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GENETIC GAINS FROM TREE IMPROVEMENT OF PONDEROSA PINE IN SOUTHERN IDAHO

Gerald E. Rehfeldt

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U.S. Department of Agriculture, Forest Service

THE AUTHOR

GERALD E. REHFELDT is a plant geneticist at the Forestry Sciences Laboratory, Moscow, Idaho. Primary emphasis of his research is on the ecological genetics of Northern Rocky Mountain conifers.

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RESEARCH SUMMARY

Potential gains from tree improvement of ponderosa pine in southern Idaho were assessed after 16 years of field testing. From a comparison of progenies of 268 half-sib families from 37 populations growing at four test locations, genetic gains in 16-year height were related to (1) seed collections within seed zones, (2) seed collections from selected populations within seed zones, and (3) seed orchards developed after family trials.

Analysis of population differentiation provided bases for re-evaluation of seed transfer guidelines. In general, seed for reforestation may be transferred from the collection area (1) \pm 750 ft (230 m) elevation, (2) \pm 50 miles (0.7 degrees) latitude, and (3) \pm 60 miles (1.2 degrees) longitude. In addition, a gain of about 4 percent in 16-year height can be expected from seed collections in populations of highest mean performance.

Quantitative genetic analyses provided estimates of the additive genetic variance and phenotypic variance required for predicting gains in 16-year height after seed orchards are developed from family trials. Depending on the intensity of family selection and individual selection within families, genetic gains of 8 to 14 percent can be expected from seed orchards. Realization of these gains requires seed orchards to be composed of less than 150 genotypes.

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INTRODUCTION

The basis for a practical tree improvement program of ponderosa pine in southern Idaho is contained in 16-year old family evaluation tests. As detailed in preceding publications (Wang 1967; Wang and Patee 1974, 1976; Rehfeldt 1980), primary objectives of the tests are: to develop seed zones and seed transfer guidelines that account for genetic adaptations to natural environments, to identify outstanding individual trees and populations from which wind-pollinated seeds will provide genetic gains to artificial reforestation, and to provide materials and information prerequisite to future breeding programs.

The present analyses of 16-year height utilize experimental materials more fully described in a series of papers that have assessed performance at ages 3, 8, and 11. Test plantations currently require thinning; therefore, it is appropriate to consider alternative plans for the future research program and for development of seed orchards.

MATERIALS AND METHODS

Wind-pollinated cones had been collected from 1 to 10 trees in each of 37 populations. Populations were separated by about 1 000 m in elevation and 2 degrees in latitude and longitude; they also represented habitat types that ranged from the relatively dry *Pinus ponderosa/Purshia tridentata* to the relatively moist *Abies grandis/Vaccinium globulare*. Thereby, much of the geographic distribution and ecological amplitude of the species in southwest Idaho was represented. Seedlings from 268 families were planted in four-tree row plots in each of 10 blocks at four planting sites. About 1.5 m separated trees within rows; 3 m separated rows. Test sites included Idaho City (1 200 m elevation), Holcomb (1 100 m), in the southern portion of the region; and Boulder Creek (1 450 m) and Jack's Creek (1 650 m) in the north. Since the last report of this series (Rehfeldt 1980), the plantation at Boulder Creek was thinned: the two shortest trees in each family plot were removed, and, at Jack's Creek, three replicates of exceptionally low survival were destroyed.

Statistical analyses for assessing population differentiation and quantitative genetics were made on the 16-year height of individual trees. An appropriate analysis would involve calculation of main effects for sites and populations; nested effects of blocks in sites and families in populations; four interactive effects; and variance within plots. As explained previously, however, imbalances in the original design were accentuated by survival percentages that ranged from 22 to 80 percent at the four test sites. Because missing data were excessive, least squares analyses were required for accurate estimation of variance components. Yet, the large size of the matrix needed for a single analysis precluded inversion. Consequently, statistical analyses were completed in separate stages.

Population differentiation was assessed from a least square analysis of variance (table 1). One population, represented by a single family, was excluded from analyses. In addition to assessing differentiation, this analysis allowed calculation of least square means for populations within and among planting sites. These means were used in all subsequent comparisons of population performance; they reflect the height expected if an equal number of observations had been available for each population in each block at all planting sites.

Table 1.--Form and results of analysis of variance of population performance for height at age 16

Source of variance	Degrees of freedom	Components expected in each mean square	Mean square	F	
Sites	3	σ_E^2	$+ 203.43\sigma_{B/S}^2 + 1503.95\sigma_S^2$	489,559	3.38**
Blocks in sites	30	σ_E^2	$+ 203.43\sigma_{B/S}^2$	144,829	18.21**
Populations	35	$\sigma_E^2 + 43.74\sigma_{PS}^2 + 174.21\sigma_P^2$		27,335	3.44**
Populations x sites	105	$\sigma_E^2 + 43.74\sigma_{PS}^2$		7,952	1.55**
Residual	6125	σ_E^2		5,124	

**Statistical significance at the 1 percent level of probability.

Patterns of population differentiation were related to physiognomic criteria of the seed source by multiple regression:

$$Y_i = b_0 + b_1X_1 + b_2X_2 + b_3X_3$$

where

Y_i = least squares mean for population i on all sites as calculated in preceding analysis,

b_0 = intercept,

b_1 to b_3 = regression coefficients,

X_1 to X_3 = independent variables of elevation (meters), latitude (degrees -40) and longitude (degrees -100), respectively.

Effects of habitat types (recurring plant communities of potential climax) on population differentiation were also tested in multiple regression analyses. For these tests, the previous model was adjusted by including constant terms for each habitat type represented by the 36 populations. But, as shown previously (Rehfeldt 1980), inclusion of the effects of habitat types did not improve the fit of the data to the model. Habitat types apparently have little effect on differentiation and are subsequently ignored.

The regression model presented above was also used on least squares mean height of populations from each of the four sites. As detailed later, however, the mean height of populations between ages 11 and 16 was so strongly correlated among sites that the results of the separate regression analyses essentially duplicated those presented previously (Rehfeldt 1980). Consequently, results of separate analyses for each site are not presented.

Guidelines for seed transfer were developed from patterns of population differentiation. According to techniques used previously (Rehfeldt 1979), the analysis of variance allows calculation of the least significant difference (lsd) among population means that provide for statistical detection of mean differences at given levels of probability (Steele and Torrie 1960). A value of lsd was calculated at the relatively low level of probability of 0.2 in order to guard against making the error of accepting no differences among populations when differences actually exist. Then, the expression $lsd(0.2)/b$, where b is the regression coefficient, provides the distance in elevation, latitude, and longitude associated with mean differences at the 80 percent level of probability. These distances are proposed as guidelines for limiting seed transfer.

Possible genetic gains within seed zones were estimated from quantitative genetic analyses made for each site according to a model of random effects (table 2). These analyses allowed estimates of family heritabilities, individual heritabilities, and genetic gains expected after alternative plans of seed orchard development. Estimates of genetic gains from family selection and individual selection within families followed Namkoong (1979).

Table 2.--Form of analyses of variance for quantitative genetics

Source of variance	Expected mean squares ²
Blocks	$\sigma_W^2 + k_1 \sigma_E^2 + k_5 \sigma_B^2$
Populations	$\sigma_W^2 + k_1 \sigma_E^2 + k_3 \sigma_{F/P}^2 + k_4 \sigma_P^2$
Families in populations	$\sigma_W^2 + k_1 \sigma_E^2 + k_2 \sigma_{F/P}^2$
Experimental error ¹	$\sigma_W^2 + k_1 \sigma_E^2$
Within	σ_W^2

¹Contains all sources of variance involving interaction of blocks

²where:

	<u>Holcomb</u>	<u>Idaho City</u>	<u>Boulder Creek</u>	<u>Jack's Creek</u>
$k_1 =$	1.88	1.90	1.89	1.56
$k_2 =$	11.36	16.04	16.29	4.70
$k_3 =$	12.01	16.83	16.75	5.27
$k_4 =$	74.50	109.04	110.47	30.45
$k_5 =$	334.56	377.89	397.03	177.01

RESULTS AND DISCUSSION

Population Differentiation

Analyses of population differentiation readily detected mean differences among populations across all planting sites (table 1). But, main effects of sites were also significant, and populations tended to perform differently at the various planting sites. The interaction apparently arises from expression of differential adaptations of populations at planting sites that encompass a large elevational (550 m) and latitudinal (> 1 degree) range.

Least square mean heights and physiognomic criteria of the seed sources are presented in table 3. These means are representative of mean performance across all four test sites, and, therefore, they are confounded by interactions between genotype and environment. But, simple correlation coefficients (r) of mean height for populations at each site and least square means ranged from 0.64 to 0.85. The high values of these correlation coefficients suggest that confounding of means by genotype-environment interactions is small. Least square means apparently reflect an average performance suitable for assessing differentiation in relation to physiognomic criteria of the seed source. But, because the correlations were not perfect, differentiation also was assessed from performance at each site.

Table 3.--Location and least square mean height of populations according to origin

Popula- tion	Location	Latitude	Longitude	Elevation	16-year height
Number		Degrees	Degrees	Meters	cm
1	Anderson	44.55	116.20	1520	292
2	Mill Creek	44.45	116.30	1370	294
5	Camp Creek	44.62	115.65	1830	286
6	Crawford	44.53	115.97	1460	296
9	Warm Springs Ridge	43.85	115.88	1520	296
11	Lester Creek	43.62	115.38	1830	281
14	Sagehen	44.32	116.23	1580	308
15	Third Fork	44.37	116.33	1250	309
16	Powellson Creek	44.78	115.87	1770	293
17	Circle Creek	45.05	116.27	1280	311
18	Bear Creek	43.95	115.47	1830	275
19	Idaho City	43.72	115.72	1460	301
22	South Fork Payette River	44.07	115.50	1220	299
23	Mill Creek	44.67	116.87	1250	309
24	Pine Creek	44.70	116.83	1160	309
25	Babbit Creek	43.80	115.72	1950	283
26	Mica Creek	44.60	116.27	1520	285
27	Cabin Creek	44.63	116.27	1370	331
28	Mud Creek	45.05	116.38	1520	308
29	Rough Creek	44.90	116.48	975	314
35	Dutch Creek A	43.80	115.37	1520	289
38	Circle "C"	45.05	116.27	1220	318
39	Meadow Valley	44.98	116.22	1220	318
41	Dutch Creek B	43.73	115.45	1980	288
42	Trail Creek	43.60	115.75	1190	315
46	West Fork Creek	44.30	115.87	1370	286
47	Garden Valley	44.07	115.93	1040	315
50	Bumgartner	43.62	115.08	1310	271
53	Camp Creek	44.88	115.70	1220	320
54	Zena Creek	45.07	115.75	1520	271
20A	Idaho City	43.77	115.72	1280	296
20B	Idaho City	43.87	115.83	1280	282
21A	Hazard Creek	45.18	116.30	1070	321
21B	Scriver Creek	44.17	116.00	1310	318
43A	Rice Creek	45.75	116.33	1430	301
43B	Fleming Creek	44.03	116.10	1310	296

In the multiple regression analysis, elevation, latitude and longitude of the seed source accounted for 51 percent of the variation in mean performance of populations (table 4). Visual examination of the residuals from regression suggested that transformations of the independent variables would not necessarily improve the fit. The regression statistics show that for an elevational gradient of 1 000 m, mean height of populations decreases by about 10 percent; and across a geographic interval of one degree of latitude or longitude, mean height changes by 3 percent and 2 percent, respectively.

Since the simple correlations (r) of population means at age 16 with those at age 11 were 0.78, 0.89, 0.93, and 0.91 at Jack's Creek, Holcomb, Boulder Creek, and Idaho City, respectively, it is not surprising that multiple regression models that fit mean performance at each site to physiognomic variables essentially duplicated results of similar models for height at age 11 (Rehfeldt 1980). Moreover, models that involved mean values of 16-year height across all sites (table 4) accounted for more variance than those models involving 11- or 16-year height at a single site. Undoubtedly, analyses that combined observations from all sites provided better estimates of population means and greater statistical power than previous analyses that were made for each site separately.

Table 4.--Results of multiple regression analyses for relating population performance to physiognomic criteria of the seed source

Variable	Regression coefficient (b)	$\frac{lsd_{(0.2)}}{b}$
Elevation (X_1)	-0.026	466 m (1500 ft)
Latitude (X_2)	8.791	1.4 ⁰ (100 miles)
Longitude (X_3)	5.134	2.3 ⁰ (120 miles)

$b_0 = 268.84$
 $R^2 = 0.51$
 $s_{y \cdot x} = 10.99$

Statistical analyses have detected differences among populations in 16-year height and have related differentiation to geographic and ecologic conditions of the seed source. The applicability of these results to practices of seed zoning depends on the degree by which tree height reflects adaptations to the natural environment. While there is little doubt that seed zones should be based on numerous adaptational characteristics, no data other than height are available for ponderosa pine in southern Idaho. But, adaptations in ponderosa pine may be manifest much like adaptations in Douglas-fir of north Idaho: the growth, phenology, and cold hardiness of populations are so highly intercorrelated that variation among populations in a single character reflects numerous characters (Rehfeldt 1979). Consequently, it is assumed that observed patterns of variation in 16-year height of ponderosa pine are adaptive.

Table 4 reveals the distance in elevation, latitude, and longitude that is associated with mean differences among populations equal to a value of $lsd_{(0.2)}$. At minimum distances of 1,533 ft (466 m) elevation, 100 miles (1.4 degrees) latitude, or 120 miles (1.9 degrees) longitude, differences among populations are detectable with a probability of 80 percent. Or as a corollary, seed for afforestation may be transferred from the collection area: + 750 ft (230 m) elevation, + 50 miles (0.7 degrees) latitude and + 60 miles (1.2 degrees) longitude.

Yet, it should be recognized that the recommended seed zones are based solely on the probability of detecting differences in height among populations. Not only do these zones fail to account for traits other than height, they also fail to account for administrative factors such as patterns of land ownership or location of future planting programs. However, these guidelines can be altered readily provided that an increased risk of maladaptation is recognized. A difference in height of about 10 percent can be expected from populations separated by 1 000 m (table 4); populations separated by 1 degree of latitude or longitude can be expected to differ by 3 percent and 2 percent, respectively.

Genetic gains from tree improvement are readily attained by collecting seeds for reforestation from natural stands of proven genetic value. For instance, if the present region is divided into four zones separated at 1 400 m elevation and 44.3 degrees latitude, a gain in height of about 4 percent could be expected within zones when seed collections are made from the following populations:

<u>Zone</u>	<u>Superior populations*</u>
Low north	27,38,53,21A
High north	14**,28
Low south	42,47,21B
High south	14**,19

*Coded in table 3.

**Suitable for both northern and southern zones.

Quantitative Genetics

All mean squares associated with the main effects of families at each planting site (table 5) were statistically significant at the 1 percent level of probability. As a percent of the sum of variance components, the family variance accounted for about 4 percent of the total variance and slightly more variance than effects of populations. Still, the use of these results to estimate genetic components of variance (table 6) needs explanation.

Because of the methods of calculation, bias is introduced at four levels into estimates of the additive genetic variance, phenotypic variance, and, consequently, heritabilities. First, the assumption is implied that families were composed of half-sibs. But, progenies of wind-pollinated trees are slightly more closely related than actual half-sibs (Namkoong 1966); thus, additive genetic variances (table 6) are slightly overestimated.

Table 5.--Results of analyses of variance of 16-year height for each location

Source of variance	Holcomb			Idaho City			Boulder Creek			Jack's Creek		
	d.f.	Mean square	σ^2	d.f.	Mean square	σ^2	d.f.	Mean square	σ^2	d.f.	Mean square	σ^2
Blocks	7	544,147	1604	9	213,488	1037	9	154,743	363	5	178,051	945
Populations	36	19,786	127	36	21,302	97	36	30,265	128	36	22,499	315
Families/ Populations	198	10,350	249	207	10,689	218	207	16,171	340	193	12,907	464
Experimental error ¹	1186	7,527	2002	1826	7,198	1924	1852	10,632	3804	470	10,726	2338
Within	2041	3,762	3762	2948	3,542	3542	2095	3,442	3442	710	7,078	7078

¹Contains sources of variance involving interactions of blocks.

Table 6.--Genetic components of variance for each location.
Calculations follow Namkoong (1979)

	Holcomb	Idaho City	Boulder Creek	Jack's Creek
Additive genetic variance:				
$\sigma_A^2 = 4\sigma_{F/P}^2$	996	872	1360	1856
Total phenotypic variance:				
$\sigma_T^2 = \sigma_W^2 + \sigma_E^2 + \sigma_{F/P}^2$	6013	5684	7586	9880
Family phenotypic variance:				
$\sigma_{TP}^2 = \frac{\sigma_W^2}{k_2} + \frac{\sigma_E^2}{k_2/k_1} + \sigma_{F/P}^2$	992	661	1000	2746
Heritability of families:				
$h_F^2 = \frac{.25 \sigma_A^2}{\sigma_{TP}^2}$	0.27	0.33	0.34	0.17
Heritability of individuals:				
$h_I^2 = \frac{\sigma_A^2}{\sigma_T^2}$	0.17	0.15	0.18	0.19

Secondly, since estimates of additive genetic variance from single planting sites are confounded by interactions of genotype and environment (Namkoong and others 1966), present estimates (table 6) may be subject to bias. But, genetic gains for ponderosa pine in southern Idaho will accrue within seed zones, and, therefore, appropriate estimates of heritabilities should be inflated by the effects of the genotype-environment interaction (Namkoong 1979).

Thirdly, estimates of the phenotypic variance apparently do not contain components of variance due to genotype-environment interaction. It is likely, however, that some of the effects of a genotype-environment interaction expected within seed zones are contained within the interaction of blocks and families. Whereas the mean height of trees varied 63 cm among planting sites, mean differences associated with blocks ranged from 67 cm to 105 cm at the various planting sites. Significant mean differences among blocks (table 5) arise partially because blocks were arranged according to aspect at each site. Thereby, blocks reflect a variety of sites typical of the seed zone represented by each planting site. Therefore, the interaction among blocks and families (table 5) likely reflects genotype - environment interactions within seed zones as well as sampling errors.

Finally, sampling errors are magnified by the experimental design. Only four trees were planted in each block at each test site. As reflected by harmonic means (k_1 in table 1), an average of two or fewer trees remain. Thus, family plots poorly reflect family means in each block; experimental errors (block interactions) are magnified; and phenotypic variances are greatly exaggerated in relation to the additive genetic variance.

Thus, there is little doubt that the genetic components of variance (table 6) are only approximate. But, particularly if each planting site is considered as a representative of a single seed zone, errors of estimate can be absorbed without invalidation of statistical analyses.

Results of analyses of variance (table 5) and calculations of genetic components of variance (table 6) are similar to those from age 11 (Rehfeldt 1980). Most of this correspondence can be traced to the high correlation of individual tree heights ($r = 0.86, 0.88, 0.91,$ and 0.83 at Jack's Creek, Boulder Creek, Idaho City, and Holcomb, respectively) and family means ($r = 0.81, 0.88, 0.89$ and $0.81,$ respectively) between data at age 11 and age 16. In fact, analyses of variance of the deviation from regression of 16-year on 11-year height detected no differences among blocks, families, or their interaction; all of the variance was attributable to experimental errors or to variation within family plots. Nevertheless, as observed for ponderosa pine in California (Namkoong and Conkle 1976), the proportion of the total variance attributable to families within populations has decreased between ages 8, 11, and 16. This reduction occurred because error variances (within plots and experimental error) increased. In fact, while error components of variance doubled between ages 11 and 16, family variance components increased in absolute size by only 50 percent. Consequently, estimates of additive genetic variance are less; phenotypic variances are greater; heritabilities are less; and expected gains are smaller at age 16 than at age 11.

Genetic gains in 16-year height that are expected after interpollination of trees chosen under various intensities of family and individual tree selection are detailed in figure 1. These gains were calculated for family selection by:

$$\Delta G = ih_F^2 \sigma_{TP}$$

and for selection of individuals within selected families by:

$$\Delta G = 0.75ih_I^2 \sigma_T$$

where

ΔG = genetic gain in units of measure

i = selection intensity; a constant relation to the proportion of the population selected (Namkoong 1979).

h_F^2, h_I^2, σ_T and σ_{TP} are defined in table 6.

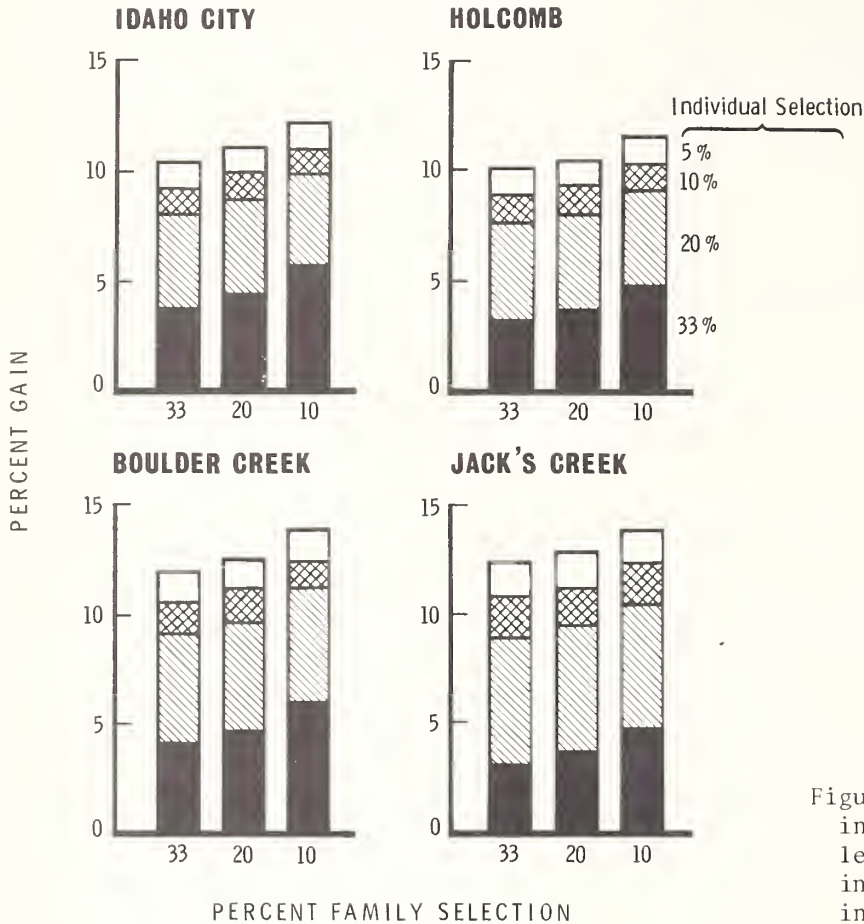


Figure 1.--Expected gains (ordinate) in 16-year height from alternative levels of family selection (bars) and individual selection (shading) within families for each planting site.

Gains presented in figure 1 are expressed as a percentage of the mean height of only those trees at each planting site that represent the seed zone within which that site lies. A 3 to 5 percent gain over local seed sources can be expected after intermatings of the tallest families. And, gains of 10 to 15 percent seem likely in progenies of the best performing individual trees within selected families. Relatively high gains will be realized, however, only if seed orchards are composed of relatively few genotypes (fig. 2). And therefore, an additional investment will be required to develop clonal seed orchards.

These results attest to potential genetic gains at several levels of tree improvement for ponderosa pine. First, seed transfer guidelines account for natural adaptation of populations and reduce losses in productivity from maladaptation. These guidelines limit seed transfer to + 750 ft (230 m) elevation, + 50 miles (0.7 degrees) latitude, and + 60 miles (1.2 degrees) longitude. Secondly, a 4 percent gain in 16-year height can be attained by collecting seeds for reforestation from populations of proven genetic potential. And, thirdly, depending on the intensity of selection, gains from 8 to 14 percent can be expected in the next generation from seed orchards developed from select individuals within selected families.

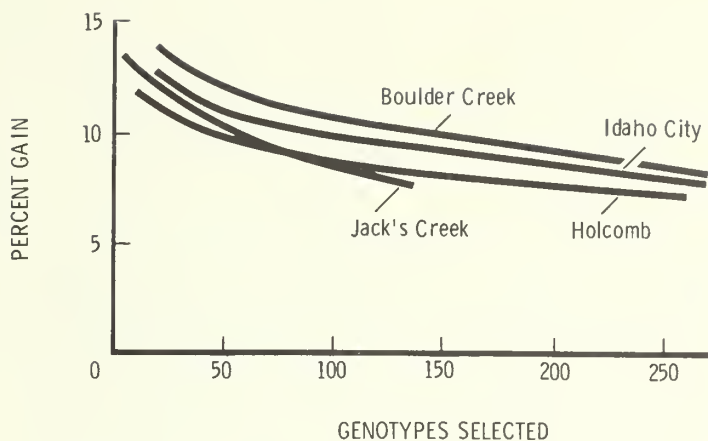


Figure 2.--Approximate relationship between percent gain in 16-year height and number of genotypes selected for seed orchards at each planting site. The number of genotypes was derived from the various combinations of family and individual tree selection detailed in figure 1.

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The 16-year heights of ponderosa pine progenies from 268 half-sib families representing 37 southern Idaho populations were compared on four test sites. Analyses of population differentiation showed that a genetic gain in 16-year height of about 4 percent will result from collections of seed in selected populations. But seed for reforestation should not be transferred more than 460 m elevation, 1.4° latitude or 2.4° longitude. Quantitative genetic analyses implied that genetic gains of 8 to 14 percent can be expected in the height of 16-year-old progeny of selected families and individual trees.

KEYWORDS: genetic variation, ponderosa pine, heritability, genetic gain, seed zoning

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