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M. THOMPSON CONKLE

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Abstract. Ponderosa pine progenies from parents restricted in latitude but spanning 7,000 feet of elevation show significant growth differences in plantations at low-, mid-, and high-elevation test sites. At low- and mid-elevation sites tree heights and diameters of progenies from high-elevation parents were the smallest; those from the low-elevation parents, intermediate; and those from mid-elevation seed parents, largest. At the high-elevation site, trees from mid- and high-elevation sources grew equally well, whereas trees from low-elevation parents showed poorest growth. The variation associated with elevation zone of parent trees accounted for 8 percent of the total experimental variation. About 9 percent of the total was attributed to the interaction between parent tree elevational zones and plantations. Height rankings of progenies for different ages showed little change over the 29-year growth period of the study in low- and mid-elevation test sites. But at the high-elevation test site, height means for zone groups shifted with age as the relative heights of the higher elevation progenies increased. ***Forest Sci. 19:31–39.***

Additional key words. *Pinus ponderosa* Laws., elevational transect, genetic adaptation, genotype and environmental interaction.

IN an exploratory study at the Institute of Forest Genetics near Placerville, California, Austin (1932) showed a decline in the vigor of ponderosa pine (*Pinus ponderosa* Laws.) progenies as the seed source elevation increased. In the late 1930's a rigorous and larger study was begun to determine whether this relationship was generally true. Open-pollinated seed was collected from ponderosa pines growing along a west-east transect on the Sierra Nevada encompassing an elevational change of 7,000 ft. About 10 parents were sampled for each 1,000-foot change of elevation. In 1938 the seeds were planted in nurseries at low-, mid-, and high-elevation test sites within the original collection transect. Plantations were later established next to the nurseries.

Two earlier reports (Mirov *et al.* 1952, Callaham and Liddicoet 1961) dealt with data from trees at younger ages from this study. The initial report (trees were then 12 years old) clearly identified progeny growth trends related to the seed parent elevation. In all plantations progenies from mid-elevation parents averaged taller than progeny from low-elevation parents, and both were taller than trees from high-elevation parents. Mirov *et al.* (1952) concluded that "the optimum seed collection zone lies between 1,500 and 3,500 feet on the west slope of the Sierra Nevada." The second report (trees were then 20 years old) drew similar conclusions, with one noticeable exception. At the high-elevation plantation trees from the higher elevation seed parents were improving in relative performance and nearly equalled heights of the previously taller mid-elevation progenies. At 29 years, progeny from mid-elevation parents continue to rank tallest in all plantations but are challenged at the high elevation site by progenies from higher elevation seed parents.

Seed parent elevation affects wood characteristics of these same progenies. Wood

The author is Geneticist, Pacific Southwest Forest and Range Experiment Station, Forest Service, USDA, P.O. Box 245, Berkeley, California. Manuscript received June 20, 1970.

specific gravity for the 29-year-old trees decreased as elevation of seed parents increased (Echols and Conkle 1971). Echols (1972) found that the influence of elevation of seed parents on progeny tracheid length was not significant.

The Elevational Transect. The transect, inland about 100 miles from the coast, lies within the gently rising peneplane constituting the western slope of the Sierra Nevada. Elevation changes at a rate of about 170 ft per mile. Rain, which occurs principally during winter, increases as elevation increases to an annual total of nearly 50 inches at the 4,500-foot elevations. Snow rarely falls below 2,000 ft but increases to nearly 400 inches per year at the 7,000-foot elevation. Temperatures show a frost-free period of 260 days at low elevations and of less than 100 days at 6,000 ft elevation.

Parent Trees. Open pollinated cones were collected from 72 seed parents (Mirov *et al.* 1952). Most parent trees grew between latitude 39° 30′ and 39° 00′ N., longitude 120° 00′ and 121° 10′ W. (35 miles south to north, 65 miles east to west), and between elevations of 125 and 6,919 ft.

Test Plantations. The highest plantation (H) is at an elevation of 5,650 ft on a south-facing slope. The middle elevation plantation (M) is on the grounds of the Institute of Forest Genetics near Placerville, California, at 2,730 ft elevation near the crest of a ridge. The lowest plantation (L) is at elevation 960 ft on a north-facing slope which grades from 25 to 45 percent.

Experimental Design. Seedlings (2–0) were transplanted from nurseries adjacent to each plantation in the spring of 1940. Each plantation plot represented a 1,000-foot elevational zone and contained 16 trees in a 4-tree by 4-tree square. Plots included either one or two seedlings from each of nearly 10 families. Spacing was 8 feet between trees within a plot and 16 feet between plots. Zonal plots were randomly located within each of four replications. A total of 448 (16 trees per plot × 7 zone groups × 4 replications) seedlings were established at each plantation. Some of the dead transplants were replaced the year after outplanting.

Callaham and Liddicoet (1961) reported slight, random mortality within L and M plantations after 20 years, but progeny of trees from the low-elevation sources had some mortality in the H plantation. Trees were measured after the 25th growing season. After these measurements trees were systematically thinned to eight per plot. Trees in plots were again measured after their 29th growing season.

Data Analysis. The major analysis centers on height growth. Relative contributions of the various sources of variation were derived from expectations of mean squares (Scheffe 1959). Observations of individual trees were analysed by assuming that plantations and elevational zone groups were fixed effects and that replications within plantations, families within zone groups, and trees within families were random effects.

Results

Zonal Performance—Tree Height. Survival of trees from any zone group during the first 25 years never dropped below 84 percent, a value found for trees of a low-elevation source at the H plantation. After thinning neither the L or H plantations had mortality. Six trees in the M plantation died, but mortality was not related to seed parent elevation.

Strong trends of mean heights for the tree groups representing the various elevational zones exist in each plantation (Fig. 1). Differences between zone groups and plantations were statistically highly significant for heights at both 25 and 29 years. The relationship between height means for zone groups within the plantations was virtually constant for both ages.

At the L plantation trees from the 2,500-foot zone group were superior in height for both ages. Progeny of parent trees local to the plantation area, those from the 500-foot and 1,500-foot zones, were surpassed on the average by trees from the 2,500-foot zone group. Progeny of trees from the

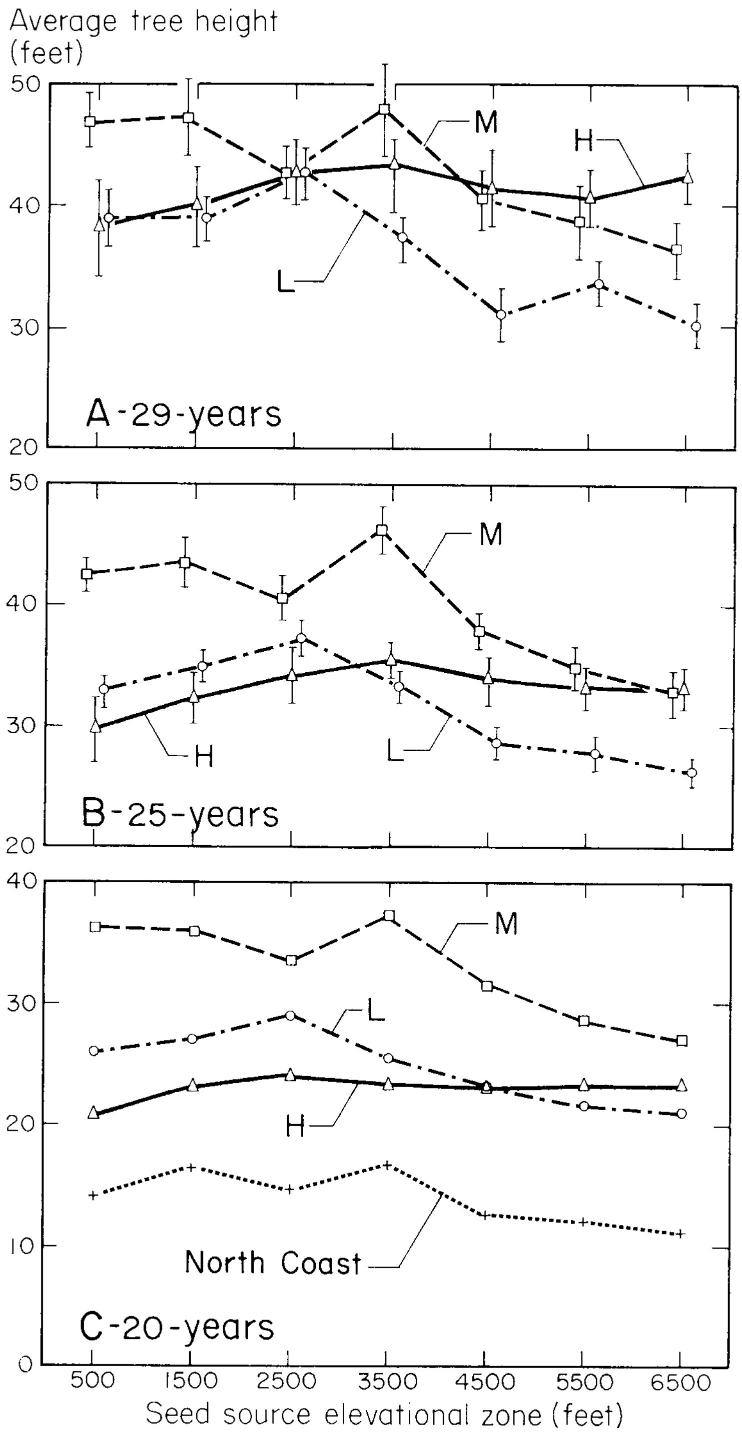

FIGURE 1. *Heights of trees grown from seed from seven elevational zones, planted at low (L), middle (M), and high (H) elevations, after 29, 25 and 20 years. (Ranges delineate 95 percent confidence limits for means.)*

TABLE 1. Combined analysis of variance and variance ratios for heights at four ages.

Item	Degrees of freedom	5 years Percent of total	20 years Percent of total	25 years Percent of total	29 years Percent of total
Plantation	2	38.3**	42.3**	22.1**	8.3*
Zone	6	11.7**	6.4**	9.2**	8.3**
Families within zone	65	0.9	4.7**	3.3**	
Zone × plantation	12	0.4	6.7**	8.2**	9.1*
Zone × replications in plantations	54	3.4**	5.7**	9.0**	17.1**
Families within zone × plantation	130	7.5**	0.0[1]	0.0[1]	
Replications within plantations	9	4.1**	4.4**	6.1**	6.5**
Families within zone × replications in plantations	579	0.0[1]	0.0[1]	2.1	
Trees within families in zone groups	478	33.7	29.8	40.0	
Trees within zone groups	583				50.7

* = Mean square ratio statistically significant at 5 percent level.
** = Mean square ratio statistically significant at 1 percent level.
[1] Negative components were taken to be zero when calculating percent values.

higher elevations, 4,000 feet and above, had the smallest mean heights.

Heights in the M plantation of trees from the 2,500-foot zone group were significantly shorter than trees from the 1,500-foot and 3,500-foot zone groups. In the M plantation trees of the 3,500-foot elevational zone group were the tallest. In the M plantation as in the L plantation trees from the 4,500-foot zone group and above were the shortest.

In the H plantation, trees of the 3,500-foot zone group were the tallest. The height growth of trees representing the 4,500-foot, 5,500-foot, and 6,500-foot zones in the H plantation was comparatively better than in M or L plantations. Mean heights for trees from seed zone groups 2,500 ft and higher were, for practical purposes, similar. Trees from the 500-foot and 1,500-foot zone group averaged 10 percent shorter than those in the tallest zone group.

To compare the various groups over several ages, zonal means were determined for the trees at 20 years of age (Fig. 1-C). Curves for 20, 25, and 29 years showed that the over-all heights of progenies at the H plantation improved in relation to the other two plantations.

Callaham and Metcalf (1959) reported the performance of trees, age 20 years, from these same seed sources growing in the north Coast Range of California (Fig. 1-C). The plantation, near Willits, is at 1,800 ft elevation and lies 140 miles to the northwest of the three Sierra Nevada plantations. Trees in the north Coast plantation were growing much more slowly than those at the Institute of Forest Genetics plantation, but the relationship of growth rate to seed source was similar.

Sources and Magnitude of Variation—Tree Heights. The combined analyses of variance and ratios of individual sources to the sum total were summarized for four ages (Table 1).

For 5-year heights the significant sources of variation were plantations, replications in plantations, and elevational-zone groups. Zone groups accounted for about 12 percent of the total sum of variances, whereas the interaction between zone groups and plantations was not statistically significant. Zonal means were nearly uniform across plantations for the very early ages (Mirov *et al.* 1952). Characteristically, the mean for the 2,500-foot elevational zone group was the highest. The mean for the 6,500-foot zone group was the lowest. Other zone groups were intermediate, with an increase from the mean height of the 500-foot zone groups to the 2,500-foot zone groups, then

TABLE 2. Analysis of variance and variance ratios for tree heights at various ages, for three planations.

Item	Degrees of freedom	H Plantation 5 years	H Plantation 20 years	H Plantation 25 years	M Plantation 5 years	M Plantation 20 years	M Plantation 25 years	L Plantation 5 years	L Plantation 20 years	L Plantation 25 years
Zone	6	13.9**	0.0[1]	0.0[1]	22.6**	34.1**	34.1**	24.3**	31.2**	33.2**
Families within zone	65	7.6*	4.7*	2.9*	15.6**	8.2*	4.4*	7.4*	7.6*	6.5**
Zone × replications	18	3.7*	19.1**	25.0**	9.0*	3.9*	3.6*	4.6*	14.5*	10.4*
Families within zone × replications	191	0.0[1]	0.0[1]	0.3	0.0[1]	0.0[1]	4.4	0.0[1]	0.0[1]	3.9
Trees within families	157	74.8	76.2	71.8	52.8	53.8	53.5	63.7	46.7	46.0

* and ** = Mean square ratio from analysis of variance significant at 5 and 1 percent level, respectively.

[1] Negative components were taken to be zero when calculating percent values.

a decrease in mean height for the groups from the 2,500-foot to 6,500-foot zone.

As plantations developed, the trees in zones in M and L plantations maintained their original relationships. The significant interaction between plantations and zone groups for the 20-year heights arose with the relatively good performance of trees from the higher elevation seed sources in the H plantation. In the M and L plantations, trees from these zones had the shortest heights.

The 20- and 25-year analyses showed significant variation for the same components. The magnitude of the between-plantations component was less for 25- than 20-year heights because of the steady increase in tree growth at the H plantation. The zone-group component of the analysis of 25-year heights was significant and larger than the component for families within zone groups.

The analysis of variance of the 29-year-data corresponds to that for the 25-year analysis. The components for zone groups and the interaction between zone groups and plantations were highly significant and of the same magnitude. The effect of plantations is reduced at this age.

The combined analysis points to plantation differences, to the magnitude of the zonal component, and to the interaction between zone groups and plantations. The zone group component (H plantation) was highly significant and relatively large at 5 years, but was negative for 20- and 25-year analysis (Table 2). Families within zones were a significant source of variation at all three measurement periods, accounting for 2.9 percent of the total variance within the H plantation at age 25.

In contrast, the zonal component for M and L plantations was highly significant and accounted for a large proportion of the total variation. The zonal component was about four times larger than the component for trees in families within zone groups. The interaction between zonal groups and replications increased (Table 1) during the growth history of the study.

Significant variation was found between families within elevational zone groups. When single-family mean heights were compared for 20- and 25-year-old trees in the three plantations, some families showed relatively good growth in all plantations, and others, relatively poor growth. The data indicate that tree improvement can profit from a parental selection in combination with a zonal selection.

TABLE 3. Correlation between tree-height means for seven zone groups at three plantations at various ages.[1]

Tree age years	Tree age, years 5	7	12	20	25
		H Plantation			
3	.95	.81	.59	–.12	.14
5	—	.93	.63	–.23	.04
7	—	—	.79	–.14	.02
12	—	—	—	.43	.45
20	—	—	—	—	.98
		M Plantation			
3	.89	.83	.80	.84	.87
5	—	.99	.96	.85	.91
7	—	—	.97	.97	.91
12	—	—	—	.99	.96
20	—	—	—	—	.98
		L Plantation			
3	.95	.93	—[2]	.95	.92
5	—	.99	—[2]	.97	.98
7	—	—	—[2]	.97	.98
12	—	—	—	—[2]	—[2]
20	—	—	—	—	.96

[1] A correlation of 0.75 or greater is needed to state with 95 percent confidence that the correlation differs from 0.

[2] Data missing.

TABLE 4. Correlation between individual tree-height means at various ages.[1]

Tree age years	Tree age at time of measurement, years 5	7	12	20	25
		H Plantation			
3	.73	.49	.28	.16	.12
5	—	.76	.44	.24	.19
7	—	—	.77	.47	.37
12	—	—	—	.75	.62
20	—	—	—	—	.93
		M Plantation			
3	.59	.43	.30	.28	.25
5	—	.92	.74	.64	.60
7	—	—	.87	.76	.70
12	—	—	—	.90	.84
20	—	—	—	—	.94
		L Plantation			
3	.72	.61	—[2]	.42	.41
5	—	.88	—[2]	.62	.60
7	—	—	—[2]	.73	.68
12	—	—	—	—[2]	—[2]
20	—	—	—	—	.93

[1] Most correlations based on 448 observations; the minimum was 411. Correlations of 0.10 or greater differ significantly from 0 (95 percent confidence level).

[2] Data missing.

Correlations between Height Measurements at Different Ages. For the H plantation, correlations between zonal mean heights for different ages (Table 3) were not close and in some instances, negative. Contrasting with the low and negative correlations in the H plantations were the high positive correlations between zonal mean heights in the M and L plantations.

Throughout the experiment the tree-height relationships for different elevational-zone groups within the M and L plantations remained constant and predictable. The best performance has been for the progeny of trees from zones between 2,000 and 4,000 feet elevation. Therefore, identification of the best seed collection areas for commercial planting up to 5,000 feet elevation in the Sierra Nevada can be made early in the growth of the trees.

Individual tree means within the plantations showed significant correlations of heights for different ages (Table 4). Here, as noted for zonal means, the M and L plantations had consistently higher correlations than the H plantation for comparable ages. Within both the M and L plantations correlations between tree heights at 25 years of age and 5 years and older were close.

Zonal Performance—Tree Diameter. Variations in tree diameter between locations, between elevational zone groups, and for the interaction of locations and zone groups were statistically significant. Analyses showed major variation associated with trees within families in zone groups.

Zone group means for diameters (Fig. 2) followed trends similar to those for heights. Correlations between height and diameters for the zonal groups were 0.82 for trees in the L, 0.88 in the M, and 0.72 in the H plantation. Diameters of trees in the H were significantly larger and the trees had greater taper than those from M and L plantations.

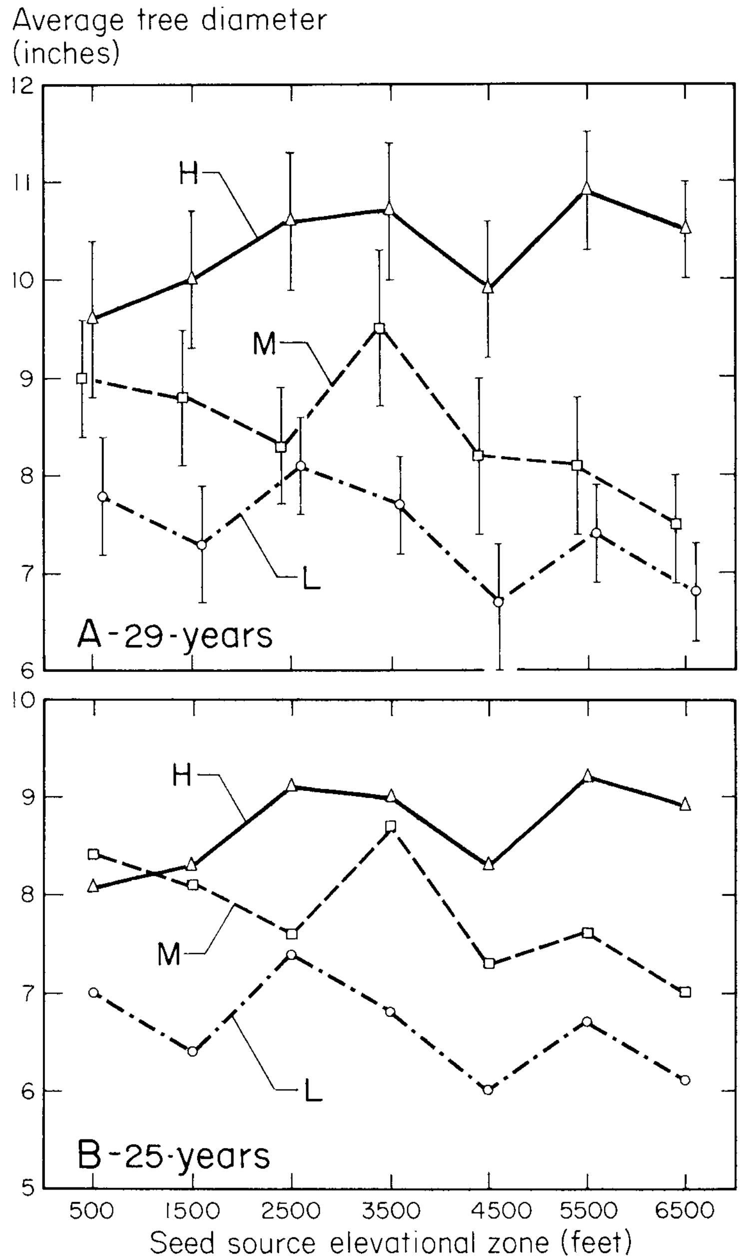

FIGURE 2. *Diameters of trees grown from seed from seven elevational zones, planted at low (L), middle (M), and high (H) elevations, at ages 29 and 25. (Ranges delineate 95 percent confidence limits for means.)*

Discussion

Clausen *et al.* (1940) concluded that four statistically distinct climatic races of *Achillea lanulosa* could be recognized from the central Sierra Nevada of California. They collected plants from an elevational transect 60 miles to the south of the ponderosa transect and like the ponderosa test, *Achillea* was grown in gardens at low-, mid-, and high-elevation sites. For Clausen *et al.*

(1940) individual ecological races took on discrete form: "Individual plants, having all the characteristics of their neighboring races, seem to have immigrated from a higher or sometimes lower altitude. The plants' physiological range of tolerance has been sufficient to enable them to withstand the apparent change. Other individuals, having only one or two characters of a neighboring race, would seem to represent hybrid recombinations." Thus the climatic race, like other kinds of ecotypes, was a basic ecological unit, just as the species is the basic taxonomic unit.

Ponderosa pine and *Achillea* show similar growth responses with changes in the elevation of parent sources. *Achillea* plant height decreased as elevation of collection increased. The race of *A. lanulosa* from 3,000 feet was the tallest at the low-elevation test site. Individual plant mean heights of *Achillea* from one elevational race were represented in heights of plants in adjacent races.

It is difficult to interpret the variation in ponderosa pine as ecotypic variation. Tree heights means from adjacent zone groups overlapped in value. Zone groups cannot be considered to contain trees so uniquely adapted as to view individual variants within a group as having migrated from an adjacent zone or having resulted by hybridization with trees from the adjacent zone. Tree growth in each of the three plantations followed clinal trends. Factors in the environment common to an elevational zone appeared to select similar sets of physiologically conditioned traits. The net result is growth patterns and trends characteristic of particular parent-tree elevational groups.

Wells (1964a,b), reporting the nursery phase of a study of geographic variation between seed sources of ponderosa pine, and Wright *et al.* (1969), reporting on the plantation phase of the same study, did not find predictable differences between low- and high-elevation sources in other sections of the natural range of ponderosa pine. Wright *et al.* (1969) suggests that the gentle rise in elevation over a relatively long distance in the Sierra Nevada acts as a barrier to large scale migration and permits genetic differentiation. Two observations tend to support their statements: (1) gradients in environmental factors in the Sierra Nevada are relatively continuous and lack abrupt changes, and (2) the magnitude of change in environmental factors is large within the transect area. They suggest that elsewhere in the range, slopes are abrupt and migration distances are not sufficiently large to encourage genetic differentiation.

Their hypothesis has not been rigorously tested in pine. But Beals (1969) came to a similar conclusion in his comparison of vegetational changes along steep versus gentle slopes in Ethiopia. Distribution of species along a gentle slope tended to have bell shaped curves, grading gently from one to the next. But distribution of vegetation on steep slopes tended to have abrupt discontinuities.

Application.

In the ponderosa pine study, trees from low-elevation parents were surpassed in height by trees from mid-elevation parents at all test locations. Progeny from high-elevation parents had poor growth in the low- and mid-elevation test sites. But progenies of trees from a relatively restricted area were tallest in all three planting sites. Thus, from 29 years of growth data, the practical conclusion is that for planting up to 5,000 ft elevation the optimum seed collection zone lies between 2,000 and 4,000 ft elevation on the west slope of the Sierra Nevada. Above 5,000 ft elevation the growth of mid-elevation sources was nearly equaled by high-elevation sources. Since (1) the plantings are at mid-rotation age, later adaptational differences may develop, and (2) in the absence of a significant growth advantage of mid-elevation seed sources, the present recommendation would be to use high-elevation seed sources for planting above 5,000 feet elevation.

Trees showing consistently good growth in all three plantations are from central areas of the ponderosa pine population. At lower elevations, selection probably favors pine adapted to the drier site conditions and longer growing season. At the highest elevations, past environmental selection pressures probably favored "hearty" genotypes. But in the central portion of the population, where growth conditions are more nearly optimum, where stands are closed, and tree-to-tree competition is intense, selection probably favored genotypes capable of rapid height growth. The tree breeders' emphasis on vegetative vigor, namely height growth, would favor mid-elevation phenotypes for future artificial regeneration. If the growth relationships noted in this study continue through rotation age, they would indicate that mid-elevation genotypes are sufficiently adapted to lower and higher elevations to recommend these general seed collection areas for west slope Sierra Nevada regeneration. This conclusion is similar both to previous experimental results (e.g. Wells and Wakeley 1966) and a thesis advanced by Namkoong (1969) that strictly local races may be non-optimal in terms of vegetative growth.

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Literature Cited

Austin, L. 1932. Heredity variations in *Pinus ponderosa*, an abstract of an address before the California Botanical Society. Madroño 2: 62–63.

Beals, E. W. 1969. Vegetational change along altitudinal gradients. Science 165:981–985.

Callaham, R. Z., and A. R. Liddicoet. 1961. Altitudinal variation at 20 years in ponderosa and Jeffrey pines. J Forest 59:814–820.

———, and W. Metcalf. 1959. Altitudinal races of *Pinus ponderosa* confirmed. J Forest 57:500–502.

Clausen, J., D. D. Keck, and W. M. Hiesey. 1940. Experimental studies on the nature of species. 1. Effect of varied environments on western North American plants. Carnegie Inst Washington Publ 520, 452 p.

Echols, R. M. 1972. Effects of elevation and seed source on tracheid length in young ponderosa pine. Forest Sci 19:46–49.

———, and M. T. Conkle. 1971. The influence of plantation and seed-source elevation on wood specific gravity of 29-year-old ponderosa pines. Forest Sci 17:388–394.

Mirov, N. T., J. W. Duffield, and A. R. Liddicoet. 1952. Altitudinal races of *Pinus ponderosa*, a 12-year progress report. J Forest 50:825–831.

Namkoong, G. 1969. Nonoptimality of local races. *In* Tenth South Forest Tree Impr Conf Proc 1969:149–153.

Scheffe, H. 1959. The analysis of variance. John Wiley & Sons, New York. 477 p.

Wells, O. O. 1964a. Geographic variation in ponderosa pine. I. The ecotypes and their distribution. Silvae Genet 13:89–103.

———. 1964b. Geographic variation in ponderosa pine. II. Correlations between progeny performance and characteristics of the native habitat. Silvae Genet 13:125–132.

———, and P. C. Wakeley. 1966. Geographic variation in survival, growth, and fusiform-rust infection of planted loblolly pine. Forest Sci Monograph 11. 38 p.

Wright, J. W., W. A. Lemmien, and J. N. Bright. 1969. Early growth of ponderosa pine ecotypes in Michigan. Forest Sci 15:121–129.