Heights of Selected Ponderosa Pine Seedlings During 20 Years

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MANY silviculturists and geneticists, concerned with the problem of increasing the rate of production of forest plantations, advocate or practice the selection of the larger seedlings in the nursery bed. Such selection implies a hypothesis that size of seedlings is positively correlated with size of the same plants at some more advanced age. Two tests were established at the Institute of Forest Genetics to determine whether seedlings selected as tallest within one-parent progenies maintain a growth superiority.[1]

MATERIALS AND METHODS

Low Selection Intensity

Trees used to study the effects of selection at a low intensity were planted in part of the isolation strips surrounding a larger test (Callaham and Liddicoet, 1961). Plantations were established at 2,730 and 5,650 feet on the western slope of the Sierra Nevada in El Dorado County, California. All trees in this study were derived from open-pollinated seed from a single seed tree of *Pinus ponderosa* Laws., growing at an elevation of 3,400 feet, ½ mile east of Camino, El Dorado County, California.

In any study of the genetic effectiveness of selecting seedlings within progenies, size of seed is a variable which must be taken into account (Langner, 1939). Many investigators[2] have shown that size of 1- or 2-year pine seedlings is directly related to size of seed. In this study seed-size effects were reduced by using only seed of a single size-grade. After cleaning, the seed was screened for size, and only seeds of average size, that is, grade 18 (200 seeds occupied 18 cubic centimeters), were sown.

Sowings were all made in 1938, on May 1 ("early sowing") and May 25 ("late sowing") at the nursery of the Institute of Forest Genetics adjacent to the 2,730-foot plantation, and on May 26 at the nursery adjacent to the 5,650-foot Pyramid plantation. Seedlings were measured 75 days after sowing in each nursery. Hence, these seedlings were measured in July and August before growth had ceased. Within each nursery plot of six seedlings, those with the longest and the shortest epicotyls (that portion of the stem of a 75-day-old seedling above the whorl of cotyledons) were noted.

At two years of age the seedlings were transplanted to borders of the nearby plantation sites. Seedlings were grouped in four-tree row-plots; each plot contained two pairs of seedlings from a single nursery plot. The seedlings with longest and shortest epicotyls at 75 days comprised one pair and were assigned at random to the ends of the group of four trees. The seedlings with next-tallest and next-shortest epicotyls were planted in the center of the group. Fourteen row-plots were established at each of two plantations, giving 112 seedlings for study.

Measurements were taken to determine the relation between seedling and tree characters. After 75 days in the nursery, heights were measured from the ground to the cotyledons and to the tip of the epicotyl. At the same time the number and length of cotyledons were recorded. Total heights of the trees were determined at two, five, 12, and 20 years from sowing.

Moderate Selection Intensity

Another study of seedling selection within ponderosa pine progenies was started at the Institute in 1937 as part of a progeny test of ponderosa pines (Callaham and Hasel, 1961). One-parent progenies of 81 seed trees were grown in the nursery. Seed size was not controlled within progenies. Each progeny comprised 54 seedlings, 18 in each of three replications. Sixteen two-year-old seedlings from one nursery replication were outplanted into each of the three plantation replications. The 16 trees were arranged in a 4 x 4 square with 7.5 feet between trees and a blank row surrounding each progeny. Planting followed a systematic design: the tallest seedling in a nursery replication always was planted at the northwest corner of the square; the shortest seedling at the southeast corner; and the two seedlings closest to average height at the southwest and northeast corners. Heights and diameters were measured when the trees were 15 years old.

RESULTS

Low Selection Intensity

Seedlings having longest epicotyls after 75 days in the nursery generally produced taller trees than seedlings with shortest epicotyls at two, five, 12, and 20 years (Table 1), but differences in mean height of trees from these two classes of seedlings were not significant after two years. The delay in sowing of 24 days in the same nursery exerted about the same significant effect on two-year height as epicotyl selection, but this effect of time of sowing quickly lost its significance. We found no significant difference in heights at 12 or 20 years. Thus, neither length of the epicotyl after 75 days nor date of sowing had a significant relation to growth at five, 12, and 20 years.

Paired trees in the plantations during 20 years showed numerous shifts and reshifts from taller to shorter or *vice versa* (Table 2). In more than half of the pairs, the seedling with short epicotyl had exceeded its long-epicotyl partner in height growth within 20 years. The number of shifts does not depart significantly from half the number of pairs. About one-third of these reverted to the original seedling superiority. All in all, this experiment indicates that epicotyl

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[1] Conception and design of these tests can be attributed to Lloyd Austin who directed the work through the fifth year of growth. Later plantation measurements and analyses were made under the direction of the authors. Statistical analyses were performed by Rita R. Taylor and Simon Stiassney.

[2] Mitchell, 1934; Spurr, 1944; Righter, 1945; Fowells, 1953; Callaham and Hasel, 1961; and many others.

length after 75 days cannot be used to predict height of ponderosa pines at 12 or 20 years.

Height at 12 and 20 years can be predicted rather well from height at five years or later. Regression and correlation analyses were used to relate height measurements to one another (Table 3). Height at one age can be used to predict height at the next measurement age. That is, height at two years predicts about 20 to 40 percent of the variation in height at five years; height at five years predicts about 40 to 60 percent of the variation at 12 years; height at 12 years predicts about 65 to 90 percent of the variation at 20 years. However, as the interval between measurements on young trees increases, the accuracy of height prediction decreases. Note that height at two years predicts only two to nine percent of the variation in height at 12 years. Multiple correlations do not add appreciably to the accuracy of prediction from simple correlations.

Table 1.--Mean height (feet) of ponderosa pine, by age, plantation elevation, epicotyl length at age 75 days, and time of sowing

Age	Plantation at 2,730 feet				Plantation at 5,650 feet	
	Early sowing		Late sowing			
	Long epicotyl	Short epicotyl	Long epicotyl	Short epicotyl	Long epicotyl	Short epicotyl
75 days	0.12	0.02	0.13	0.05	0.07	0.01
2 yrs.	1.2	0.9	1.0	0.8	0.6	0.4
5 yrs.	3.4	2.9	3.2	3.0	2.3	2.0
12 yrs.	18.7	17.5	17.0	15.8	10.4	10.2
20 yrs.	36.9	35.2	33.4	30.1	23.3	23.7

Table 2.--Shifts in height superiority over 20 years for 60 pairs of trees selected at age 75 day for long (L) and short (S) epicotyls

Shift	No. of pairs shifting superiority between ages				
	75 days 2 yrs.	2 yrs. 5 yrs.	5 yrs. 12 yrs.	12 yrs. 20 yrs.	Total
L to S	6	11	15	4	36
L to S to L		2	5	6	13
L to S to L to S				1	1

The number and length of cotyledons have been suggested as juvenile characters which might be related to subsequent growth (Wettstein, 1949; Haskell, 1961). Mitchell (1934) reported no correlation between number of primary cotyledons and seedling weight. These relationships were tested with the data on hand (Table 4). Within this selected one-parent progeny, cotyledon number and heights at two and 20 years were not related. On the other hand, a small but significant 16 to 24 percent of the variation (r^2) in seedling height at two years was related to variation in cotyledon length. If additional studies verify this relationship between cotyledon length and early growth, allowance must be made for cotyledon length in evaluations of genetic differences in early growth. After 20 years cotyledon length and height growth no longer were related.

Moderate Selection Intensity

After 13 years in the plantation, trees from seedlings selected as tallest or smallest among 16 to 18 after two years in the nursery were taller or smaller on the average than trees selected as average seedlings. Hypotheses that heights, diameters, and volumes at 15 years of age were equal for tallest and shortest 2-0 seedlings were rejected at the 99 percent probability level by sign tests (Siegel, 1956). Similar tests showed that trees from the tallest seedlings grew taller than trees from seedlings closest to average height, and the latter also grew faster than trees from the smallest seedlings. Thus, the three classes of seedlings retained their rankings at 15 years with significant distinction between tallest, average, and shortest.

Seedling size and position in the plantation square are statistically confounded in this test. However, results of other analyses suggest that neither is the northwest position the most favorable nor is the southeast position the least favorable. Therefore, the results probably do show genetic differences in growth potentials.

Seedling size also influenced survival after outplanting. From 132 plantation squares, tallest trees were missing in only six squares, and average trees in only six or seven; thus, survival was 95 percent. Shortest trees were missing in 25 squares for a survival of 81 percent.

Many of the smallest seedlings produced aberrant runts or dwarfs. Selection of the smallest seedlings was selection for major genetic defects in the direction of dwarfing.

DISCUSSION

Efficiency of mass selection in bringing about genetic improvement of a given character depends upon the heritability of the character, its genetic correlation to other characters, and the intensity at which selection is exercised. In the case of height growth of these open-pollinated

Table 3.--Coefficients of simple and multiple determination (r^2 and R^2) for height, at 2, 5, 12, and 20 years, of end and center trees in groups of four trees planted at two locations

Age comparisons	Institute		Pyramid	
	Ends	Centers	Ends	Centers
20 on 12	.883**	.752**	.647**	.674**
20 on 5	.560**	.021	.117	.186
20 on 2	.119	.084	.003	.020
12 on 5	.559**	.064	.416**	.421**
12 on 2	.089	.032	.053	.016
5 on 2	.328**	.202*	.410**	.176*
20 on 2, 5, 12	.889**	.793**	.701**	.704**
20 on 5, 12	.888**	.758**	.700**	.692**
20 on 2, 5	.570**	.084	.161	.188
12 on 2, 5	.583**	.070	.473**	.448**

* Correlation and regression coefficients significant at the 95 percent probability level.

** Correlation and regression coefficients significant at the 99 percent probability level.

Table 4.--Coefficients of correlation (r) between number and length of seedling cotyledons and subsequent heights of trees at two plantations

Cotyledon	Height	Institute	Pyramid
number	2-year	-0.105	-0.008
number	20-year	-0.239	-0.186
length	2-year	0.487**	0.399**
length	20-year	0.215	-0.062

**Correlation and regression coefficients significant at 99 percent probability level.

ponderosa pines, broadsense heritability has been estimated as 0.39 (Callaham and Hasel, 1961). That is, about 39 percent of the variation in height growth at 15 years could be genetically determined, and the remainder would be environmentally induced. Thus, it is not surprising that low intensity selection (the best one of four to six seedlings or the best of the remaining two to four) did not result in significant improvement in height growth. For the same reason it is not surprising that moderate intensity selection (the best of 16 to 18 seedlings or the top six percent) did result in significant genetic improvement in height, diameter, and volume. These results offer promise that mass selection of seedlings within progenies at moderate intensities of five to 10 percent or at the high level of less than one percent may lead to substantial genetic improvement in forest trees. During progeny tests, the best trees of each progeny should be preserved for second generation progeny tests to capitalize on this opportunity for genetic improvement.

This type of selection within one-parent progenies is not comparable with what Ellertsen (1955) referred to as selection of "super-seedlings" or what Zobel *et al.* (1957) called "outstanding nursery seedlings." Since the time of Fabricius (1931 and 1938), silviculturists and geneticists have engaged in mass selection of the best individuals in nursery seedbeds. Such selection differs substantially from the conditions of tests reported here. Nowadays this extremely intense selection is aimed at finding the best of many thousands of seedlings raised from bulk seed collections. Seedlings under selection germinate from seeds of many sizes, and they are highly diverse genetically, coming from many geographic areas and individual trees. Under such conditions it is difficult to be certain that "super seedlings" do not come from extra large seeds or do not represent geographic race contamination. These conditions all differ from the circumstances of our studies; hence, evidence of demonstrable genetic improvement from mass selection of moderate intensity within progenies cannot be compared with genetic improvement through the "super seedling" approach.

Our studies do indicate how long we must carry these "super-seedling studies" and progeny tests to determine the relation between juvenile and mature expressions of character. As the trees become older, superiority of individual trees is less likely to be overcome. Correlations between consecutive total height measurements should become higher. Growth comparisons probably need not be carried much beyond the time at which crowns close and individual trees assert dominance. If tests are planted at wide spacing, reducing and postponing competition between trees, then one might continue tests until a correlation coefficient of 0.8 or higher was obtained between measurements at five-year intervals. For our ponderosa pines, 20 years seems to be long enough to wait. Where widely divergent growth curves are expected, as from different geographic sources, one may have to wait until rotation ages are attained.

In contrast to findings from other studies, total height at two years could not be used to predict height at 12 years for individual trees in this study. Rohmeder (1952) selected the tallest individuals within one-parent progenies grown from seed of the same size. His tallest seedlings at one or two years maintained their superiority of height growth at 11 years. Fowells (1953) selected large, medium, and small 1-1 transplants from among 1-0 seedlings of a single size class. These transplant classes maintained their rankings of largest, medium, and smallest through 11 years of age when the test was terminated. Callaham and Hasel (1961) showed for a series of 81 one-parent progenies that a significant relationship existed between average height growth of a progeny in the second year and average total height at 15 years. Many of the studies showing a significant relation between heights of seedlings and of older trees have been based on averages for progenies or large classes where considerable genetic diversity existed among the progenies or classes. Perhaps our insignificant correlation between heights at two and 12 years stems from the fact that we analyzed a few individuals all from a single one-parent progeny. Juvenile-mature correlations in height growth may be quite significant for predictions of growth of progenies but not for predictions of growth of individuals within progenies.

SUMMARY

Seedlings selected within one-parent progenies for height growth at a low selection intensity (about 20 percent) did not grow to be tallest at 20 years. Heights of the tallest and shortest of four to six seedlings selected 75 days after sowing in the nursery were compared when two, five, 12, and 20 years old. Twenty-eight such comparisons were made. After 12 and 20 years, trees from seedlings with tallest and shortest epicotyls at 75 days did not differ significantly in height. Hence, selection of seedlings from one-parent progenies at the low intensity of one out of four to six on the basis of early epicotyl growth does not give measurable genetic or practical gain. For these trees cotyledon number was not related to tree height at two through 20 years.. About 20 percent of the variation in seedling height at two years was related to length of cotyledons, but length of cotyledons and height at five, 12, or 20 years were not related.

The study also sheds light on the age at which superiority of height growth can be evaluated. Each measurement of height was closely correlated with the next; hence, heights after 75 days are good indicators of heights at two years, *et seq.* Neither heights at 12 nor at 20 years were significantly correlated to total height at two years. Of the variation in heights at 20 years about half could be predicted from heights at five years and about three-quarters from heights at 12 years.

Seedlings chosen at a moderate selection intensity (about six percent) did show significant differences in height, diameter, and stem volume at 15 years. The seedlings were selected as tallest, closest to average, and smallest, among 16 to 18 seedlings of one-parent progenies after two years in the nursery.

Literature Cited

Callaham, R. Z. and A. A. Hasel. 1961. *Pinus ponderosa*—height growth of wind pollinated progenies. Silvae Genetica 10(2): 33-42, illus.

Callaham, R. Z. and A. R. Liddicoet. 1961. Altitudinal variation at 20 years in ponderosa and Jeffrey pines. Jour. Forestry 59(11): 814-820, illus.

Ellertsen, B. W. 1955. Selection of pine super-seedlings—an exploratory study. Forest Sci. 1: 111-114.

Fabricius, L. 1931. Planzenauslese im Saatbeet. Forstw. Centralb. 53: 449-457.

——— 1938. Planzenauslese im Saatbeet (II). Forstw. Centralb. 60: 297-304.

Fowells. H. A. 1953. The effect of seed and stock sizes on survival and early growth of ponderosa and Jeffrey pine. Jour. Forestry 51(7): 504-507, illus.

Haskell, G. 1961. Seedling morphology in applied genetics and plant breeding. Bot. Rev. 27(3): 382-421.

Langner, W. 1939. Zuchtung auf Wuchsigkeit (Theorie einer Auslese als Beitrag zur Forstpflanzenzuchtung). Forstw. Centralb. 61: 313-318.

Mitchell, H. L. 1934. Pot culture tests of forest soil fertility. Black Rock Forest Bul. 5, 138 pp., illus.

Righter, F. I. 1945. *Pinus:* the relationship of seed size and seedling size to inherent vigor. Jour. Forestry 43: 131-137, illus.

Rohmeder, E. 1952. Die Mogleichkeiten einer Wachstrumssteigerung bei den Baumarten Kiefer und Fichte durch das Massenausleseverfahren der fruhzeitegen Pflanzengrossensortierung. Zeit. f. Forstg. u. Forstpflanzenz. 2:22.

Siegel, Sidney. 1956. Nonparametric statistics: for the Behavioral Sciences. McGraw Hill, 312 pp.

Spurr, Stephen H. 1944. Effect of seed weight and seed origin on the early development of eastern white pine. Jour. Arnold Arboretum 25(4): 467-480, illus.

Wettstein, W. 1949. Selektion von Kiefern nach 4 Jahren. Zuchter 19: 205-206, illus.

Zobel, B. J., Goddard, R. E., and Cech, F. C. 1957. Outstanding nursery seedlings—a progress report. Texas Forest Service Res. Note 18, 14 pp., illus.

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