis to which they referred. Some seed trees were represented by progenies from two or three crop years.

Ripe cones were collected in 1934 and again in 1936 from selected trees. The cones were opened by suncuring. The extracted seed was cleaned, and the volume of a representative sample of 200 sound seeds was determined. Then the seed was placed in dry cold storage until it was sown in the nursery. Special care was taken to identify and to separate the seed lots from each tree in each crop year.

The nursery phase of the investigation commenced with the planting of unstratified seed in the spring of 1937. The nursery was sown in a triple lattice design (DAY and AUSTIN, 1939). Six seeds of a progeny were sown at each of six planting spots in each of 9 replications: 324 seeds of each progeny. A record was made of the time required for the germination of at least one seed in each of 3 of the 6 spots of a replication. The resulting seedlings were thinned to one per spot; the most westerly seedling at each spot always was retained. Heights of these seedlings were measured at the end of the first season and height and diameter after the second growing season in the nursery. The 2-year data were analyzed by Mrs. KAY BRECHEEN under the supervision of the junior author in 1938.

Using this analysis as a guide, AUSTIN chose 81 progenies for outplanting on the grounds of the Institute. The majority of the progenies were selected for their superiority in seedling height growth and volume. Some progenies were selected to show the effect of crop year of the seed on progenies from the same tree; others to show the influence of either seed size or germination time on subsequent growth. Selections also were made from the largest and smallest progenies in each elevational zone, with respect either to height growth during the second season or to stem volume. Progenies of isolated, possibly self-pollinated, seed trees were included, as were progenies representing several trees which were close neighbors in the field.

Following the suggestion of Dr. F. YATES, AUSTIN laid out this plantation in a 9 × 9 (double lattice) design with three replications. Sixteen trees of each progeny in a 4 × 4 arrangement comprised a plot. Plots were separated from one another and from the single border rows by blank rows. Nine of the progeny plots were grouped together in a block. Nine such blocks made up a replication. One of the 3 replications was rendered useless by insect-caused mortality of many trees. Thus, 32 trees of a progeny, 16 trees in each of 2 replications, were available for measurement.

Dr. J. W. DUFFIELD, formerly geneticist at the Institute, supervised the 15-year measurements and data compilation in the fall of 1951. Tree height was measured with a range rod to the nearest foot; diameter at breast height was measured with calipers to the nearest 0.1 inch. Dr. K. R. NAIR, Forest Research Institute, Dehra Dun, India, subjected DUFFIELD's data to statistical analyses. His results have been confirmed by our more detailed analysis.

Most recently the plantation progeny data have been subjected to multiple regression analyses by the junior author. Mean second-year height growth was computed for the 32 seedlings of a progeny transferred to the plantation. The actual differences between 1-year and 2-year measurements of total height were used. The total height measurements were not block-corrected for the position of the seedling in the nursery according to the formulae of DAY and AUSTIN (1939). Mean height of each progeny at 15 years was computed for the survivors of the original 32 seedlings. These analyses produced the bulk of our results.

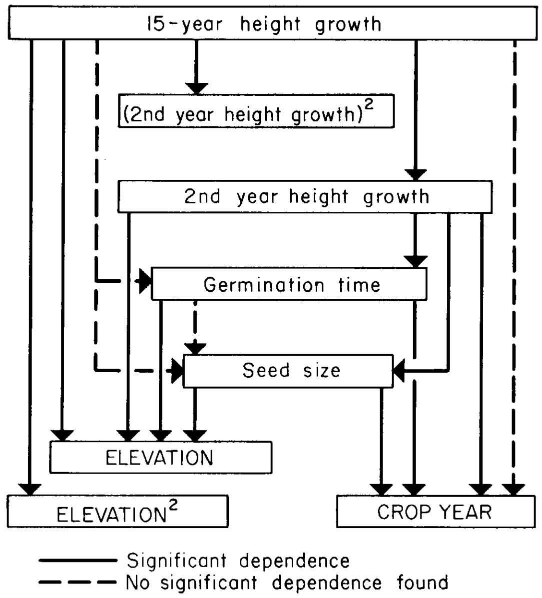

Figure 2. — The relationships tested.

The Results of the Study

The scope and results of the analyses which were made are depicted in *figure 2*. Multiple regression analyses showed the effect on second-year and 15-year height growth of variation in seed size, time for seeds to germinate, elevation of seed source, and crop year. In addition, the 15-year performance of progenies was analyzed to detect the exceptional nature of some offspring.

A word of caution at the onset: In all cases the results of this study apply only to the population of seed-tree progenies represented in this particular study. The seed trees represented in the nursery phase of this study comprise a sample of the trees bearing 10 or more cones systematically selected with respect to elevation and latitude. The seed trees represented by progenies in the plantation phase of this study are a biased selection from this systematic sample. These successive selections give us a population whose average characteristics may be quite different from the average of the wild population of seed trees. Only with considerable caution and statistical reservation can the results of either phase of the study be applied to the natural population from which the seed trees were selected.

Second-year Height Growth

Height growth in 0.01-foot units during the second year in the nursery, H, was related to the following variables:

Z_1 = number of days from sowing until at least one seed in each of 3 of the 6 seed spots in a plot had germinated;

Z_2 = elevation of seed source to the nearest 100 feet;

Z_3 = seed size expressed as cubic centimeters per 200 seeds.

Separate equations showing the relationships were derived for the progenies representing the 1934 and 1936 seed crops. The equation for the 1934 crop is

$$\hat{H}_{34} = 47.12 - 0.4409\, Z_1 - 0.2152\, Z_2 + 0.5360\, Z_3, \qquad (1)$$

and for the 1936 crop

$$\hat{H}_{36} = 53.99 - 0.5751\, Z_1 - 0.2161\, Z_2 + 0.3552\, Z_3. \qquad (2)$$

Equation *(1)* represents 423 means based on 54 seedlings each; equation *(2)*, 223 means of 54 seedlings each. Each of these means was corrected before analyses for environmental variation in the nursery beds (DAY and AUSTIN, 1939).

The three independent variables accounted for an average 50 percent of the variation in second-year height growth. The independent effect on height growth of each variable was highly significant statistically. FOWELLS (1953) in a study started in 1938 found a similar significant relation between seed size and seedling growth for ponderosa pine.

A parallel analysis was made using 2-year stem volume as the dependent variable. $(\text{Diameter})^2 \times (\text{height})$ was taken as directly proportional to volume. The regressions in this case accounted for 63 percent of the variation in stem volume. The use of second-year height growth as the dependent variable is retained, however, because it is much easier to measure in practice than stem volume.

The 1936 seeds were slightly larger and germinated faster than the 1934 seeds. The mean difference in seed size was 0.86 cc. per 200 seeds; the difference in germination time was 4.21 days. Both of these differences are statistically significant, but part of each difference may merely reflect the mean difference in elevation of the progenies of the two crops. The mean elevation of the 423 progenies in the 1934 crop was 2,843 feet and of the 223 progenies of the 1936 crop was 2,452 feet.

Only for the variable Z_3 did the partial regression coefficents differ significantly in equations *(1)* and *(2)*. The importance of germination time and elevation in determining second-year height growth did not vary from one crop year to the other; however, the positive influence of seed size on growth was significantly stronger in seeds of the 1934 crop. Yet, for a given set of values of the three independent variables, the estimates *(1)* and *(2)* are almost identical. The differences in the partial regression coefficients and the constant terms tend to be compensating within the range of the data. Absolute crop year differences in second-year height growth are related to smaller seed and slower germinations in 1934 seed.

Correlation analyses using the 1934 and 1936 data showed for each crop a highly significant statistical correlation between germination time and elevation and between seed size and elevation. Germination was delayed and seed size diminished as the elevation of the seed source increased. The small negative correlation found between size of seed and germination time was not statistically significant.

The use of $(\text{elevation})^2$ as an additional variable in calculations of the curvilinear regressions of 2-year seedling measurements and of the above correlations with seed size and germination time probably would have accounted for additional variation. This was not done because other studies (MIROV *et al*, 1952) have shown the curvilinear elevational effect on seedling growth. The above results do indicate that within an elevation class, the best seedling progenies have mothers producing large quick-germinating seeds. These results confirm indications from an earlier (1929) progeny test at the Institute. Seedlings that were largest in the 1929 seedbed generally came from relatively large seed which had germinated early.

Fifteen-Year Height

One of the main purposes of the plantation phase of this study was to test the reliability of predicting subsequent progeny performance on the basis of seedling measurements. The 1929 progeny test had given indications on this; the best progenies in the seedbed in most cases still were the best progenies in the plantation, at least up to 10 years later. With the present data, an answer can be obtained for the question: Is the 15-year height related to second-year height growth?

AUSTIN selected the plantation progenies for particular reasons. One group of 28 progenies included progenies selected from the 5 most vigorous progenies in 500-foot elevational zones. Vigor was based either on 2-year stem volume or on second-year height growth. Other groups of progenies were selected on the basis of particular combinations of seed size and germination time. The selection of progenies within arbitrary groups was random in some cases; in other cases no record was made as to whether selection was random. In submitting the plantation data to a multiple regression analysis we assume that all selections were at random. On this basis our regression equations can be used in predicting the 15-year heights of nursery progenies that were not carried over into the plantation.

For this special population the effects on 15-year height of seed size, of germination time, and of second-year height growth were determined through a regression analysis. Data for 80 plantation progenies were used.[4] Seed size and germination time did influence final height indirectly through their significant effect on second-year height; however, they did not have a direct effect on 15-year height. This finding is in agreement with RIGHTER (1945) and with FOWELLS (1953). Both reported that the effect of seed size on seedling growth was not apparent after the sixth year. Second-year height growth was the only one of our independent variables showing a significant effect on later growth.

Both second-year height growth and its square contributed significantly to 15-year height. Averages of 32 trees of each of 80 plantation progenies were used in the derivation of equation *(3)* by least squares:

$$\hat{Y}_1 = 0.9554\, X_1 - 0.0094\, X_2 - 0.0581 \qquad (3)$$

= estimated 15-year height in feet;

X_1 = average second-year height growth in 0.01-foot units for the 32 nursery seedlings which were outplanted;

$X_2 = (X_1)^2$

The partial regression coefficients of both independent variables were statistically significant; each had a significant effect independent of the other. The analysis of variance of Y_1, expressed in terms of the mean of 16 trees in a single plot is:

Source of Variation	Sum of Squares	df	Mean Square	F	P
Regression on second-year height growth	552.82	2	276.41	[1] 23.25	<0.001
Deviation from regression	*915.84*	77	*11.89*	[2] 2.45	<0.01
Total, between progenies	1,468.66	79	18.59		
Between plots within progenies	389.00	80	[3] 4.86		

[1] F = 276.41/11.89;
[2] F = 11.89/4.86;
[3] Average variance between plots of the same progeny.

[4] Eighty-one progenies were represented in the plantation, but part of the nursery data for one progeny were lost. Analyses involving both nursery data and plantation data are based on 80 progenies; those involving just plantation data are based on 81 progenies.

The progeny deviations from regression exceed the plot variance within progenies, based on 2 replications of the same progeny in the plantation. However, both second-year height growth and its square do account for a very significant 37.2 percent of the curvilinear variability in 15-year height.

NAIR found in his analysis that elevation of the seed tree accounted for most of the variability in the 15-year height of the progeny. When we use elevation and its square as independent variables, the equation for 81 progenies is:

$$\hat{Y}_2 = 21.84 + 0.1506\, X_3 - 0.00347\, X_4 \quad (4)$$

= estimated 15-year height in feet;

X_3 = elevation of seed tree in hundreds of feet;

$X_4 = (X_3)^2$

The analysis of variance of Y_2 is:

Source of Variation	Sum of Squares	df	Mean Square	F	P
Regression on elevation	600.86	2	300.43	[1]) 26.99	<0.001
Deviation from regression	*867.90*	*78*	*11.13*	[2]) 2.29	<0.01
Total, between progenies	1,468.76	80	18.36		
Between plots within progenies	389.00	80	[3]) 4.86		

1) $F = 300.43/11.13$;
2) $F = 11.13/4.86$;
3) Average variance between plots of the same progeny.

This significant curvilinear relationship of height growth with elevation of the seed source is shown in *figure 3*. The curve of 15-year height is essentially parallel to that of 12-year height (MIROV *et al*, 1952, fig. 7). The two curves show a maximum growth about at the same elevation, but the 15-year curve does not drop as much for higher seed source elevations.

Here we have shown that the use either of second-year height growth or of elevation of seed trees will account for a very significant proportion of the variation in 15-year height. Of the two variables, elevation of seed tree is a little more effective. If information on elevation of seed tree is not available, then second-year height growth in the nursery will serve about as well in predicting progeny vigor.

The next step is to find if the combined effect of second-year height growth and elevation of seed source will

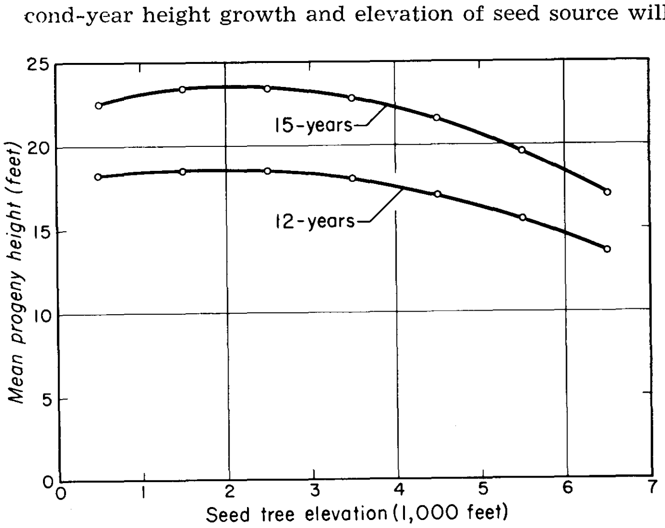

Figure 3. — Mean heights of 15-year-old progenies grown at Institute of Forest Genetics (2,730 feet in elevation) in relation to altitude of seed source. (Curve for 12-year-old heights taken from MIROV *et al.*, 1952.)

further improve the regression estimate. The partial regression coefficients for second-year height growth and its square are not significant in such a multiple regression. But, when the square of second-year height growth is dropped as a variable, second-year height growth becomes highly significant; elevation is significant; and (elevation)^2 is highly significant. The equation is:

$$\hat{Y}_3 = 16.08 + 0.1496\, X_1 + 0.1242\, X_3 - 0.002672\, X_4 \quad (5)$$

= estimated 15-year height in feet;

X_1 = average second-year growth in 0.01-foot units for the 32 nursery seedlings which were outplanted;

X_3 = elevation of seed tree in hundreds of feet;

$X_4 = (X_3)^2$

The analysis of variance of Y_3 is:

Source of Variation	Sum of Squares	df	Mean Square	F	P
Regression on second-year height growth and elevation	722.30	3	240.77	[1]) 24.52	<0.001
Deviation from regression	*746.36*	*76*	*9.82*	[2]) 2.02	<0.01
Total, between progenies	1.468.66	79	18.59		
Between plots within progenies	389.00	80	[3]) 4.86		

1) $F = 240.77/9.82$;
2) $F = 9.82/4.86$;
3) Average variance between plots of the same progeny.

The mean square deviation from regression on elevation alone has been reduced from 11.13 to 9.82 by using the additional variable, second-year height growth. These three variables in combination account for the most variation, 49.2 percent, in 15-year height.

Heritability of Height Growth

Another significant fact was gleaned from the foregoing calculations: the heritability of height growth is gratifyingly high. Heritability is the portion of variation due to genetic differences among sources in relation to the total varation in this study:

$$\text{heritability} = \frac{\sigma^2 \text{ Genetic}}{\sigma^2 \text{ genetic} + \sigma^2 \text{ environment}}$$

The progeny deviations from the regression on elevation were 11.13. This value is an estimate of the total variance after elevational effects were removed. The average variance between plots of the same progeny, 4.86, is an estimate of the environmental variance. The difference between these two values, $11.13 - 4.86 = 6.27$, is the genetic variance within elevations for 2 replications of each progeny. Hence, the best estimate of genetic variance is 6.27/2 or 3.135. Substitution gives

$$\text{heritability} = \frac{3.135}{3.135 + 4.86} = 0.392$$

Nearly 40 percent of the variation in progeny heights within elevational zones is genetically controlled.

Of course this heritability estimate pertains only to this refined test of open-pollinated progenies. It is encouraging though to note that SQUILLACE and SILEN (1960) estimated heritability of ponderosa pine height growth to be 0.362. They analyzed ponderosa pine studies designed differently and intended for different purposes. Their heritability calculations provided the stimulus and format for the calculations presented here. The concurrence of results gives real hope that selection of progenies demonstrating outstanding height growth will lead to substantial improvement in this character.

Prediction of 15-Year Height

Equation *(5)* may be applied to predict the 15-year height of any of the 1937 nursery progenies which were not outplanted. Such prediction may be applied only to the seedlings grown under the conditions of this particular experiment. The predicted heights would be those resulting from growth during the same 15-year period, 1937 through 1951. This application may be made to the 600 progenies representing 546 seed trees which were not included in the plantation phase of this study.

The estimated variance of $\hat{Y}_3$, obtained through the application of equation *(5)* to a set of values X_1, X_3, and X_4, will be:

$$s_{\hat{Y}_3}^2 = 9.82\ [1/80 + 0.000356184\ (X_1 - 37.125)^2 + 0.000518490\ (X_3 - 29.500)^2 + 0.000000116453\ (X_4 - 1239.400)^2 - 0.000098158\ (X_1 - 37.125)\ (X_3 - 29.500) + 0.000003432\ (X_1 - 37.125)\ (X_4 - 1239.400) - 0.000014852\ (X_3 - 29.500)\ (X_4 - 1239.400)] \qquad (6)$$

Then $\hat{Y}_3 \pm 2\, s_{\hat{Y}_3}^2$ is the range for a set of X_1, X_3, and X_4 values. The odds are 19 to 1 that the true value of Y for each set of values from this population of 600 progenies will be included in this range.

For a single progeny the variance of the estimate, $\hat{Y}$, is $(s_{\hat{Y}_3}^2 + 9.82)$. The odds are 19 to 1 that the range $\pm 2\ s_{\hat{Y}_3}^2 + 9.82$ would include the actual measure of Y, had that progeny been carried over to the plantation.

This procedure of predicting $\hat{Y}$ will be used to screen the remaining 600 nursery progenies to detect outstanding seed trees. Such trees if detected will be brought into the future breding program of the Institute. Thus, the superiority of seed trees whose progenies were not included in the plantation may be evaluated.

Outstanding Progenies in the Plantation

Some of the best progenies in the plantation could have been detected at 2 years of age on the basis of their height growth in the second year. The 16 outstanding progenies were selected from the 80 represented in the plantation. These progenies are arranged by 15-year height in *table 1.*

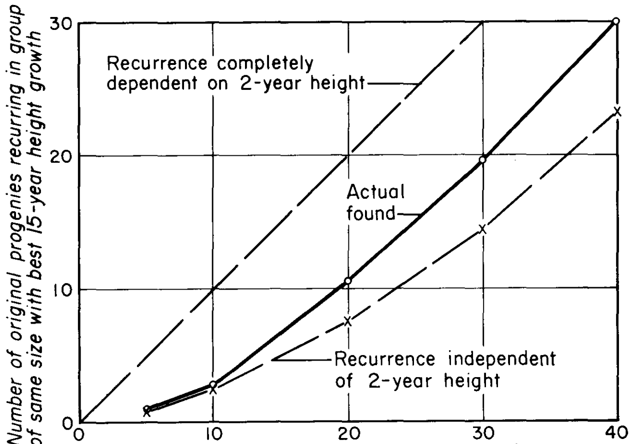

Figure 4. — The number of progenies recurring as best at 15 years, from groups of different sizes selected as best in their second year of growth.

Table 1. — Ranking of progenies[1] in terms of measured 15-year height (y), second year height growth, predicted 15-year height $(\hat{y})$; and residuals $(y-\hat{y})$

y		Second-year height growth		$\hat{y}$		$(y-\hat{y})$		Elevation	Progeny identific. number
Rank	Feet	Rank	0.01 feet	Rank	Feet	Rank	Feet	100 feet	
1	28.5	21-23	42	18-20	23.6	[2]1	4.9	32	726
2	27.3	24-27	41	23-25	23.3	[2]4	4.0	12	432
3	26.9	41-46	36	35	22.7	[2]2	4.2	15	322
4	26.5	8-9	47	12-13	24.0	10	2.5	9	212
5	26.3	55-57	33	45-48	22.1	[2]3	4.2	26	735
6-7	25.9	16-17	44	18-20	23.6	11	2.3	10	257
6-7	25.9	4-7	48	6-10	24,2	17	1.7	9	239
8-9	25.4	35-40	37	36-38	22.6	7	2.8	10	266
8-9	25.4	8-9	47	12-13	24.0	21	1.4	9	221
10	25.3	4-7	48	6-10	24.2	25	1.1	10	275
11-12	25.2	50-54	34	45-48	22.1	[2]6	3.1	10	284
11-12	25.2	4-7	48	4-5	24.4	29	0.8	35	744
13-14	25.1	35-40	37	30-34	22.9	13	2.2	15	394
13-14	25.1	16-17	44	14-15	23.9	24	1.2	15	376
15	25.0	1	33	1	25.4	49	-0.4	21	468
16	24.8	2-3	51	3	25.0	44	-0.2	30	596

[1]) A range of ranks, i. e., 4—7, shows two or more progenies had the same value for a particular measurement.

[2]) Vigor significantly exceeds expectation from equation *(5)*. Prospectively very superior progenies.

The corresponding second-year height growth and predicted height *(equation 5)* are shown, together with progeny ranking on these bases. Ranking among 80 progenies based on second-year height growth may be compared with the ranking based on heights at 15 years.

A direct method was used to assess the efficiency of nursery selection. The method chosen was to determine the recurrence of the best nursery progenies as the best plantation progenies. All of the best nursery selections might prove to be the best in the plantation; one might claim 100 percent efficiency in such selection. This maximum level is illustrated by the dotted line in *figure 4.* The zero level would be achieved if second-year and 15-year growth varied independently. The dashed line in *figure 4* shows the maximum number of progenies expected to appear as best in the plantation from 19 out of 20 random selections in the nursery. Only in 1 out of 20 plantation samples should the number of recurring progenies exceed the values shown by this line if the two growth measurements truly were independent.

Selection of the best progenies in the nursery resulted in a significant increase over random nursery selection (solid line *figure 4*) in detection of the best plantation progenies. We ranked each progeny according to its second-year height growth and its ultimate 15-year height (*figure 5*). The results of nursery selection both on the basis of second-year growth and on equation *(5)* expectation were practically identical. If the best 16 progenies (20 percent of the 80 progenies in the plantation) had been selected on either basis from the nursery, 8 of these selections would be among the 16 tallest progenies at 15 years. Actually this recurrence is significantly better than the recurrence expected from random selection. The probability of getting more than 6 in 16 from random selection is 0.015; of getting more than 7 is 0.0024. The 8 obtained could happen by chance alone only if a 1 in 417 event occurred. Differences for other size groups are at least equally conclusive *(figure 4)*. Out of the 40 progenies that were tallest at 15 years, for example, 30 would have been predicted on the basis of second-year height growth, but only 23 would

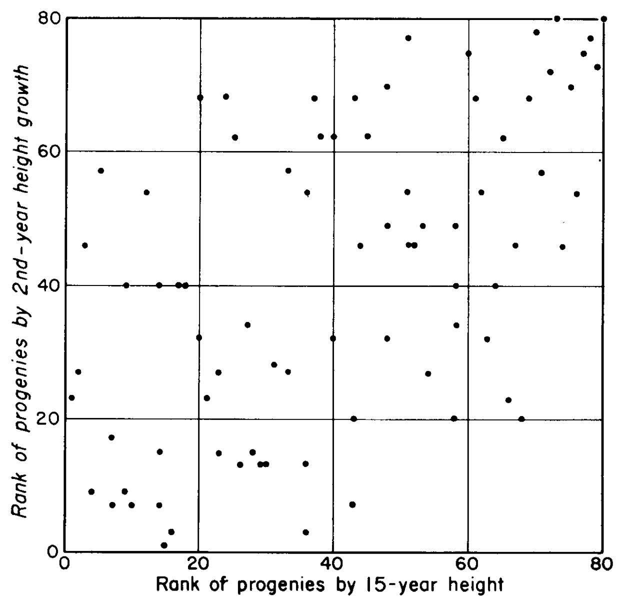

Figure 5. — Rank of each progeny by second-year height growth and by 15-year heights.

be expected in a random selection of 40. Thus, the value of progeny selection is demonstrated.

Next we refined the criterion of selection of progenies showing inherent rapid growth. We used deviations of actual growth from expected growth in the second year. The regressions presented in equations *(1)* and *(2)* provided a basis for predicting seedling growth of progenies. The 80 progenies were ranked by deviations of actual second-year growth from the expectation of the appropriate equation *(1)* or *(2)*. Then the deviation of progenies from expected 15-year heights, based on equation *(5)*, were arranged by rank. When 15-year rank was plotted against second-year rank *(figure 6)*, no trend was discernible. Seedling progenies which exceeded expected growth in the the second year did not hold their superiority through 15 years. Selection by using deviations from expected second-year height growth was genetically less effective

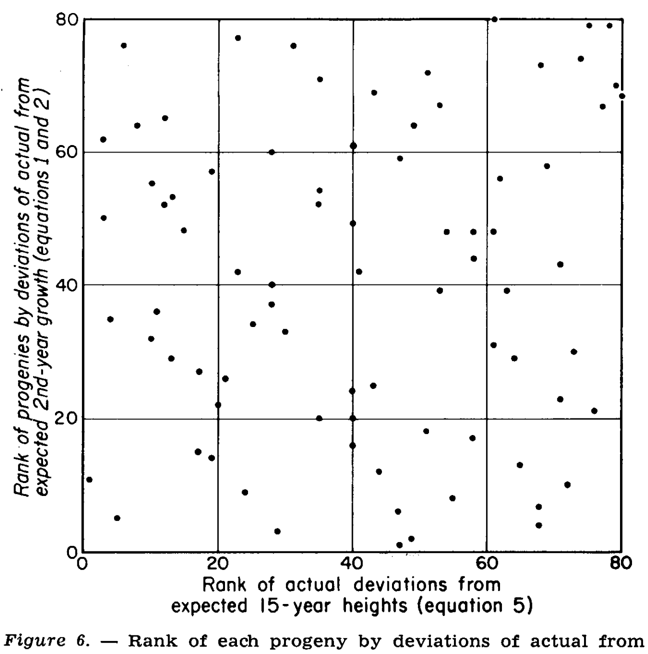

Figure 6. — Rank of each progeny by deviations of actual from expected growth.

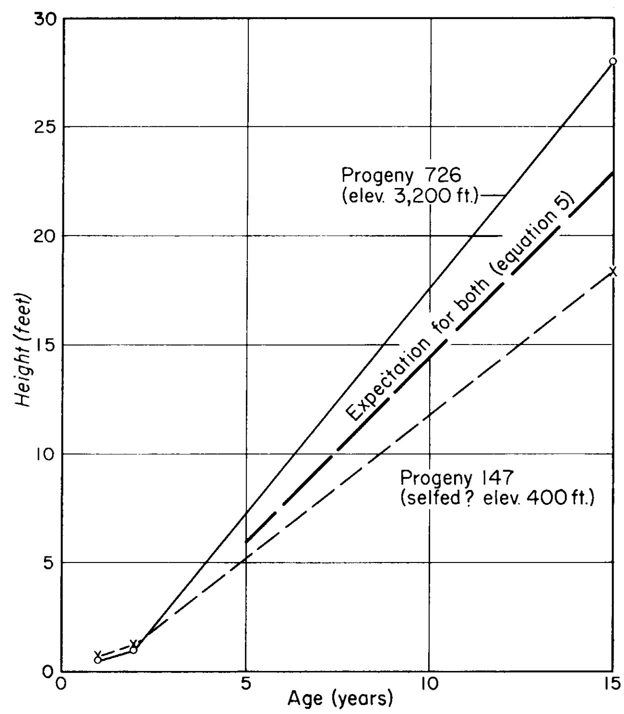

Figure 7. — Growth of the best and next to poorest of 81 progenies. The same 15-year heights were expected for both based on second-year height growth, elevation and (elevation)².

than selection using actual second-year growth. Furthermore, this refinement in selection, in addition to being valueless, would be expensive and difficult.

The selection of outstanding progenies on the basis of elevation alone would not be efficient. Elevations of the best 16 progenies range from 900 to 3,500 feet, and average 1,700 feet. The optimum elevation indicated by equation *(5)*, holding second-year height growth constant, is 2,500 feet. The conclusion having practical application is that "local" seed from the 2,500-foot zone would provide progenies that averaged best in vigor; however, inclusion of certain seed trees from a wider elevational range would provide even better progenies.

Five of the best progenies have been marked *(table 1)* as having significantly better 15-year vigor than expected on the basis of their second-year growth and the elevation of their seed source. The growth of the best progeny, number 726, is shown in *figure 7*. The significance of deviation from expectation was based on the average variance within progenies in the plantation, i. e., 4.86. If for any progeny $(y - \hat{y}) \geq 2\sqrt{\frac{4.86}{2}} = 2\,(1.56) = 3.12$, then we considered the progeny to have deviated significantly from expectation.

Relative Vigor of Progeny Groups

As described previously, groups of progenies were selected, on various bases, from the nursery for outplanting. The average deviation of 15-year heights of n progenies in a group is

$$\bar{d} = \frac{1}{n} \sum_{i=1}^{n} (y_i - \hat{y}_i).$$

$C_n = 2\sqrt{\frac{1.56^2}{n}}$ is a criterion to provide guidance in selecting groups of progenies whose performance is considered better than equation *(5)* expectation. If $\bar{d} \geq C_n$, we have considered the group performance superior. Because the n progenies themselves were included in computing the regression, no probability statement is made regarding statistical significance.

Crop year of the seed was one of the bases of selection. The objective was to show the influence on growth, if any, of seed collected in different years from the same trees. Fifteen seed trees were included in this test. In this case each plantation plot was split. One-half included trees from the 1934 crop; the other half from the 1936 crop. NAIR made an analysis of variance of these split plot data. He did not find a significant effect of crop year on 15-year height.

Groups of progenies were outplanted to determine the effect of two factors on later growth: (1) *germination time* when seed size is held constant, and (2) *variation in seed size* when germination time is constant. These groups of progenies performed in close accordance with expectation from equation *(5)*. This is in line with a multiple regression analysis presented earlier; seed size and germination time had no direct effect on 15-year height.

Twenty-eight progenies were randomly selected from the *5 largest nursery progenies in 500-foot elevational zones*. For this group

$$\bar{d} = + \frac{5.5}{28} = + 0.196, \quad \bar{d} < C_n = 2 \sqrt{\frac{2.43}{28}} = 0.590.$$

The conclusion is that the group performance accords with expectation under equation *(5)*. A similar conclusion was drawn from analysis of the data for a group of the 4 smallest progenies; each had been randomly selected from the *5 smallest within their elevational zones*. These limited tests led to this conclusion: the most vigorous and least vigorous nursery progenies did not exceed or fall below expectation in the plantation. These groups of progenies did not become progressively better or poorer than expected on the basis of equation *(5)*.

Nine progenies from one district were selected for plantation testing. Their mothers had grown on 3 field plots having an elevational range from 933 to 1,148 feet. For this group

$$\bar{d} = + \frac{14.7}{9} = + 1.63, \quad \bar{d} > C_n = 2 \sqrt{\frac{2.43}{9}} = 1.04$$

The nine progenies selected from this district performed better than expected, considering their second-year height growth and elevation. This district, particularly these three plots, deserves further study as a possible area for the selection of superior seed trees.

Isolated and possible self-pollinated seed tree progenies were carried over to the plantation. For this group of 6 progenies from low elevations

$$\bar{d} = - \frac{9.5}{6} = - 1.583, \bar{d} > C_n = 2 \sqrt{\frac{2.43}{6}} = 1.272$$

These progenies from isolated seed trees have performed progressively poorer than expected on the basis of equation *(5)* Progeny 147 ranked 79th in deviations of 15-year height from expected. It came from one of these isolated seed trees. This progeny did well in the nursery, but failed in subsequent development *(figure 7)*.

Progenies of *seed trees that were close neighbors* in the same field plot were grouped for comparison. In a group from one field plot, 9 progenies were represented; 7 progenies constituted a group from another field plot. Groups of 3 or 4 trees represented other plots, In none of the groups did the average 15-year height differ appreciably from expectation. In no case did the progeny from a particular seed tree differ significantly from the progenies of neighboring trees.

Discussion of Results

The report by MIROV *et al* (1952) adequately presents and discusses the evidence of elevational variation for 12-year old ponderosa progenies at the Institute. Of course, the fact that the results of this study confirm their conclusions is not surprising. The seed used in their study represented a sample of the seed collected for this study. Furthermore, the trees were grown under essentially the same environmental conditions. The results presented in this article do show that their conclusion as to the curvilinear influence of elevation on growth apply equally well to 15-year old progenies.

The statistical validity of predicting 15-year heights from second-year height growth is perhaps the most significant finding of this study. Much work must be done before general equations for such prediction can be formulated. The particular prediction equations developed here apply only to progenies grown for this study. Yet, the development and refinement of such methods of prediction for other species should be forthcoming. If this comes to pass, forest geneticists can shorten the period of waiting before reporting the results of their studies of heritable growth differences. JOHNSSON (1951), WENGER (1955), and others already have evidence for other tree species that strong correlations exist between growth increments in succeeding years.

As is typical of science today, our prediction equations based on second-year growth may be outmoded before they are developed and applied. We were 20 years in demonstrating this correlation. New work on very young seedlings soon may provide a better tool. SCHRÖCK and STERN (1953) with detailed measurement and analysis have shown significant growth differences between progenies in the first weeks after germination. The development and extension of such a technique would provide the ultimate in prediction if: (1) the first growth cycle can be adjusted for the major environmental influence of seed size, and (2) a high correlation exists between this adjusted first cycle and all subsequent cycles to maturity. SCHMIDT (1957) recently has reviewed this and other work on the early diagnosis of differences in patterns of growth.

If methods of prediction can be developed, progeny testing could proceed more economically. Extensive screening could be done in the laboratory or nursery. Only the most promising progenies would have to be plantation tested for general site adaptability. Tests of plus trees having known site adaptability also could proceed at a much faster pace; for progeny growth capabilities could be determined in a few years in the nursery. No further delay for plantation testing would be needed. All of this is with the proviso that further verification of the results of this work is forthcoming.

The biological significance of these prediction equations lies in the fact that differences in inherent growth potentials of progenies can be recognized in 2-year old seedlings. Fast-growing seedlings on the average proved to be the fastest growing trees 13 years later. Elevation of seed source was one factor demonstrated to have a significant influence on all of this growth. In fact, much of the significance attributed to second-year growth in determining later growth may merely reflect the inherent influence of elevation on seedling growth. This factor, elevation, is but a numerical expression of inherent differences in growth potential. Trees are adapted to live in their part of a continuously varying environment; hence, they differ in their growth potentials.

These prediction equations also enable one to select progenies which perform significantly better than expected. Thus, after a few years, geneticists can detect trees whose progenies would reach their grand period of growth earlier. The continuation of our study will show whether or not these early starters produce at maturity: (1) more or less wood at standard rotation ages or (2) average amounts of wood at shorter or longer rotations. Only the future will tell. Here again, the proof of the tree is in the growing; predictions based on laboratory tests can go just so far.

Forest geneticists have displayed some reticence to extrapolate from seedling growth measurements to an evaluation of the growth potential of progenies. Seed size and germination time have a dominant influence on early seedling growth; hence, the belief that early growth rate is an ephemeral condition (RIGHTER, 1945; FOWELLS, 1953). This study shows that average progeny growth rate in the second year serves as an indicator of inherent growth potential. FOWELLS (1953) made a similar general observation for 9-year old ponderosa and Jeffrey pines. Progenies we selected as best in second-year growth proved to be best at 15 years *(figures 4 and 5)*. Probably the environmental effects of seed size and germination time are less on second-year growth than they are on total 2-year growth as measured by RIGHTER. Thus, hereditary differences do show through as early as the second year.

Crop year of the seed had considerable influence in depressing seedling growth. Foresters generally have not been aware of this fact. The general decrease in germinability of seeds as they age is well recognized, but foresters have not realized that a concomitant decrease in seedling vigor exists. ENGLER (1903-05) was one of the first to report this relationship. STONE (1957) has undertaken recent work on this point. He suggests that age of the seed may actually be a key factor determining the survival of the seedling. Forest geneticists should beware lest they confound an experiment by using seed from different crop years. Cold-stratification of seed prior to sowing equalizes the germination time of seed of different ages, but does not equalize the rate of development of the seedlings. Differences between progenies should not be blindly ascribed to genotypic differences when age of seed is not constant.

The reader should use caution in testing or applying the results of this study. The experimenter must realize first that only second-year height growth measurements of the nursery seedlings were used in this study, not two-year measurements. Further, he must realize that the design of the nursery in which these seedlings were grown was exceedingly complicated. Because of the design, much of the environmental variation in the seed beds was equally distributed among the many progenies. Just growing 54 seedlings of a progeny and selecting the tallest at 2 years is not enough. Rigid control of environmental variability must be maintained.

For example, the seed used in this study was not cold-stratified prior to sowing. Had this been done, perhaps the early genetic differences in growth would have been even more strikingly apparent. The time required for the unstratified seed to germinate was a significant factor in the determination of seedling growth. The complication introduced by this variable was considerable.

Dr. N. T. MIROV, who has been on the staff of the Institute since before this study was started, immediately recognized the physiological problem involved in this delayed germination (MIROV, 1936). He realized that stratification of the seed might solve our problem. Accordingly, he made a small test of the effect of stratification. The results of his test of stratified and unstratified seed from 4 of the seed trees used in this study are presented with his kind permission in *figure 8*. His test led to our recognition that for progeny testing pine seeds must be stratified to assure uniform and rapid germination. We now stratify hard pines for two months and white pines for three months before sowing in the nursery.

Some discussion should be made of the considerations developed by a study of open-pollinated progenies. Our purpose is not to criticize the originator of this study, Mr.

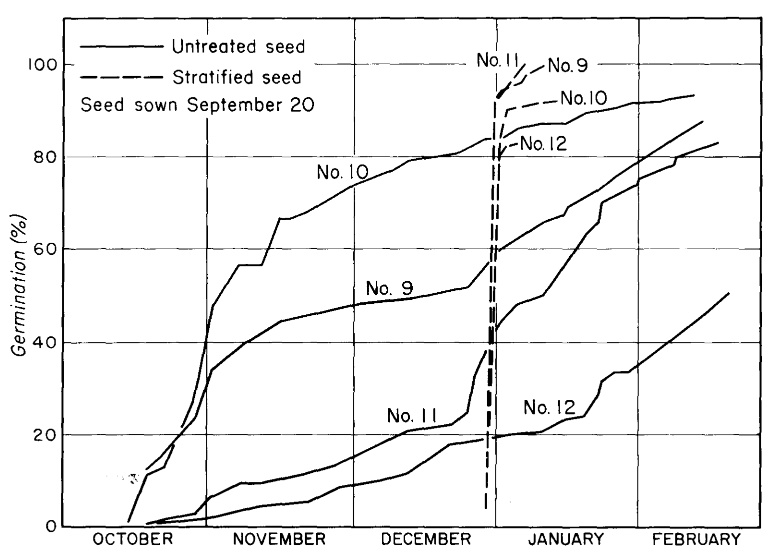

Figure 8. — The rate of germination of stratified and unstratified seed from 4 neighboring seed trees. (Courtesy Dr. N. T. MIROV.)

LLOYD AUSTIN; from the records which he left we know that he appreciated all of the limitations of such tests.

Foremost is the fact that we have not tested just maternal differences. Even if we allow that each cone is pollinated by a randomly selected cross-section of the pollen-bearing trees in the vicinity of the mother tree, we cannot escape the fact that such a cross-section of male parents probably shows considerable elevational variation. Therefore, we have not tested various females using a common male denominator, but rather we have tested these females using males of variable potentials. Of course this procedure accentuates elevational effects and masks individual genetic differences.

We have shown that progenies resulting from particular combinations of known females and unknown males appear to be much better than others; thus, we have accomplished one of the original objectives of the study. Yet to be demonstrated is whether or not outstanding progenies will be produced year after year by these particular females and their unknown mates. AUSTIN had planned to repeat his study several years in succession to answer this question. On the basis of what we know now, only certain progenies would have to be repeated each year. Probably these would have to be carried only through their second year in the nursery.

Artificial crosses to one male would have provided a better test of the superiority of individual trees. Seed produced through such a breeding program undoubtedly would have produced more uniform progenies. Admittedly far fewer progenies could have been included in the study. But with the reduction in variance within progenies smaller differences between progenies might have been detected as significant.

If we assume that the maternal and paternal contributions to growth potential are equal, then the procedure of crossing each female naturally or artificially with her close neighbors tends to magnify the elevational differences between females. Smaller elevational and other genetic differences would be expected if all of the females had been mated artificially with any one male. Thus, the wind-pollinated seed serves quite well for a test of elevational variation, but not so well for a test of seed-tree potentials.

Summary

In 1937 at the Institute of Forest Genetics LLOYD AUSTIN began a comprehensive study of the heritable variation in ponderosa pine. The wind-pollinated progenies of 627 seed trees were grown for two years in the nursery. Progenies of 81 of these seed trees were carried on to the plantation phase of the study. Data taken on progenies included among other items: seed size, time for seeds to germinate, elevation of the seed source, second-year height growth, and 15-year heights. Many people participated in the compilation and analysis of these data over the past 20 years.

Ultimately multiple regression analyses provided the bulk of the results presented in this report. Seed size, germination time, seed-tree elevation, and crop year of the seed all were shown to have significant effect on the growth of progenies in their second year. However, variation in height after 15 years was significantly associated only with height growth in the second year and with the elevation of the seed source and its square.

Equations were developed for predicting 15-year height from second-year performance and elevation of the seed source. The best equation accounted for only 49.2 percent of the variation in 15-year height. About 39 percent of the variation in 15-year heights could be attributed to heritable genetic differences between progenies.

Analyses of the expected and actual 15-year performance of progenies indicated that some had made relatively good growth; other relatively poor growth. Within these groups certain progenies exhibited exceptional growth patterns. All progeny groupings were set up at the beginning and not at the end of the plantation phase of the experiment.

A group of progenies from isolated seed trees grew exceptionally poorly. The depression in growth may be the result of inbreeding, but further investigation is needed on this point.

A group of progenies from one district showed exceptionally good growth, indicating that this district may be a very good seed source.

Other progeny groups were made up of progenies having the same seed size but varying germination time or having the same germination time but varying seed size. No important deviations from regression expectation were found for these groups of progenies.

This study indicates that seed trees producing relatively large seed which germinates rapidly tend to produce progeny having superior progeny height growth during the second year. However, these factors cannot be used to select the tallest progenies at 15 years. To select 15-year progenies that are prospectively best, select in the nursery on the basis of second-year height growth alone or in combination with elevation of the seed tree.

Zusammenfassung

Titel der Arbeit: *Pinus ponderosa: Höhenwachstum frei abgeblühter Nachkommenschaften.*

1937 begann LLOYD AUSTIN am Institut für Forstgenetik mit umfassenden Untersuchungen über die erbliche Mannigfaltigkeit bei *Pinus ponderosa*. Frei abgeblühte Nachkommenschaften von 627 Mutterbäumen wurden 2 Jahre in der Baumschule angezogen und 81 Nachkommenschaften davon auch bis zum Dickungsalter weiter verfolgt. Die an den Nachkommenschaften ermittelten Daten umfaßten unter anderem: Korngröße, Keimdauer, Höhenlage der jeweiligen Herkunft, Höhenwuchs im Jahre 2 und Höhe im Alter 15. An der Erfassung und Auswertung dieser Daten nahmen im Laufe der letzten zwanzig Jahre viele Leute teil.

Abschließende multiple Regressionsanalysen ermöglichten die Berücksichtigung der in dieser Arbeit enthaltenen großen Menge von Ergebnissen. Korngröße, Keimdauer, Höhenlage des Mutterbaumes und Erntejahr hatten alle einen signifikanten Einfluß auf das Wachstum der zweijährigen Nachkommenschaften. Die Variation im Höhenwachstum nach 15 Jahren war jedoch nur noch mit der Höhe der zweijährigen Pflanzen und der Höhenlage des Mutterbaumes gesichert korreliert.

Zur Vorhersage der Gesamthöhe im Alter 15 aus der Leistung im Alter 2 und aus der Höhenlage der Herkunft entwickelte man Gleichungen, von denen die beste nur 49,2 Prozent der Gesamtvariation der Höhen im Alter 15 erfaßte. Etwa 39% davon kann man auf vererbbare Differenzen zwischen den Nachkommenschaften zurückführen.

Analysen der erwarteten und der tatsächlichen Leistung der Nachkommenschaften mit 15 Jahren lassen erkennen, daß einige verhältnismäßig gute, andere relativ schlechte

Wuchsleistungen gezeigt haben. Innerhalb dieser beiden Gruppen gibt es gewisse Nachkommenschaften mit einem außergewöhnlichen Wachstumsverlauf. Alle Nachkommenschafts-Gruppierungen wurden zu Beginn und nicht zum Abschluß der Freilandbeobachtungen dieses Versuches vorgenommen.

Eine Nachkommenschaftsgruppe aus isoliert stehenden Mutterbäumen wuchs ungewöhnlich schlecht. Die Wuchsdepression dürfte die Folge von Inzucht sein, jedoch sind in dieser Angelegenheit weitere Untersuchungen notwendig.

Eine Gruppe mit Nachkommenchaften eines Bezirkes wuchsen besonders rasch und ließen dadurch erkennen, daß dieser Bezirk eine besonders geeignete Herkunft darstellt.

Andere Gruppen wurden aus Nachkommenschaften gleicher Korngröße aber unterschiedlicher Keimdauer, oder aus Nachkommenschaften gleicher Keimdauer aber verschiedener Korngröße gebildet. Bemerkenswerte Abweichungen von der Regressions-Erwartung konnten für diese Gruppen nicht festgestellt werden.

Diese Untersuchungen zeigen, daß Nachkommenschaften von Mutterbäumen mit großen, schnell keimenden Samen i. a. im zweiten Jahr von überlegener Wuchskraft sind. Diese beiden Kriterien können jedoch nicht benutzt werden, um auch die höchsten 15j. Nachkommenschaften zu finden. Um die voraussichtlich besten 15j. Nachkommenschaften zu erfassen, sollte man in der Baumschule allein auf der Basis des Höhenwachstums im Alter 2 oder in Verbindung mit der Höhenlage des Mutterbaumes selektieren.

Résumé

Titre de l'article: *Pinus ponderosa — croissance en hauteur de descendances obtenues par pollinisation libre.*

En 1937, Lloyd Austin a commencé à l'Institut de Génétique forestière une étude complète de la variation héréditaire chez *Pinus ponderosa.* Les descendances, après pollinisation libre de 627 porte-graines ont été élevées pendant 2 ans en pépinière. Les descendances de 81 d'entre eux furent mis en place sur le terrain. Les données recueillies sur les descendances comprenaient notamment: la grosseur des graines, la vitesse de germination, l'altitude des arbres-mères, la hauteur des semis de 2 ans et la hauteur totale à 15 ans. De nombreux chercheurs ont recueilli et analysé les résultats au cours des 20 dernières années.

En définitive, des calculs de régression multiple ont permis d'obtenir l'ensemble des résultats présentés dans ce rapport. La dimension des graines, la vitesse de germination, l'altitude des porte-graines et l'année de récolte ont une influence significative sur la croissance des descendances au cours de la deuxième année, mais la variation de la hauteur à 15 ans n'est liée de façon significative qu'avec la hauteur à 2 ans, l'altitude des porte-graines et son carré.

Diverses formules ont été établies pour le calcul de la hauteur à 15 ans d'après la heuteur à 2 ans et l'altitude des porte-graines. La meilleure de ces formules ne rend compte que de 49,2% de la variation de la heuteur à 15 ans, environ 39% de la variation de la hauteur à 15 ans, peut être attribuée à des différences héréditaires entre les descendances.

L'analyse des hauteurs à 15 ans obtenue d'une part par le calcul, d'autre part par les mesures, montre que certaines des descendances ont une croissance assez bonne, d'autres une croissance assez faible. A l'intérieur de ces groupes, certaines descendances manifestent une vitesse de croissance exceptionnelle. Les groupements des descendances ont été établis au début et non à la fin de la phase plantation de l'expérience.

Un groupe de descendances provenant d'arbres isolés ont montré une croissance extrêmement faible, cela peut être un effet de l'autofécondation, mais de nouvelles recherches sont nécessaires sur ce point.

Un groupe de descendances provenant d'une région manifeste une croissance exceptionnelle, cette région représente donc une très bonne source de graines.

D'autres groupes furent constitués avec des descendances ayant la même grosseur de graines mais des vitesses de germination différentes ou la même vitesse de germination mais des grosseurs de graines différentes. On n'a constaté, pour ces groupes de descendances aucun écart important par rapport aux estimations obtenues d'après les calculs.

Cette étude montre que des porte-graines qui produisent des graines relativement grosses, à germination rapide, donnent en général des semis qui à 2 ans ont la plus forte hauteur. Mais ces facteurs ne peuvent pas être employés pour choisir les meilleures descendances à 15 ans. Pour sélectionner les descendances qui auront la meilleure hauteur à 15 ans, il faut faire une sélection en pépinière sur la base de la hauteur des semis de 2 ans seule ou combinée avec l'altitude des porte-graines.

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