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Altitudinal Variation at 20 Years in Ponderosa and Jeffrey Pines

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Early returns from a study of altitudinal variation of pines along an elevational transect in California indicated middle elevation sources grew best regardless of the elevation of planting, seeming to contradict the old maxim, "Local seed source is best" (*6*). Later returns bring some support for the maxim as local seed sources assert themselves after 20 years. Nonlocal seed sources do not keep up the growth pace or are hard hit by environmental factors.

The 20-year results reported here add to the earlier report some striking plantation differences on the one hand, and some interesting elevation trends on the other. Here also are 20-year data on Jeffrey pine; early performance of this species has yet to be summarized.

For 20 years, ponderosa (*Pinus ponderosa*) and Jeffrey (*P. jeffreyi*) pines from different altitudinal sources have been "pitted against one another" in a test of survival and growth. The test is limited to a narrow transect on the west slope of California's Sierra Nevada. The elevation of the 89 ponderosa seed trees ranged from 125 to 6,919 feet. Three Jeffrey pine progenies each representing a different number of seed trees were included:

Progeny	Seed trees	Elevation Range	Elevation Mean
	(No.)	(Feet)	(Feet)
1	3	3,450	3,450
2	13	5,720-7,450	6,635
3	5	7,735-8,235	7,860

All progenies were grown from seed sown in 1938 at low-, medium-, and high-elevation planting sites—960, 2,730, and 5,650 feet above sea level. Other features of the study including plantation design have been described (*6*).

In the fall of 1957 every tree was measured and several characters were recorded. Height and diameter growth vary significantly with altitudinal source and with elevation of planting. For other characters, the outstanding results emerge from the highest plantation. Up high, lean and breakage of the main stem are most pronounced in low-elevation sources. All trees have more branches there than at lower plantings. Furthermore, they grow slower and retain their needles longer. The net result is a more fully-clothed, dense-crowned tree at higher elevations.

Height Growth

Ponderosa pine.—After 20 years, the influence of seed source on height had changed at the 5,650-foot plantation (Fig. 1). Elevation of seed source no longer significantly influenced growth. The growth of all sources started leveling off. We computed the curvilinear regression of growth on altitude of seed source and altitude squared. This curve still accounts for more variation in height than does a linear regression using altitude alone; however, the difference is not significant as it was after 12 years (Table 1).

Height growth at the 960-foot and 2,730-foot plantations seems to be following the course suggested by the earlier measurements (Fig. 1). Certainly the highest sources are falling farther behind. The highly significant effects of altitude and its square on height growth were shown by curvilinear regressions. Use of both independent variables also accounted for significantly more of the variation in height growth than did the use of altitude alone (Table 1).

One further observation on heights deserves mention. The progeny having 5,765 feet as the mean elevation of its seed trees grew less than the progeny having 5,555 feet as a mean parental elevation. This occurred at each of the three plantations. Four seed trees are represented in the slower growing progeny and 10 in the faster growing progeny. The mean elevation difference between these progenies is only 210 feet—not enough to account for the growth difference. Perhaps differences in microsite of the parental trees could be correlated with this genetic difference in height growth. Regardless of the forces leading to the origin of this genetic difference, here is a strong illustration that factors other than elevation must be considered in selecting seed trees. The next step needed is to examine the genetic adaptations to microsites—localized ecotypic variations (*10*).

At 20 years, evidence is appearing of inherent differences in growth curves associated with seed source elevation. Trees with low-elevation seed-parents take off rapidly. Trees with high-elevation seed-parents start more slowly; they seem to be dropping ever farther behind at low elevations. Conversely, at

Table 1.—Relation Between 20-year Height and Both Seed-Tree Altitude and Altitude Squared

Item	Plantation elevation, Feet: 960	2,730	5,650
Coefficient of multiple correlation, R	0.642[1]	0.591[2]	0.065
Superior curved line fit, F	11.068[1]	5.609[2]	1.519

[1]Highly significant; probability <.01.
[2]Significant; probability <.05.

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high elevations, as in the story of the hare and the tortoise, the local sources have caught up to the fast-starting lowlanders. Perhaps in the next 10 years they will forge ahead. This long wait for results is in sharp contrast to the quick returns realized by Squillace and Bingham (*10*). In only a few years their progeny tests showed the superiority of high- over low-elevation progenies at their highest planting site.

Jeffrey pine.—In general, Jeffrey pine, as a species, is considered to be inherently more slow growing than ponderosa pine. But recently a contradiction to this assumption appeared (*3*). In 1937 a plantation similar to these three was established in the Coast Range of California at 1,830 feet above sea level. The Jeffrey pine progenies were from the same trees as the ones in this Sierra study. At the Coast Range plantation, Jeffrey pines grew taller in 20 years than ponderosa pines from the same elevations. However, in the Sierra test, no Jeffrey pine progenies equalled ponderosa progenies from the same elevation.

However, we must note that the Jeffrey tests in the Sierra were not an integral part of the ponderosa tests. At the Coast Range planting the two species were mixed together in a randomized design. At each Sierra plantation the Jeffrey test was located along one margin of the ponderosa test; furthermore, this margin usually was a poorer site. Particularly at the middle-elevation planting, Jeffrey did not have a fair chance. Thus, the Jeffrey progenies did not have an equal opportunity with ponderosa to sample randomly the site differences within each plantation. One cannot degrade Jeffrey pine by comparing the height growth curves in Figures 1 and 2. We still do not have a rigorous Sierra test of ponderosa and Jeffrey progenies from the same elevation.

Differences in growth between the three progenies tested were highly significant at the 960-foot and 2,730-foot plantations; the progeny from the highest source grew slightly less. At the 5,650-foot plantation, progeny growth differences, although greater, were not quite significant (F=5.06) at the .05 level ($F_{.05}$=5.14).

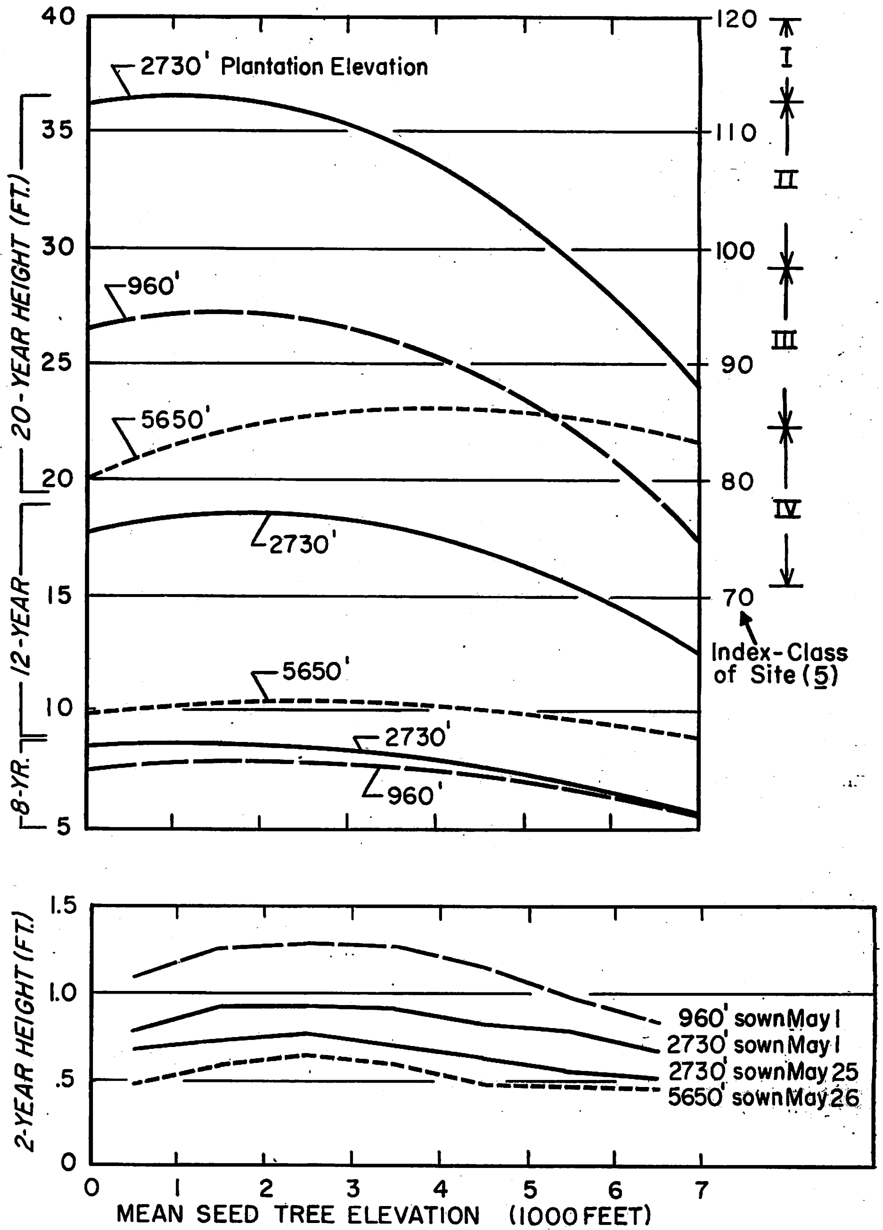

FIG. 1.—Ponderosa pine progeny heights up to 20 years of age in relation to seed tree altitude.

The performance of the highest elevation Jeffrey progeny at the lowest elevation of planting is remarkable. The parent trees were subalpine residents, but the progeny did well on a low, hot, dry site. Incidentally, their half-sib relatives were the ones which attained such an outstanding growth rate at the low-elevation plantation in the Coast Range (*3*).

In the Sierra Nevada, Jeffrey pines normally intermingle with ponderosa pines at the upper edge of the ponderosa zone and grow on up to 8,000 or 9,000 feet (*4*). Below the normal range of the species, one finds isolated pockets of Jeffrey pines. The lowest elevation Jeffrey source, 3,450 feet, was from such an isolated site where soils were derived from serpentine rocks. In

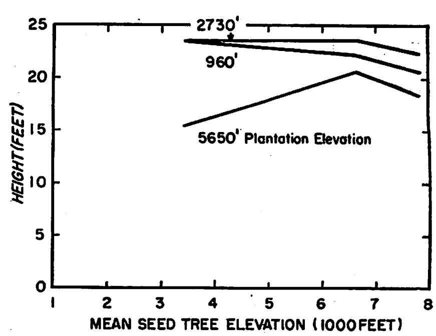

FIG. 2.—Jeffrey pine progeny heights at 20 years of age in relation to seed tree altitude.

the Sierra this progeny grew well at the 960-foot and 2,730-foot plantations on nonserpentine soils (Fig. 2). This progeny, like the low-elevation ponderosas, certainly suffered on being elevated.

Results of this test, like those of the ponderosa test, demonstrate the existence of genetically different populations at different elevations. Selective forces related to elevation have been a factor in their evolution. In the particular elevational transect under study, topographic and climatic changes are gradual and continuous. Ponderosa and Jeffrey pines exist as a continuous population on this tilted plain. The logical induction from the data is that the pattern of genetic variation is clinal.

Genetics in Site Classification

All foresters know that site varies as soils, slope, aspect, climate, etc. change. What about *genetics* and site? Because the conventional measure of site is tree height at a given age, as Mirov, Duffield, and Liddicoet (*6*) indicated, a forester's measure of site includes the genetic capacity of a tree to utilize and to tolerate the environment in which it grows. This genetic capacity varies as individual trees vary or as trees from different geographic sources vary. Traditional site index estimates growth capacity for native trees. What will happen to this traditional measure as nonnative trees are established in plantations?

The yield at a given location will vary with the kind of tree planted there. Using the height regressions presented earlier, we find that the same planting site can vary by one or two classes (*5*), depending on the genetic stock used (Table 2). Conversely, estimating quality of different planting sites by using genetically similar plants has its limitations. Assuming the 1,000-foot source as a basis the three plantations would have ranged from site I to site IV (Table 2). The higher elevation sources would have shown sites II to III or III to IV. One must constantly remember that every source —actually each tree—has a different kind of reaction and tolerance range to all factors of its environment. All trees of a species are not identical just because men call them all by the same name. Each tree provides a genetically different yardstick for measuring the environmental factors of site.

Furthermore, the results illustrate the need for caution in calling any planting site "uniform." Analysis of variance in height growth within elevational progenies at each plantation showed a highly significant variation due to what may be called microsite variations in the 2,730-foot and 5,650-foot plantations. The lowest plantation was rather uniform. Only because the design of this study incorporated replication and randomization were we able to obtain meaningful answers on this point.

The range of site index on each plantation after 20 years was considerable (Table 3). Ponderosa "local stock" was planted at four random locations in each plantation. The middle-elevation planting site showed the most internal variation. On this southerly exposure, the gentle upper slopes (9 percent) were significantly better, site I, than the steeper (29 percent) lower slopes, site II. This site variation occurs in a total horizontal distance of 400 feet. Incidentally, foresters faced with such rapid changes in environment will have great difficulty in finding good genotypes through phenotypic selection in wild stands. To pursue this point further, even if one finds a superior genotype in microsite III, can he expect it to be superior in a microsite I at the same elevation or a microsite III at another elevation?

TABLE 2.—VARIATION IN SITE INDEX AND CLASS[1] AT EACH PLANTATION DEPENDING ON ELEVATION OF SEED SOURCE USED FOR SITE ESTIMATION

Plantation elevation (Feet)	Seed source elevation—feet			
	1,000	3,000	5,000	7,000
960	94.6—III	93.4—III	86.7—III	73.3—IV
2,730	113.4—I	110.4—II	102.0—II	88.0—III
5,650	82.9—IV	85.8—III	85.8—III	83.2—IV

[1]Based on theoretical 20-year tree heights from regressions for each plantation and on Meyer's (*5*) site index (100-year).

TABLE 3.—VARIATION IN SITE INDEX AND CLASS BASED ON HEIGHT AT 20 YEARS FOR "LOCAL" PONDEROSA PINE AT EACH PLANTATION

Plantation elevation	Seed source elevation	Mother trees of progeny	Range in four progeny replications		
			Height	Site index	Site class
Feet	*Feet*	*No.*	*Feet*		
960	618	9	23.7-28.3	87.5-96.6	III
	783	1	18.9-27.1	77.4-94.2	IV⟶III
	783	1	23.5-26.0	87.0-92.0	III
2,730	2,719	5	32.2-41.3	104.4-122.6	II⟶I
	2,748	1	32.4-41.0	104.8-122.0	II⟶I
5,650	5,555	10	21.4-25.3	82.8-90.6	IV⟶III
	5,765	4	18.5-22.4	76.3-84.8	IV⟶III
	6,250	1	18.8-23.8	77.1-87.6	IV⟶III
	6,322	1	23.6-26.4	87.2-92.8	III

Diameter Growth

Ponderosa pine.—At all three plantings, d i a m e t e r s at breast height showed elevational distributions similar to heights (Fig. 3). The variation in diameters due to elevation was statistically significant at the lower two plantings but not at the highest planting. At the lower plantations, high-elevation progenies grew more slowly than middle-elevation progenies, but at the upper planting they held their own and now seem to be surging ahead.

The most striking outcome was the generally large diameters for all progenies. If one determined site class by Meyer's table of diameters at age 20, every progeny at every one of the plantations would measure up to site I (4.6 inches and larger). This contrasts with the wide diversity in site as measured by heights.

The explanation seems simple. Meyer's tables are based on natural stands with highly variable spacing between trees. In these tests, wide, uniform spacing (8 feet) was maintained between all trees. Wide initial spacing promotes such rapid diameter growth (*12*).

Diameters, like heights, were significantly smaller on some of the adverse microsites of the upper two plantings. The range in average diameters for the four replications was:

at 2,730 feet........6.59 to 7.59 inches
at 5,650 feet........5.79 to 7.04 inches

Jeffrey pine.—Diameters of the Jeffrey progenies were strikingly uniform by contrast (Fig. 3). Elevation generally had little effect. Only at the highest planting did high-elevation stock approach a significant increase in diameter over the low-elevation stock.

Stem Taper

By combining the foregoing two characters, one obtains an expression of stem taper. Following Weidman (*13*), we divided mean height in feet by mean diameter in inches for each progeny.

Analyses of data for both ponderosa and Jeffrey pine show significant changes in stem taper (Fig. 4). As elevation of seed source increased, the progenies became stockier at each plantation. Between planting elevations, all sources were stockiest at the highest plantation.

What causes the significant changes in stem taper associated with elevation? In the 960- and 2,730-foot plantations, mean progeny height was closely related to diameter (Fig. 5). Tallest progenies were slimmest (form 5.0); shortest progenies were stockiest (form 4.0). Continued growth at the present relative rates may produce changes in taper, as expressed here. Data presented by Weidman (*13*) and by Squillace and Silen (*11*) show such a change over 20 years. They followed changes in dominant trees of ponderosa from three Bitterroot, Montana, sources grown in northern Idaho. Their taper values after 20 and 40 years were:

Source	*20 years*	*40 years*
4,000 feet	4.57	6.10
5,000 feet	4.68	6.37
7,200 feet	4.41	5.95

As in California, the highest elevation trees were stockiest, and the middle elevation trees slimmest. This order was maintained to age 40 in northern Idaho.

At the 5,650-foot plantation, the interaction between environment and genes produced much stockier progenies regardless of the source elevation (Fig. 5). This stockiness reflects a change in relative rates of diameter and height growth from conditions at the lower plantations. Probably temperature, moisture, and wind conditions during the periods of height and diameter growth influence this change. Future measurements from these plantations may clarify the importance and nature of genetic and environmental influences on stem taper.

Branch Number

Ponderosa pine.—In an attempt to assess the influence of elevation on limbiness, we counted the total number of limbs produced on the main axis at the first two whorls behind the leader—the branches produced in 1956 and 1957. Counts from the ground were made on the outer 12 trees in each group of 16 trees. The average total number of branches per tree for the four replications of a progeny was the statistic subjected to analysis of variance.

Elevation of planting, not source elevation, very significantly influenced the number of branches produced (Fig. 6). The average number of branches produced at the three plantations was:

Plantation	*Branches*
960 feet	6.9
2,730 feet	7.1
5,650 feet	8.4

Elevation of the seed parent did not contribute significantly to the number of branches. Only at the

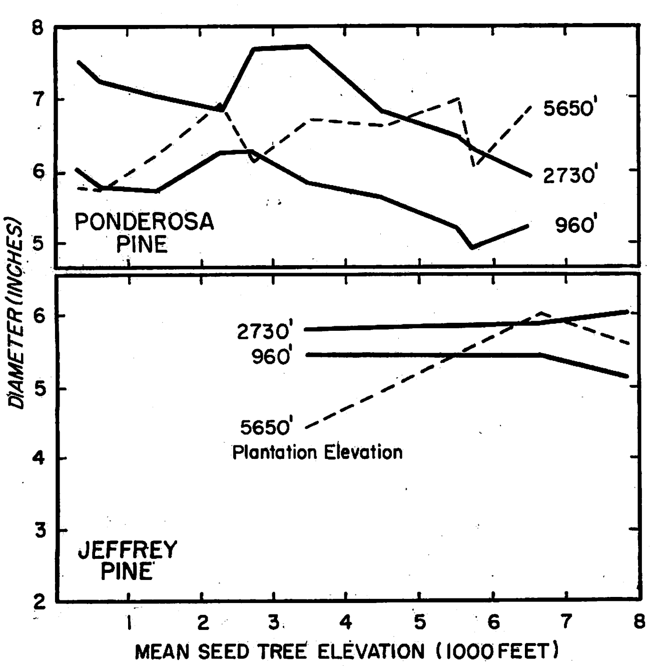

FIG. 3.—Progeny diameters at 20 years of age at three elevations of planting.

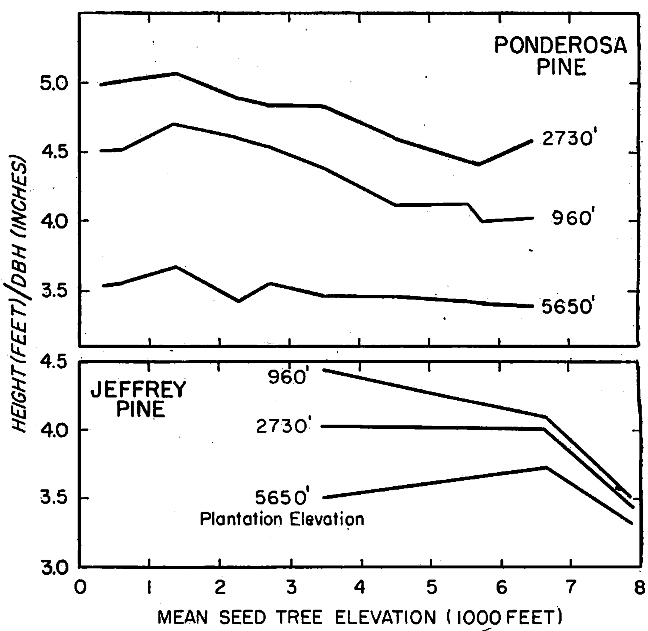

FIG. 4.—Stem form of elevational sources at three plantation elevations.

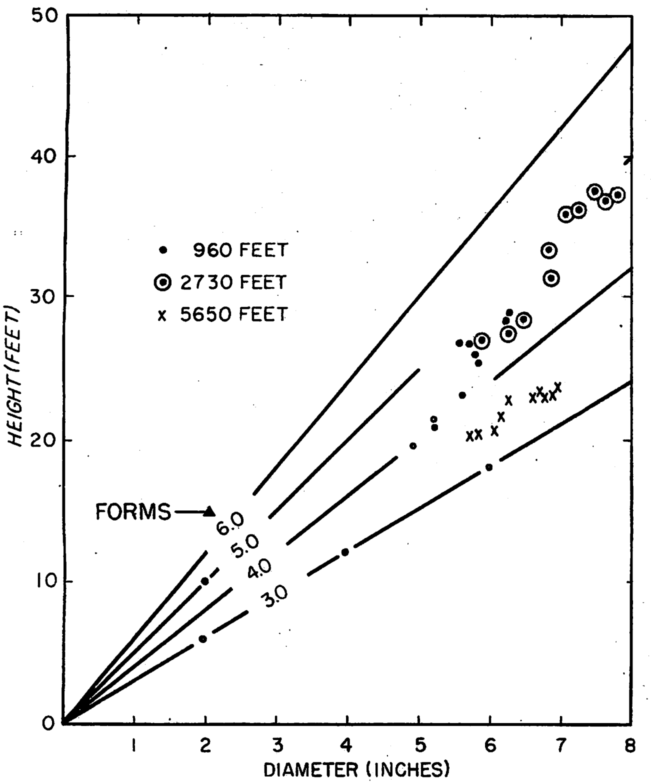

FIG. 5.—Stem form (height/diameter) for ten progenies from different elevation sources planted at three elevations.

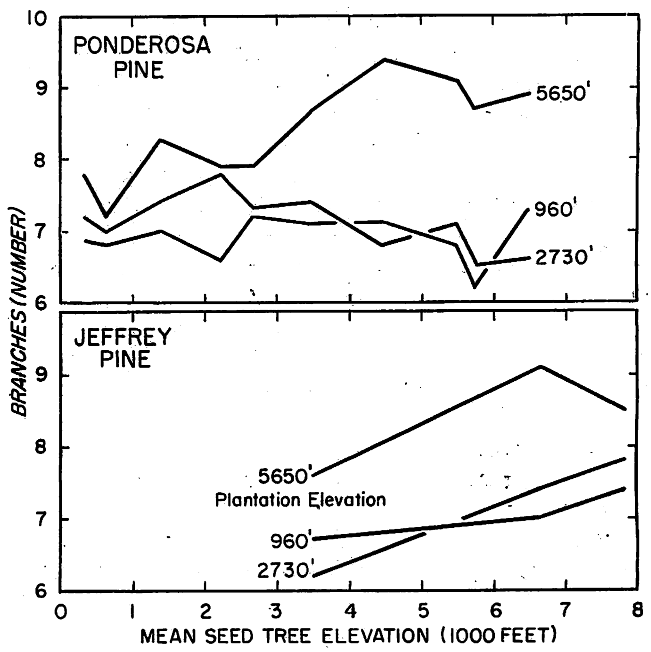

FIG. 6.—The average total number of branches produced in the 19th and 20th growing seasons at three elevations of planting.

5,650-foot plantation did the data suggest an increase in number of branches as seed source elevation rose.

One other unexplained fact was gleaned from the data by means of a sign test (*9*), comparing the number of branches produced in 1957 with the number produced in 1956. At the two lower plantings significantly more branches were produced in 1957; fewer in 1956. At 5,650 feet the 1956 complement was larger, but the difference was not significant. The test suggests (1) a strong influence of environment on branch number and (2) a variation in this influence with both year and elevation.

Jeffrey pine.—Seed source elevation did significantly influence the number of branches produced by Jeffrey pine. Progenies of the lowest sources (3,450 feet) had fewest branches at all three plantations. Just as for ponderosa, all sources produced significantly more branches at the highest planting. The plantation means were:

Plantation	*Branches*
960 feet	7.1
2,730 feet	7.0
5,650 feet	8.4

Sign tests did not reveal significant differences between the numbers of 1956 and 1957 branches.

Needle Retention

Ponderosa pine.—The 12 outside trees in each block of 16 were inspected for needle retention in the fall of their twentieth growing season. The average number of seasons of retention for 48 trees in the 4 replicated blocks at each plantation was the statistic subjected to an analysis of variance.

The relation of needle retention to plantation elevation had extremely high significance. The 5,650-foot plantation trees retained their needles nearly twice as long as the trees planted at the two lower plantings. The average number of seasons needles were retained at each plantation elevation were:

Plantation	*Ponderosa*	*Jeffrey*
960 feet	1.92	2.30
2,730 feet	2.11	2.57
5,650 feet	3.80	3.27

Many authors (*1, 2, 7, 13, 14*) have noted this longer retention in natural stands and plantations at higher elevations.

At each plantation the progenies from different elevations had uniform needle retention. The over-all average number of seasons of needle retention varied regularly but insignificantly by elevation of seed source:

4 lowest sources	2.7 seasons
4 middle sources	2.6 seasons
2 highest sources	2.5 seasons

These data provide another illustration of the low heritability and high environmental control of this character (*1, 13*).

Jeffrey pine.—The pattern of results in ponderosa pine nearly was duplicated in Jeffrey pine. Trees from all elevations retained their needles longest at the highest plantation. The regular but insignificant trend in over-all average number of seasons of retention according to elevation of seed source was reversed:

3,450 feet	2.6 seasons
6,635 feet	2.7 seasons
7,860 feet	2.8 seasons

Lean

Ponderosa and Jeffrey pines.—In their native habitats these pines normally are erect straight-boled trees. At the 5,650-foot plantation, many trees were starting to lean or to bend over. We rated every tree at each plantation according to this subjective system:

Rating	*Description*
0	No lean.
1	Slight lean, up to 5°, having very little effect on future straightness.
2	Moderate lean, 6 to 20°, perhaps having some effect on future straightness.
3	Sharp lean, 20 to 45°, probably enough to reduce commercial value.
4	Horizontal, more than 45°.

The percentage of trees from each seed source given each rating was calculated. Such statistics are not distributed normally and conventional analyses could not be followed.

Examination of the data (Fig. 7) shows a much greater incidence of lean in low-elevation progenies at the highest plantation. At the lower plantings the trend is not dominant; all sources performed about the same. Perhaps the deep snow pack with its tendency to slide downhill may be related to the more frequent lean of stems at the highest plantation.

The development of lean over the next decade will be interesting to follow. Trees will grow larger; crowns will become more crowded; the snow pack no longer will provide shelter to the crowns from winter's blasts and may push on the stems. High-elevation sources probably will stand straightest. Schmidt (*8*), in a comparable study of 17-year-old *Pinus sylvestris* L., reports that higher elevation sources had straightest stems and most rapid recovery from leader damage.

Stem Breakage

Ponderosa and Jeffrey pines.—At the 5,650-foot planting, many trees had breaks or crooks in the main stem. This damage was rated as follows:

Rating	*Description*
0	No apparent main stem breaks.
1	Slight kink—overgrown in a few years.
2	Severe kink—eventually overgrown but only after many years.
3	Major break producing dogleg as branch turns up; commercial value limited.

These ratings represented to us breakage at progressively older sections of the stem. A slight kink seemed to have resulted from the loss of a 1- or 2-year-old leader; a severe kink, the loss of perhaps a 3- to 5-year-old leader.

Only at the highest plantation was breakage prominent (Fig. 8). Lower elevation sources broke off most frequently. Why? We do not know. Perhaps this breakage may explain the changing curves of height (Fig. 1). Careful watch should be maintained over the next few decades to determine (1) if breakage is a significant factor in

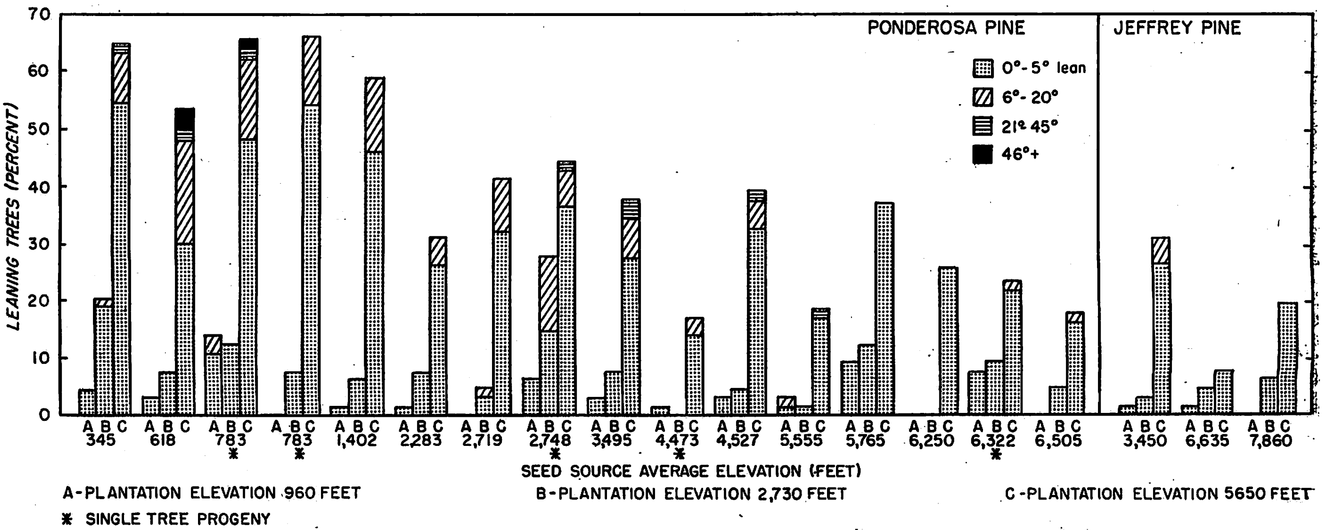

FIG. 7.—The proportion of trees in each pine progeny showing different degrees of lean.

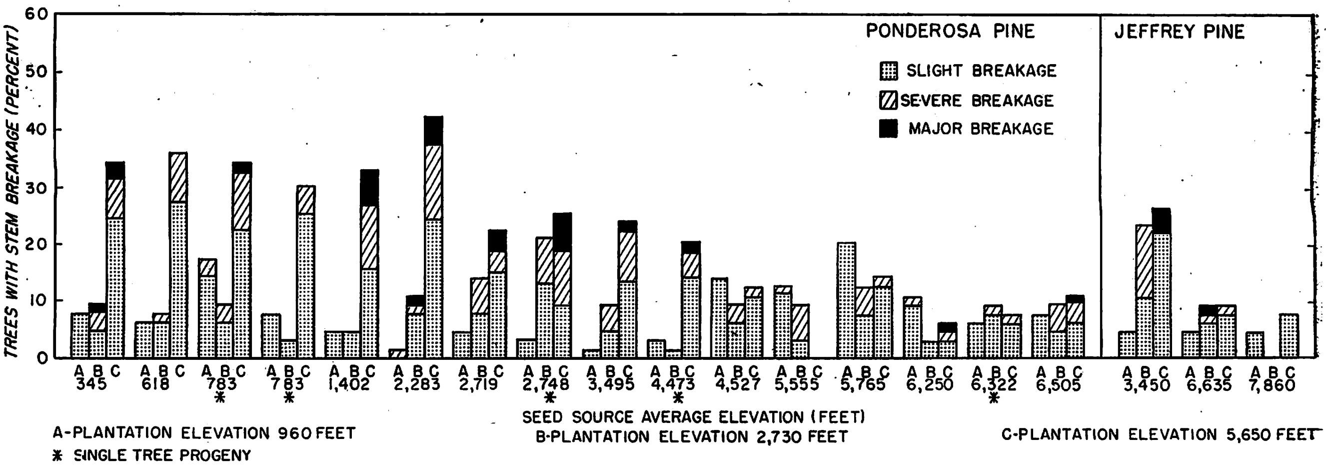

FIG. 8.—The proportion of trees in each pine progeny showing different degrees of main stem breakage.

reducing the early height superiority of middle-elevation sources, (2) what causes breakage, and (3) what effect breakage may have on final stem form.

Survival

Early plantation failures were quickly replanted; hence, the number of trees still present at 20 years (Table 4) does not reflect an accurate estimate of survival ability. Seedlings of each seed source were planted at 64 spots in each plantation. The only losses to speak of since replanting have occurred at the highest planting. The low-elevation sources seem most poorly adapted.

Summary

Progenies of ponderosa and Jeffrey pines grown for 20 years at 3 elevations show heritable differences in height and diameter growth associated with the elevation of the seed tree. Seed tree elevations varied from 125 to 6,919 feet for 89 ponderosa pines and from 3,450 to 8,235 feet for 21 Jeffrey pines. Generally local seed sources grew best at the 3 planting sites—960, 2,730, and 5,650 feet above sea level. The fastest growing 20-year-old progenies at low (960 feet) and medium (2,730 feet) elevation plantations were from seed trees growing at 1,000 to 2,000 feet elevation. They were taller than high-elevation or very low-elevation progenies. Up high (5,650 feet) the progenies from lower elevations seemed to be falling behind in height growth.

The importance of genetics in evaluating site quality is brought out. Average site class at each plantation varied by 1 or 2 classes, depending on the elevational source used for height determination.

TABLE 4.—NUMBER OF TREES SURVIVING AT 20 YEARS, BY ELEVATION OF SEED SOURCE AND PLANTING SITE

Average elevation of seed source, feet	Planting elevation 960 ft.	2,730 ft.	5,650 ft.
PONDEROSA PINE			
6,505	63	61	62
6,322[1]	64	64	64
6,250[1]	64	64	62
5,765	63	64	62
5,555	63	63	64
4,527	64	64	64
4,473[1]	64	63	64
3,495	64	63	58
2,748[1]	62	61	63
2,719	64	63	53
2,283	63	64	61
1,402	64	64	63
783[1]	64	64	59
783[1]	64	64	58
618	64	64	58
345	64	63	57
JEFFREY PINE			
7,861	64	63	62
6,635	62	64	64
3,450	64	64	45

[1]Single tree progeny.

Considerable site variation within each plantation also was detected.

Stem taper changed with elevation of planting and elevation of seed source. Progenies of highest sources were stockiest at all plantations, but all progenies were stockier at the highest plantation.

The number of branches and the number of years that needles were retained both were greatest at the 5,650-foot plantation. For ponderosa pine, neither character varied significantly with elevation of seed source. For Jeffrey pine, elevation of source did not affect needle retention but did affect branch number. Trees from the lowest source had fewer branches.

The degree of lean and breakage of stems was greatest at the 5,650-foot plantation. In this plantation low-elevation sources of both species suffered the most lean and the greatest amount of stem breakage.

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