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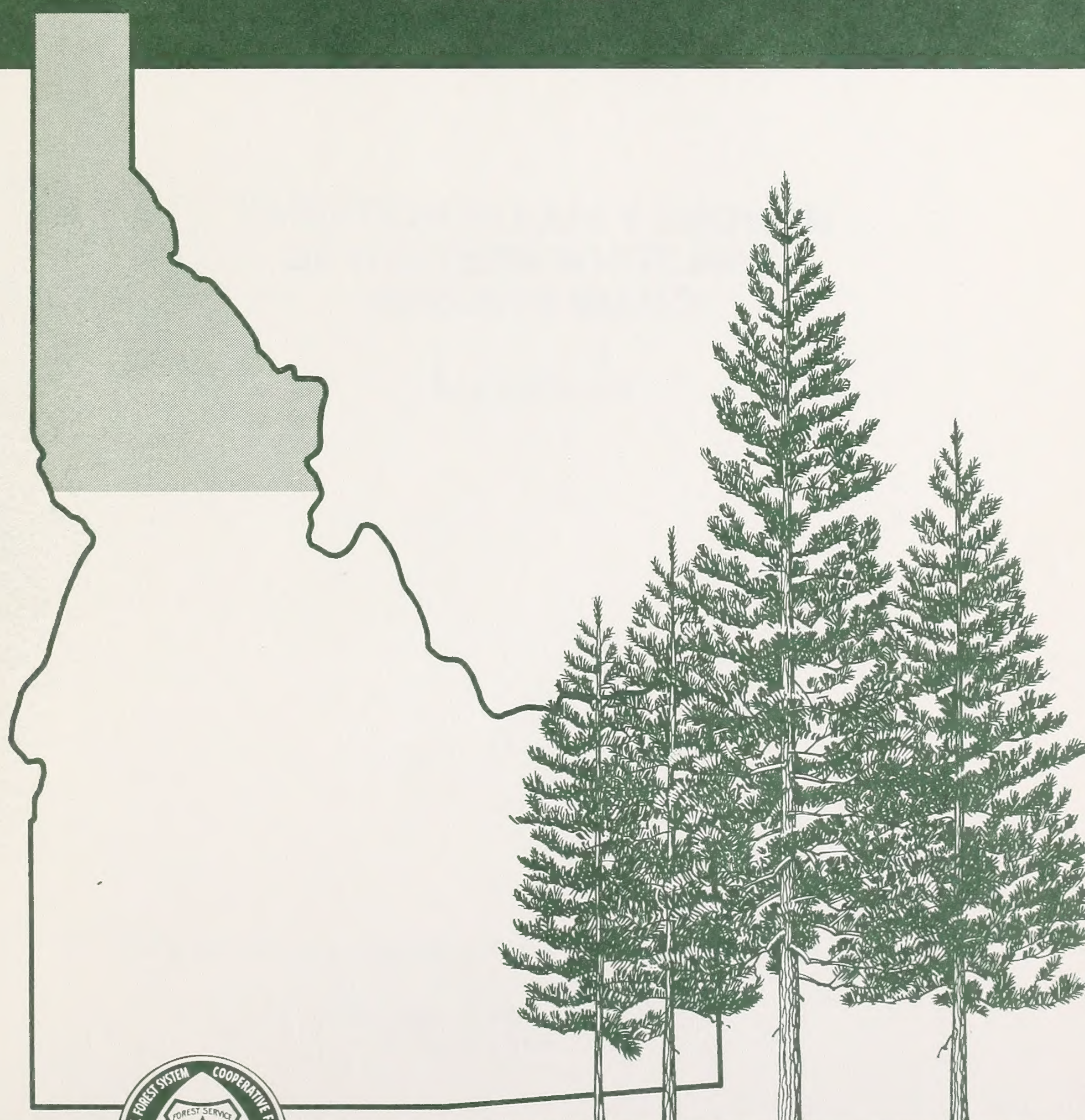
R. J. STEINHOFF



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RESEARCH SUMMARY

In nursery and field tests representing five different studies, most of the variation in height growth or other traits in any one test area was among seedlings within family plots. Of the useable genetic variation in those traits, most (60-90 percent) was related to differences among the parent trees within stands. The remaining genetic variation was spread among geographic areas, elevational zones, or stands within these categories. When differences among the latter catagories were significant, usually no pattern in the variation was apparent. Thus, although seedlings within families and family means within stands vary considerably, the lack of differences among stand means, or those for broader geographic areas, and the absence of distinct variation patterns suggests that inland western white pine is fairly uniform. However, seedlings from high-elevation parents (generally 1,375 m or higher) were significantly shorter than those of low- and mid-elevation parents in some low- or mid-elevation tests. Even when elevational effects were not significant very few high elevation families were among the tallest. Growth results to date indicate that only two seed zones are needed in north Idaho--a low zone and a high zone generally separated at 1,375 m. Within the lower zone, trees with good growth potential can be found in nearly all stands.

CONTENTS

INTRODUCTION

Western white pine (*Pinus monticola* Dougl.) has long been an important component of the forests of north Idaho, but the introduction of blister rust (*Cronartium ribicola* J.C. Fisch. ex Rabenh.) and the ensuing losses to the disease has dissuaded land managers from attempting to manage the species. Now, as efforts to produce trees resistant to the disease show some promise, land managers are again beginning to include white pine in their regeneration programs. In the long run, the natural selection process should produce trees with sufficient blister rust tolerance or resistance to allow natural regeneration. For the present and near future, however, planting of resistant seedlings will be needed.

The production and utilization of resistant planting stock involves much more than just securing an adequate level of resistance in a sufficient proportion of the seedlings to be planted. The manager wants the seedlings to survive and grow on the sites he wants to plant and he wants them to grow at a rate which fully utilizes the potential of the site. Attempting to achieve such an ideal match of seedling and site is not a realistic goal at present because of our lack of knowledge of both trees and sites. Also, the costs to approximate such a match would likely exceed the returns from greater yields as the limits of the site are approached. The realistic goal for the present is to attempt to achieve a balance that incorporates our present biological information and approximate costs with expected growth rates and economic returns.

This paper will discuss past and current investigations into variation in growth of western white pine in nursery trials and several experimental plantations. The conclusions of the research will then be translated into guidelines for distributing seed from orchards that have already been established and to evaluate alternative designs for future seed orchards.

PRIOR RESEARCH

During the past 20 years several reports on variation in western white pine have appeared. Squillace and Bingham (1958) opened the series with a report of "localized ecotypic variation" based on germination and early growth of seedlings from quite different sites within a small area. They concluded that seedlings from trees growing on poorer sites were shorter in nursery trials than those from trees growing on better sites. Germination of seeds in a sucrose solution was higher for poorer site trees than for better site trees. In a low-elevation nursery, seedlings from low-elevation trees were taller than those from high-elevation trees, but when transplanted to a high-elevation test site the seedlings from the high-elevation trees grew faster. On the basis of those findings, and other considerations, the applied program to produce blister rust resistant western white pine was subdivided into three elevational zones or breeding units with a seed orchard planned for each. These zones were: (1) Low-elevation--areas below 1,000 m; (2) mid-elevation--areas between 1,000 m and 1,250 m; and (3) high-elevation--areas above 1,250 m.

Progeny of many of the same parents used in the above studies were outplanted to two additional sites for long-term evaluation. Rehfeldt and Steinhoff (1970) found that at age 14 average growth at the two sites differed significantly and that the growth of individual progenies differed significantly but the average growth of progenies from different localities did not differ significantly.

In order to obtain materials representative of a broader range of sites, Barnes (1967) systematically collected seed and recorded data from trees in a series of elevational plots along several north Idaho streams. He reported finding significant differences in periodic annual growth rate and branch angle that were related to elevational differences along one transect. Trees in plots from 760 m elevation to 1,220 m grew at essentially the same rate, but those from 1,400 m and above were slower growing. Branch angle changed progressively from low to high plots, with trees in the lower plots having more ascending branches and those in the higher plots having more nearly horizontal branches. Differences among plots were also found in needle length and cone scale length and width, but the variation did not follow a pattern related to elevation.

Some of the seed collected by Barnes was sown in a nursery trial in Michigan. After 4 years of growth, total height of seedlings representing the various elevational and latitudinal collection areas did not differ significantly (Townsend and others 1972). Seasonal growth rates differed, but they did not fit into a pattern related to elevation or latitude. At a very low light level (130 lux) low-elevation seedlings (640 m) were less efficient photosynthetically than higher elevation seedlings (1,065 m and 1,585 m), but at higher light levels (425 and 615 lux) differences were not apparent.

MATERIALS AND METHODS

This report will present and integrate results from five studies, as follows:

1. *Elevational study*.--This study was started to further investigate the effects of elevation (as indicated in Squillace and Bingham 1958) and possibly latitude on seedling growth. Wind-pollinated seed for the test was collected from individual trees in plots (stands) at 120 m to 180 m (mostly 150 m) elevational intervals in several stream drainages in north Idaho. Although the collection locations were often along streams, they were kept out of the stream bottoms where cold air drainage effects are common. Five trees from each of 1 to 3 plots per elevation and drainage were included, for a total of 225 trees in 45 plots (fig. 1). In the Trestle Creek drainage, the plots within an elevational zone were close together (mostly within 0.5 km), but in the other areas the plots were often several kilometers apart. Further details of plot location for the Trestle Creek drainage were presented by Barnes (1967).

A nursery test for early growth and seedling traits was conducted for 3 years at Moscow, Idaho. The seed were sown at a spacing of 5x10 cm in 10-tree row plots in 4 replicates. The growing medium was a mix of forest soil, sand, and peat moss in equal proportions. The beds were watered and fertilized as needed to maintain satisfactory growth. Annual height measurements were taken after growth was completed.

Field plantations have been established at the Priest River Experimental Forest (PREF) and near the North Fork of the Clearwater River on the Canyon Ranger District (Canyon) (fig. 1). In each area, 3 test plantations were established with an elevational separation of 300 m (800 m, 1,100 m, and 1,400 m at PREF and 900 m, 1,200 m, and 1,500 m at Canyon). Aspect of the sites ranges from northeast to northwest. The field tests contain representatives of nearly all the seed collection areas and elevation zones but do not contain representatives of all the plots within elevational zones.

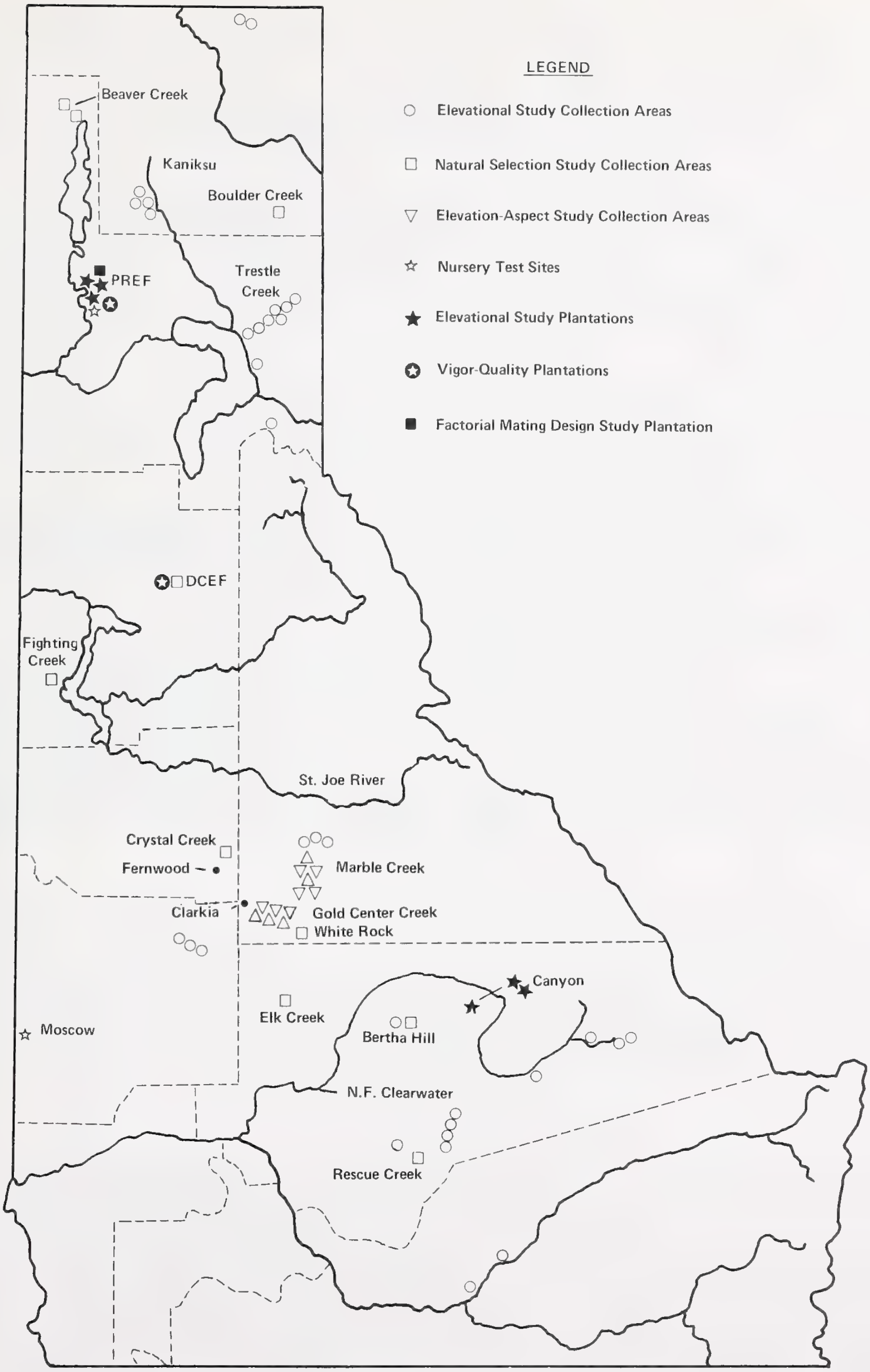

Figure 1.--Seed collection areas and test sites for the various white pine studies in north Idaho.

An additional plantation (Ida Creek) adjacent to the low PREF site contains representatives of all the families included in the nursery test. The seedlings (3-0 stock) were planted in 1971 at a spacing of 1.8 m in 4-tree row plots replicated 5 times. They were all measured at age 4 (the end of the first field growing season). The Ida Creek plot was measured again at age 6 and age 8 and the other plantations were measured at age 7.

2. *Elevation-aspect study*.--An attempt was made to evaluate the effects of environmental factors related to both elevation and aspect in this test. Study areas were located in two drainages (Marble Creek and Gold Center Creek) near Clarkia, Idaho (fig. 1). They consisted of a series of paired plots at 950 m, 1,175 m, and 1,400 m in each drainage. One member of each elevational pair had a southern exposure and the other a northern exposure. In each plot, four trees were chosen to be seed parents and three to be pollen parents. Pollen from the three trees on a plot was mixed. Each seed tree was pollinated with four pollens, the local pollen mix plus pollens from the low-, mid-, and high-elevation north-aspect Marble Creek plots. For this portion of the study seeds from the four trees on a plot were combined for each pollen type. Results of crosses among individual trees within plots are being reported elsewhere (Rehfeldt, in press).

A nursery test was conducted at Moscow for 3 years. Seed was sown in plots consisting of 2 rows of 18 planting spots. Spacing was 5x10 cm. There were two replicates.

The seedlings have been outplanted to forest test sites but have not yet been measured.

3. *Natural selection study*.--This test was originally designed for studying blister rust resistance, but its potential for studying growth variation within and between stands was soon recognized. Ten stands were located and wind-pollinated seed collected from 50 trees in each. Three of the stands are from the same general areas represented by most of the trees in the vigor-quality study (No. 5 below) and one stand corresponds to one of the elevational study collection areas (fig. 1). Six of the stands fall within the low-elevation zone of the applied program (below 1,000 m) and four within the high zone (above 1,250 m).

The seedlings were started and grown for one season in a greenhouse in 5x5x15 cm tar paper plant bands in a soil, sand, peat moss mix. They were then transplanted, still in the plant bands, in the PREF nursery site. Eight seedlings of each of the 497 families were planted at random in each of 3 replicates. Spacing was 10x10 cm. The seedlings were given routine nursery care. They were inoculated with spores of the white pine blister rust fungus (*Cronartium ribicola*) at age 3 and measured at age 4, before the disease had any noticeable effect on growth.

Other seedlings from the same families have been outplanted to a field test site but have not been measured yet.

4. *Factorial mating design study*.--This is another test that can serve both blister rust resistance breeding and growth analysis. Three factorial mating designs, one each for the low-, mid-, and high-elevation zones, were established. Four trees were used as pollen parents and approximately 40 trees were used as seed parents in each zone. However, the majority of the seedlings in the test plantation represent only 40 families from each zone (4 pollen parents x 10 seed parents).

The seedlings were grown for 6 years in replicated row plots at the Moscow nursery. They were inoculated for studying white pine blister rust resistance. No growth measurements were taken in the nursery.

The survivors from the blister rust testing were outplanted to a low (750 m), nearly flat site at PREF in 1971. A variable number (average 15) of seedlings per family were planted as single tree plots at random throughout the plantation. Growth during the 3-year period from 1973 to 1975 and height in 1976 have been measured.

5. *Vigor-quality study*.--This is the oldest of the five studies. It was started during the early stages of the program to produce blister rust resistant western white pine (Squillace and Bingham 1954). Excess seed from the program was used for this study to investigate the heritability of growth and quality traits. The parents of many of the seedlings grow in the Crystal Creek drainage near Fernwood, Idaho, at an elevation of about 870 m (fig. 1). A few others grow at three additional low sites within 45 km. Four candidates from the White Rock area at an elevation of 1,525 m near Clarkia, Idaho, were also included. Squillace and Bingham's (1958) report of "localized ecotypic variation in western white pine" was based on other seedlings of many of these same families.

Seedlings (2-1) for the 1955 outplantings were grown in a nursery in Missoula, Mont. All the others were grown in Spokane, Wash. The seedlings were not measured in the nurseries.

Three plantations were installed during the years from 1955 through 1959. Data from the 1955, 1956, and 1957 plantings at PREF and Deception Creek Experimental Forest (DCEF) are included in this report. The PREF plantation is located on a moderate (10-25 percent) north to northwest-facing slope at an elevation of 790 m. The DCEF plantation is on a steep (30-50 percent) north-facing slope at 1,110 m (fig. 1). Seedlings (mostly 2-1 transplants) were planted at a spacing of 2.4 m in 8-tree row plots in three replications at each site. Competition from native vegetation has been reduced by weeding and brush cutting at irregular intervals. The trees have been measured several times--most recently when all had been in the field for 16 years.

RESULTS

Elevational study.--The most striking feature of the nursery results is the general lack of patterns in the variation observed (table 1). Although the amount of variation present was large, much of it was related to differences among the offspring of a single tree or among the trees within a stand. This may be seen in the proportion of variance attributable to the various sources and the common significance of the "trees within stands" mean squares (table 2 and Appendix table 15). Because of the magnitude of the within-stand variation, the differences among stands, elevational zones, or geographic areas were seldom statistically significant.

Seed weight did not differ significantly from one area to another and only within the Clearwater drainage were there significant differences among elevational zones. There, seed from the higher elevation trees was lighter than that from the lower trees, with a rather consistent gradation between.

Seeds from the Trestle Creek area germinated sooner than those from other areas, but there was no pattern to the variation within areas. Whether the germination differences are inherent or were related to cone collection time or subsequent handling is unknown. Time of germination was closely related to first-year seedling height and some of the effect was still detectable at the end of the third year. All data for seedlings germinating more than 21 days after the start of germination were excluded from these and the following analyses.

Table 1.--*Elevational study nursery data*

Seed collection area	Elevation	Seed weight	Germination time	1st year height	Adjusted 1st year height[2]	2nd year height[3]	2nd year height	3rd year height	Adjusted 3rd year height[4]	Cotyledon No.	Cotyledon length	Bud burst	Bud set	Needle length
	Meters	*mg*	*Days*[1]	- - - - - -	- - - - - -	- - - -	*Millimeters*	- - - -	- - - -	- - - -	- - - -	*Days*[5]	*Days*[6]	*mm*
Clearwater	455	21.5	14	41	41	67	12	193	203	7.7	20			59
	760	19.7	14	39	40	68	13	203	218	7.7	20			57
	915	19.2	13	43	45	75	15	212	215	8.1	20			58
	1065	18.8	14	40	43	68	12	184	194	7.6	20			58
	1220	17.1	12	41	43	68	16	206	216	7.6	19	2.8	8.0	60
	1370	19.0	13	36	42	61	19	182	203	7.5	18			56
	1585	15.6	15	34	41	60	19	195	220	7.8	18			56
	$\bar{x}$	18.1	13	40	43	67	15	199	212	7.7	19			58
Trestle	640	18.6	10	45	44	78	13	217	214	7.8	20	3.3	9.3	57
	760	18.4	8	48	45	81	10	227	216	7.9	19	3.3	10.3	61
	915	19.2	6	51	46	87	9	234	214	7.9	20	2.6	9.3	62
	1065	18.7	9	46	44	77	13	223	217	8.1	20	2.8	8.9	59
	1220	18.0	8	48	46	81	9	223	212	8.1	20	3.1	9.7	61
	1400	17.8	9	45	44	76	14	221	219	7.9	20	3.6	10.4	61
	1585	18.8	10	44	43	76	10	211	211	7.9	20	2.2	7.8	61
	$\bar{x}$	18.5	9	47	45	80	11	223	215	7.9	20	3.0	9.5	60
St. Joe	915	19.0	9	48	46	80	11	222	215	7.7	20			60
	1065	18.2	10	46	46	76	10	212	209	7.9	20			61
	1220	18.0	12	41	43	70	13	212	221	8.1	19	1.8	7.8	61
	$\bar{x}$	18.4	10	45	45	75	12	215	215	7.9	20			61
Kaniksu	915	16.9	16	36	38	62	12	166	173	8.0	18			53
	1065	17.7	12	40	40	71	16	207	199	7.8	20			56
	1220	17.9	13	37	37	63	15	189	194	7.7	19	3.2	8.3	55
	$\bar{x}$	17.6	13	38	38	66	15	192	192	7.8	19			55

[1]Days after May 30, 1968.
[2]First year height adjusted for seed weight and germination time effects.
[3]Does not include lammas growth.
[4]Third year height adjusted for first year height differences.
[5]Days after April 27, 1970.
[6]Days after May 2, 1970.

Table 2.--*Percentages of total variation attributable to various sources for several seedling traits in the elevational study nursery test*

Source of variation	Degrees of freedom	Traits										
		Seed weight	Germination time	1st year height	Adjusted 1st year height[1]	2nd year height	2nd year lammas	3rd year height	Adjusted 3rd year height[2]	Needle length	Cotyledon No.	Cotyledon length
		Percent of total variation										
Trestle Creek vs. Clearwater--All Elevation Zones from 455 m to 1585 m												
Replications[3]	3		5.4	2.9	0.6	2.8	2.9	4.4	2.3	4.0	0	0.7
Areas	1	0	24.4**[4]	18.6**	2.1*	18.9**	7.1**	10.6**	0	1.5*	4.2**	3.9*
Elevation zones within area	13	12.6	1.1	2.5	0	2.1	2.0	0.4	0.1	0.6	0.7	3.2*
Stands within elevation & area	18	0	3.3	1.6	2.1	2.7	3.9*	2.8*	2.6**	0.6	0	0.3
Trees within stand, elev., & area	130	87.4	24.8**	24.1**	14.4**	19.5**	5.0**	10.9**	2.4*	5.3**	18.2**	17.3**
Experimental error[5]	471		12.4	9.3	16.9	12.2	30.9	23.4	26.1	24.5	4.2	11.7
Within plot[6]			28.6	41.0	63.9	41.8	48.2	47.5	66.5	63.5	72.7	62.9
Clearwater, St. Joe, Trestle and Kaniksu but only 915 m, 1065 m, and 1220 m Elevation Zones												
Replications[3]	3		3.7	1.9	0.4	2.5	4.5	2.3	1.2	4.8	0.1	1.7
Areas	3	0	13.2**	12.3**	1.9	10.5*	3.9	5.3	0	4.5*	0.2	0
Elevation zones within area	8	0	0.6	2.3	0	3.4	2.3	3.5	3.7	0	1.0	0
Stands within elevation & area	11	1.8	0	0	3.7	1.3	2.0	2.5	2.4*	3.2**	4.8*	6.5*
Trees within stand, elev., & area	92	98.2	28.9**	29.0**	17.5**	21.4**	3.2*	13.6**	3.9**	1.7	15.7**	21.5**
Experimental error[5]	334		21.6	10.3	11.7	14.3	30.5	22.0	20.4	21.7	5.3	9.5
Within plot[6]			32.0	44.2	64.8	46.6	53.6	50.8	68.4	64.1	72.9	60.8

[1]First year height adjusted for seed weight and germination time effects.
[2]Third year height adjusted for first year height differences.
[3]Only 2 replicates were used for cotyledon number and length analyses so degrees of freedom for replicate and error were adjusted accordingly.
[4]* and ** indicate significance at the 5 percent or 1 percent level, respectively. For detailed analyses of variance see Appendix Table 15.
[5]Includes all interaction terms involving replication.
[6]Pooled estimate from 30 to 50 plots with 5 to 10 seedlings per plot.

When the raw data for the first-year height were analyzed, the mean squares associated with areas were highly significant. This was true for both comparisons, for example, between Clearwater and Trestle where the broadest elevational range was sampled, and among all areas but utilizing only the 915 m, 1,065 m, and 1,220 m elevation zones (those common to all areas). The early germinating Trestle seedlings were taller than the later germinating seedlings from the Clearwater and Kaniksu areas. However, when first-year heights were adjusted for seed weight and germination time the variability related to areas was much reduced. The comparison of all areas using the middle elevational zones showed no significant differences, but the Trestle Creek and Clearwater areas differed at the 5 percent level when all elevation zones were considered. These adjusted means differed by only 2 mm--approximately 4.5 percent of the mean.

Subsequent height measurements taken in the second and third years followed a pattern similar to first-year height. Analyses of the raw data showed significant differences among trees within stands and among areas. There were few or no significant differences among elevations within areas or stands within elevations. When the data were adjusted to take into account first-year height differences, second- and third-year height differences among areas were not significant. In other words, the Trestle Creek seedlings, which germinated early and were tallest at age 1, were still tallest at age 3 but relative to their height at age 1 they had not grown as much as seedlings from the Clearwater and Kaniksu areas.

Whether such adjustments should be made depends on the cause of the germination time difference. If it is the result of genetic differences, no adjustment should be made. If the difference resulted from cone collecting or seed processing timing or techniques, then the adjustments would be appropriate. In the absence of information to indicate genetic differentiation of germination time, I favor use of the adjusted data.

If the range of 120- to 180-m elevational zones is combined across areas to form three broader zones called low, mid, and high (<1,000 m, 1,000-1,250 m, >1,250 m) like the classification in the following studies, then seedlings of the low zone were tallest and those of high zone were shortest. At age 3, heights by zone were: low - 220 mm, mid - 211 mm, high - 207 mm. These means did not differ significantly.

Secondary leaf length (mature third-year leaves) was the only other trait in which differences among areas were significant. Within the Trestle Creek and Clearwater areas, differences between trees within stands were significant but for the other areas they were not. Stand-to-stand differences within an elevational zone were sometimes large but seemed to occur at random. Significant cotyledon differences--number and length--were confined to trees within stands and stands within elevational zones.

Bud burst at the start of the third year did not differ significantly among stands, elevations, or areas (table 3). The highest elevation source from Trestle Creek was the first to break bud but the next to highest source was last. All buds broke within a 2-week period and most within a 5-day period. The newly emerging leaves were rapidly separated and in from 10 to 14 days the tip of the new bud was distinguishable. At that time the seedlings were classified as having set buds even though stem elongation and external bud development continued for nearly a month. No significant differences in bud set time were observed except among trees within stands.

The seedlings were 7 years old and had been in the field plots for 4 years when they were last measured. Overall survival of seedlings of Clearwater origin was about 10 percent less than that of Trestle seedlings with the differences greatest at the Canyon series of test sites. However, survival differences so far do not clearly indicate differences related to area or elevation of origin or their interactions with test site conditions. Average height ranged from 54 cm at the best site, low PREF, to 34 cm at the poorest, high PREF (table 4).

Table 3.--*Analyses of variance and percent of total variance for third-year bud burst and bud set in the elevational study nursery test*

Area	Source	d.f.	Bud burst: Mean square	Bud burst: % of total variation	Bud set: Mean square	Bud set: % of total variation
Trestle Creek (640 to 1585 m plots)	Replications	3	63.1	2.8	163.5	3.4
	Elevation	6	26.4	0.6	79.7	1.2
	Plots within elevations	7	20.8	0.9	48.0	0
	Trees within plots within elevations	28	12.1	0	52.6**[2]	8.1
	Experimental error[1]	84	16.8	29.6	20.9	4.9
	Within plot	672	5.2	66.1	16.1	82.4
1220 m plots from Clearwater, St. Joe, Trestle Creek, Kaniksu	Replications	3	14.2	2.1	104.4	5.5
	Areas	4	38.7	7.8	104.0	2.9
	Trees within areas	10	13.3*	6.3	68.7**	11.9
	Experimental error[1]	42	6.5	9.0	20.2	5.0
	Within plots	240	4.1	74.8	15.1	74.6

[1]Includes all interaction terms involving replication.
[2]* and ** indicate significance at the 5 percent and 1 percent level, respectively.

At the individual test sites the results of the analyses of total height are very similar to those from the nursery trial (table 5 presents the results for only the most variable series of sites, i.e., PREF). Most of the variability is related to differences among the families representing individual trees within stands. The variability within plots (i.e., among seedlings of the same family) is also large--nearly equaling that among plots (experimental error). This result indicates that within-family variation is large or microsite differences exert strong influences or that both are important contributors. The variation related to area of seed origin or to elevational zones within areas was very small in comparison and usually not significant.

The Trestle Creek seedlings were taller than those from the Clearwater at the low and high sites at both PREF and Canyon, but the Clearwater seedlings were as tall or taller at the mid-elevation sites. No pattern could be seen in the variation in height among seedlings related to the various elevational zones within areas. Neither was there any correspondence between elevational zones in the different areas. For example, seedlings from the highest Clearwater collections grew well at most test sites but those from the highest Trestle Creek collection grew poorly. As a group, the seedlings from

Table 4.--*Height of seedlings at age 7 in the elevational study field tests*

Seed collection		Test region and site								Overall
		Canyon[1]				PREF[2]				
Area	Elevation	Low	Mid	High	$\bar{x}$	Low	Mid	High	$\bar{x}$	$\bar{x}$
	Meters	*Centimeters*								
Clearwater	760	37	40	38	38	55	39	30	43	41
	915	42	40	37	40	53	38	34	42	41
	1065	37	41	33	37	51	35	32	40	38
	1220	41	41	35	39	50	36	33	40	40
	1370	40	43	35	40	53	34	32	41	41
	1585	44	43	38	42	54	36	34	43	42
	$\bar{x}$	40	42	36	39	53	37	33	41	40
Trestle	760	42	42	36	40	53	37	35	42	41
	915	40	42	42	41	53	35	34	41	41
	1065	45	41	38	41	57	36	36	44	43
	1220	39	41	35	39	55	39	35	44	42
	1400	42	40	37	40	56	35	34	43	41
	1585	39	39	37	38	54	37	34	42	40
	$\bar{x}$	41	41	38	40	55	37	35	42	41
Overall	$\bar{x}$	41	41	37	40	54	37	34	42	41

[1]Canyon Ranger District: low = 900 m, mid = 1,200 m, high = 1,500 m.
[2]Priest River Experimental Forest: low = 800 m, mid = 1,100 m, high = 1,400 m.

Table 5.--*Analyses of variance and percent of total variation for height of 7-year-old seedlings in the elevational study sites at PREF*

Source	d.f.	Low site		Mid site		High site	
		Mean square	% of total variation	Mean square	% of total variation	Mean square	% of total variation
Replicates	4	134	0.0	114	0.0	269	0.4
Area	1	1,013*[1]	0.8	5	0.0	793*	1.0
Elevation within Area	10	255	0.0	155	0.4	68	0.0
Rep * Area & Elev (Error 1)	44	240	2.4	131	6.0	192	6.4
Trees within Elev & Area	47	350**	6.6	140**	7.1	220**	8.2
Rep * Tree (Error 2)	170	177	5.3	79	5.2	95	2.4
Within Plot	565	149	84.9	70	81.3	88	81.6

[1]* and ** indicate significance at the 5 percent and 1 percent levels, respectively.

the 760 m Clearwater collection grew poorly at the low- and mid-elevation sites at Canyon but well at the high site. In contrast, at PREF they grew well at the low- and mid-elevation sites but poorly at the high site. However, these fluctuations are rather small--only 2 or 3 cm (5 percent) above or below the site mean--and, so far at least, appear more accidental than the result of specific tree-site interactions.

When the overall variability across sites within test regions was analyzed (table 6), the variation associated with trees within elevational zones was still predominant over that for elevational zones or areas. The site x tree interaction effect was significant at PREF. When the tree mean squares were tested against this interaction term rather than the error mean squares, the tree effects were significant at only the 5 to 10 percent level.

The average height of the seedlings over the three sites at PREF was essentially the same as that for the Canyon sites but the range at PREF was much greater. Neither group of sites shows a typical spread of conditions for the area. At PREF, growth and survival at the mid-elevation site has been reduced due to poor site quality and residual competition resulting from site preparation problems. At Canyon, the low site trees suffered from similar site preparation problems.

Table 6.--*Analyses of variance and percent of total variation for height of 7-year-old seedlings of the elevational study combined over sites at Canyon and PREF*

Source	d.f.	Canyon		PREF	
		Mean square	% of total variation	Mean square	% of total variation
Test sites[1]	2	3,829	4.9	106,038	52.2
Replicates within sites	12	302	1.1	172	0
Area	1	127	0	493	0
Site * Area	2	177	0	658	0.4
Elevation within Area	10	290	0.2	278	0
Site * Elevation	20	168	0	101	0
Rep * Area & Elev (Error 1)	132	149	2.8	188	2.0
Trees within Elevations and Areas	48	212*[2]	1.9	283	0.7
Site * Tree	94	142	2.1	213**	2.8
Rep * Tree (Error 2)	500	111	0	119	1.5
Within Plot	[3]	116	87.0	109	40.4

[1]Low, mid, and high elevation.

[2]* and ** indicate significance at the 5 percent and 1 percent level, respectively.

[3]At Canyon d.f. = 1,001, at PREF d.f. = 1,694.

In the Ida Creek plantation adjacent to the low PREF plot, where all the families included in the nursery test were planted, area differences were significant at age 4 but became less important and nonsignificant by age 6. Actually, the difference between area means remained nearly constant (2 cm between Clearwater and Trestle Creek), but as a percentage of total height that difference dropped from 7 percent at age 4 to only 2 percent by age 8.

When all the families were grouped as to low, mid, or high origin, as with the nursery data, then height at age 8 decreased from low to high elevation (101, 100, and 98 cm, respectively). These differences were not significant and that result is contrary to the findings in the adjacent low plot where the high-elevation seedlings were slightly taller than the low- and mid-elevation seedlings.

Elevation-aspect study.--Height at the end of the third year in the nursery (table 7) did not differ significantly among drainages, elevations, aspects, or pollen types. Rehfeldt (in press) also found that at age 6 differences among drainages, elevations, or aspects were not significant when tested by individual control-pollinated families within plots. Seedlings from south aspect plots in this study were generally taller than those from north aspect plots in the same drainage and at the same elevation. This was also the result for the Gold Center Creek drainage in Rehfeldt's study, but seedlings from north and south aspect Marble Creek plots were essentially equal in height.

Table 7.--*Third year height of seedlings in the elevation-aspect study*

Seed parent location			Pollen source						
			Marble Creek north aspect						
Drainage	Elevation zone[1]	Aspect	Low	Mid	High	Local	$\bar{x}$	$\bar{x}$	$\bar{x}$
			Height (millimeters)						
Gold Center Creek	Low	North	71	71	75	64	70	75	
		South	67	84	80	87	79		
	Mid	North	75	73	83	--	80	83	78
		South	76	69	87	108	85		
	High	North	73	85	65	72	74	76	
		South	71	73	84	84	78		
Marble Creek	Low	North	--	--	88	85	86	85	
		South	84	87	77	87	84		
	Mid	North	74	--	75	79	76	78	81
		South	84	78	74	84	80		
	High	North	--	--	--	75	75	78	
		South	64	84	87	84	80		
		$\bar{x}$	74	78	80	83			

	$\bar{x}$		$\bar{x}$
L	79	N	76
M	80	S	81
H	78		

[1]Low = 950 m, mid = 1,175 m, high = 1,400 m.

Overall, the seedlings produced by local pollen were taller than those produced with pollen from the north aspect plots but the differences were not significant. For the south aspect plots, local pollens produced seedlings significantly taller than those produced by the north aspect pollens. On the north aspect plots, pollen from one of the other north plots usually produced taller seedlings than did local pollen.

Among the north aspect Marble Creek plots, seedlings from the low plot were tallest but pollen from the plot produced the shortest seedlings when used on trees in other plots. For the high plot, the results were the opposite (seedlings from the plot trees were short but pollen from the plot produced tall seedlings when used elsewhere). Such reversals were probably the result of large amounts of within-plot variability coupled with the small numbers of trees chosen to be pollen or seed parents in any one plot rather than resulting from plot interactions.

Natural selection study.--In this study only growth during the fourth growing season was measured and analyzed (tables 8 and 9). The mean growth of the 4 high-elevation stands was significantly less than that of the 6 low-elevation stands (10.8 cm vs. 11.8 cm). However, the best high-elevation stands grew more than the poorest low-elevation stand. Among the 6 low-elevation stands, the 4 fastest growing ones differed significantly from the slowest growing one.

Even though the differences between elevational groups and among stands were significant, the bulk of the genetic variation (61 percent) was associated with differences among trees within stands. Of the remaining genetic variation, 28 percent was due to elevational differences and 11 percent to differences between stands within elevational zones. Overall, 62 percent of the variation was related to variation among seedlings from the same tree, 2 percent to block interactions, and 36 percent to genetic variation.

Table 8.--*Fourth year height growth of seedlings in the natural selection study*

Stand	Elevational zone[1]	Growth	Range of family means	Number of families in top 10%
		- - - - *Centimeters* - - - - -		
Beaver Creek pole	Low	12.4 a[2]	8.8-15.4	12
Crystal Creek	Low	12.2 a	9.3-14.9	9
Beaver Creek mature	Low	12.2 a	8.3-16.1	12
Montford Creek	Low	11.9 ab	9.4-15.2	7
Fighting Creek	Low	11.7 abc	9.3-16.4	3
Rescue Creek	High	11.4 bcd	8.2-14.8	3
Bertha Hill	High	11.1 cd	7.8-14.7	1
Elk Creek	Low	10.9 cd	8.2-13.7	1
Boulder Creek	High	10.8 cd	8.0-14.9	2
White Rock	High	10.6 d	7.5-13.0	0

[1]Low = below 1,000 m, high = above 1,250 m.
[2]Means not having a letter in common differ at the 5 percent level of significance.

Table 9.--*Analysis of fourth year height growth of seedlings in the natural selection study*

Source	d.f.	S.S.	M.S.	F	Variance component	Percentage of total variance
Block	2	622	311		0.09	0.005
Stand	9	3260	362	7.9*[1]	.35	.02
Elevation	1	1728	1722	9.0*	.24	.014
Stand (Elev)	8	1538	192	4.2**	.11	.006
Block*Stand	18	825	46		.11	.006
Tree (Stand)	487	15468	32	2.1**	.95	.06
Block* Tree(Stand)	969	14727	15		.00	.00
Within family	7054	108648	15		15.40	.91

[1]* and ** indicate significance at the 5 percent or 1 percent level, respectively.

Factorial mating design study.--Seedlings from crosses among mid-elevation (1,000-1,250 m) trees grew the most between ages 8 and 11 and were tallest at age 12 (table 10). As a group they differed significantly from both the low- and high-elevation families in growth and from the high-elevation families in height (table 11). The low- and high-elevation means did not differ significantly.

Approximately 90 percent of the total variability was associated with differences among seedlings within families and environmental effects. Of the remainder, 67 percent of the variability in growth and 80 percent of the variability in height was associated with differences among families within elevation zones and only 33 percent or 20 percent associated with differences among elevation zones.

Although the mid-elevation group was tallest as a whole, the tallest family was from the low-elevation group. The low group also had a higher ratio of better families than either the mid- or high-elevation groups (1/5 vs. 1/8 and 1/36 families in the top 10 percent, respectively).

Table 10.--*Growth and height of seedlings in the factorial mating design study*

Elevational zone[1]	Growth between ages 9 and 11	Height age 12
	- - - - *Centimeters* - - - -	
Low	44	101
Mid	48	106
High	45	99

[1]Low = below 1,000 m, mid = 1,000 to 1,250 m, high = above 1,250 m.

Table 11.--*Analysis of growth and height in the factorial mating design study*

Source	d.f.	M.S.	Variance: Value	Variance: Percentage of total
Growth between ages 9 and 11				
Elevational zone	2	2206**[1]	4.3	1.4
Family (Elev.)	95	432**	8.6	2.7
Within Family	1382	301	301.4	95.9
Height age 12				
Elevational zone	2	7710*	14.8	1.9
Family (Elev.)	95	1621**	59.9	7.6
Within Family	1382	716	715.7	90.5

[1]* and ** indicate significance at the 5 percent and 1 percent level, respectively.

Vigor-quality study.--The main reasons for including this study are that the trees are old enough to have reached a stable growth pattern and to show how the results have changed over the years. The mean height of the low elevation families has been consistently greater than that of the high elevation families (table 12). Significant differences during the early years, ages 4 to 8 (table 13), probably resulted from the combination of a carryover of nursery differences (Squillace and Bingham 1958) and limited competition on the recently cleared sites. By age 8 competition from the native vegetation was increasing and until age 12 or 14 when most trees were taller than the brush all families probably grew less than their potential. That competition probably was also responsible for keeping the differences between elevational zones relatively constant while between-family and within-plot variation increased more rapidly. After the trees overtopped the brush, their growth potential could be realized more fully. Then height and growth rate differences between the low and high zones again became significant.

During the last 3 years, differences between the low and high families continued to increase but at a slower rate. At the same time, differences among families within elevational zones became larger, resulting in a decrease in the significance of the elevational difference. The elevational difference exhibited in this study is probably larger than would be found if more stands, and trees, had been sampled. The results from the natural selection study reported earlier indicate that trees of the high elevation stand (White Rock) used in this study produce the slowest growing seedlings of the high elevation stands sampled. Also, most of the low elevation trees are from a stand (Crystal Creek) that produces some of the fastest growing seedlings. Thus, by chance, these results and those of Squillace and Bingham (1958) contrast the poorest high trees we have studied with some of the best low trees. Even then, the best high family has been taller than several of the low families.

Height growth of the young trees at the two sites was essentially equal until age 10 and did not differ significantly until age 16. Interactions between sites and elevational origin of the seedlings were essentially nonexistent even after the height difference between the sites became highly significant.

Table 12.--*Height and growth of young trees in the vigor-quality study at various ages*

Height at age		DCEF		PREF		Combined	
		Low elevation families[1]	High elevation families[2]	Low elevation families	High elevation families	Low elevation families	High elevation families
		Meters					
4	$\bar{x}$	0.11	0.09	0.11	0.09	0.11	0.09
	Range	0.08-0.15	0.09-0.10	0.08-0.13	0.05-0.13		
8	$\bar{x}$	0.61	0.56	0.62	0.51	0.62	0.54
	Range	0.51-0.72	0.46-0.62	0.41-0.71	0.31-0.58		
10	$\bar{x}$	0.97	0.91	0.94	0.85	0.95	0.88
	Range	0.76-0.12	0.76-1.00	0.67-1.10	0.58-1.00		
12	$\bar{x}$	1.6	1.5	1.8	1.6	1.7	1.6
	Range	1.3-1.9	1.3-1.7	1.3-1.9	1.1-1.8		
14	$\bar{x}$	2.5	2.2	2.9	2.5	2.7	2.4
	Range	2.0-3.0	2.0-2.5	2.2-3.1	2.1-2.7		
16	$\bar{x}$	3.5	3.0	4.1	3.6	3.8	3.3
	Range	3.0-4.1	2.8-3.3	3.4-4.3	2.8-4.1		
19	$\bar{x}$	5.4	4.7	6.3	5.8	5.9	5.2
	Range	4.6-6.1	4.0-5.1	5.2-6.8	4.7-6.5		
Growth between ages							
		Meters/year					
12 & 16	$\bar{x}$	0.47	0.38	0.58	0.50	0.52	0.44
	Range	0.38-0.53	0.32-0.42	0.51-0.60	0.42-0.57		
16 & 19	$\bar{x}$	0.63	0.56	0.75	0.75	0.69	0.64
	Range	0.57-0.69	0.46-0.61	0.60-0.85	0.68-0.79		

[1]Average elevation 925 m.
[2]Average elevation 1,525 m.

Table 13.--*Analysis of the effect of elevation of seed origin and test site on height and growth of trees in the vigor-quality study*

Trait measured	Test site and source of variation				
	DCEF	PREF	Combined		
	Elevation zone[1]	Elevation zone[1]	Test site[2]	Elevation zone[1]	Site X elevation[3]
Height at age:					
4	6.56*[4]	4.77*	<1	7.31*	<1
8	1.93	4.84*	<1	7.64*	1.86
10	<1	1.48	<1	2.06	1.11
12	1.96	2.39	1.53	3.46	<1
14	4.12	6.16*	7.14	8.84*	<1
16	8.98**	7.03*	12.3*	13.4**	<1
19	8.15	4.98	31.0**	10.2**	<1
Growth between ages:					
12 & 16	17.6**	14.1**	35.4**	30.0**	<1
16 & 19	5.04*	<1	109.7**	4.04	<1

[1]"F" value resulting from the comparison $\frac{\text{Elevation zone mean square}}{\text{Trees within elevation zone mean square}}$.

[2]"F" value resulting from the comparison $\frac{\text{Test site mean square}}{\text{Rep within site mean square}}$.

[3]"F" value resulting from the comparison $\frac{\text{Site X elevation mean square}}{\text{Rep within site X elevation mean square}}$.

[4]* and ** indicate significance at the 5 percent and 1 percent level, respectively.

Although the differences among families within elevational zones were large (the range between tallest and shortest varied from 10 percent to 35 percent of the mean at different ages), the differences were seldom significant because of the small numbers of families tested and large amounts of within-family variability. The variance attributable to family-by-site interactions was small and nonsignificant except at age 8. The question of family-by-site interactions is even more confusing if one also includes year of planting. A few families were planted in each of 2 or 3 years. For some of these families the seedlings planted in 1955 may have grown faster at PREF than DCEF but those planted in 1957 grew faster at DCEF or vice versa.

DISCUSSION AND CONCLUSIONS

To date all of our studies with western white pine indicate that the majority of the variation which might be utilized in a tree improvement program is related to the differences among individual trees within stands rather than to differences among stands, elevational zones, or geographic areas. When stand or area differences were significant, there did not appear to be a pattern to the variation. In most of the tests, seedlings from high elevation parent trees (generally 1,375 m or above) grew slower than those from lower elevation parents. The differences were significant in only about half of the tests and the average growth of seedlings from some high stands was good. However, if one were selecting only those families that were in the top 10 percent group for height in any one test, very few of the high-elevation families would be selected (table 14). Among the lower elevation zones there again appeared to be no pattern to the variation.

The general finding from these studies that seedlings from high elevation trees are slower growing than those from lower trees agrees with the results reported earlier by Squillace and Bingham (1958). However, these data do not agree with their findings that high-elevation families grew slower than low-elevation families in a low nursery and low plots but faster at a high plot. In the vigor-quality study, low-elevation families were significantly taller than high-elevation families at both low- and mid-test sites. While the differences in sites were not as great as in Squillace and Bingham's study, the site means did differ significantly and there was no indication of the high-elevation families growing faster at the higher site. In fact, the difference between low- and high-elevation families was greater at the higher site even though total height was less. Similarly, as mentioned above, in the elevational study high-elevation families were as tall or slightly taller than low- or mid-elevation families at the low sites but slightly shorter at the high sites. Thus, up to this time the results of the present studies suggest that groups of families representing various elevational zones perform nearly the same whether tested at low-, mid-, or high-elevation sites.

Table 14.--*Ratio of trees in top 10 percent group in various studies*

Study		Seed collection elevational zone		
		Low	Mid	High
Elevational				
Nursery		1/7	1/11	1/39
Ida Creek		1/7	1/10	1/35
PREF				
Low site		1/20	1/7	1/10
Mid site		1/4	0	1/20
High site		1/20	1/7	1/10
	$\bar{x}$	1/9	1/10	1/12
Canyon				
Low site		0	1/10	1/5
Mid site		1/20	1/20	1/5
High site		1/5	0	1/6
	$\bar{x}$	1/12	1/20	1/6
Natural selection		1/7	1/17	1/33
Factorial mating design		1/5	1/8	1/36
Overall		1/7	1/10	1/26

Chance selection and sample size appear to contribute much to the conflicting results of the various studies. The vigor-quality study generally shows a marked contrast between low- and high-elevation stands, but it mainly samples only two stands and only four trees in the high one. Subsequent results from the natural selection study where 50 trees were sampled per stand confirm the differences among the low and high stands represented in the vigor-quality study, but also show that other choices of single low and high stands could lead to the conclusion that low and high stands do not differ.

On the other hand, the elevational study sampled a much broader range of stands but again with few trees per stand. Consequently, the lack of differences among low and high stands may be too conservative. For example, two 5-tree collections were obtained from a stand at Bertha Hill at 1,585 m in the Clearwater area for the elevational study. Seedlings from one of these collections were the tallest of the Clearwater collections but those from the other were about average. The mean height of the two was only slightly less than that for the best elevational zone. However, the results from the 50-tree collection made for the natural selection study indicate that although seedlings from this stand are among the fastest growing of the high-elevation stands they are slower growing than those of five of the six low-elevation stands. Among the low-elevation stands in the natural selection study, even a 50-tree sample indicated only that seedlings of the poorest stand differed significantly from the best ones.

The results of this group of studies also differ from those found in other western conifers. Callaham and Liddicoet (1961) found that mid-elevation ponderosa pine families were tallest at low-, mid-, and high-elevation sites during the first 20 years after outplanting. However, although the high-elevation trees were doing very poorly at the low- and mid-elevation sites at age 20, at the high site they were taller than the low trees and nearly as tall as the mid trees. This pattern continued through age 29 (Conkle 1973). Conkle also found that the variance component related to elevation zones was much larger than that for families within zones at the low and mid sites but not at the high site. In our studies the family component was always much larger.

In working with Douglas-fir, Rehfeldt (1974) found that differences between low, or warm, habitat type trees and high, or cool, habitat type trees could be detected with seedlings from as few as 7 trees per stand. He also found growth differences between stands on the east and west sides of the mountain ranges along the border between Idaho and Montana.

In summary, the results from this series of tests indicate that, at least within the north Idaho portion of its interior range, western white pine has a different variation pattern than that of most other conifers that have been intensively studied. Western white pine is highly variable, but most of the variation is related to differences among the offspring of a single tree or among the trees in a stand. Although differences among stands, elevation zones, or geographic areas were sometimes significant, the proportion of the variance attributable to these sources was usually smaller than that for trees within stands.

All of the seedlings involved in the studies reported here were started under protected and irrigated nursery conditions. They escaped the variety of environmental conditions that might lead to ecotypic differentiation during the critical germination and early establishment growth phases often found when reproduction occurs naturally. Squillace and Bingham's (1958) germination test results may indicate such a differentiation, but the results reported here do not show ecotype formation for other traits.

APPLICATIONS

The results to date indicate that only two seed zones are necessary for western white pine in north Idaho, and probably for the adjacent white pine areas in northeastern Washington and northwestern Montana as well. The main, or low, zone would include all the area below 1,375 m, with the exception of the most severe sites where the upper boundary might be lowered to 1,250 m. The second, or high, zone would include all the area above 1,375 m and a limited area related to severe sites between 1,250 m and 1,375 m.

Two seed orchards, with selections related to the above seed zones, should be sufficient for the next phase of the blister rust resistance breeding program. Siblings, or vegetative propagules, of seedlings intended for either orchard should be tested at several sites to facilitate selection of those individuals or families that are both broadly adapted and fast growing.

Seed from the present low- and mid-elevation orchards can be combined and used on low- and mid-elevation sites throughout north Idaho. It can probably be used at elevations up to 1,375 m on most sites. Seed from the high orchard should be used for sites above 1,375 m. This is a conservative approach, as our results so far show little or no difference in survival or growth among seedlings of low-, mid-, or high-elevation origin at the high sites. However, long-term effects have shown up in other species.

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APPENDIX

Table 15.--*Mean squares from the analyses of variance for several seedling traits in the elevational study nursery test*

Source of variation	d.f.	Seed weight	Germination time	1st year height	Adjusted 1st year height[1]	2nd year height[2]	2nd year lammas	3rd year height	Adjusted 3rd year height[3]	Needle length	Cotyledon No.	Cotyledon length
Trestle Creek vs. Clearwater--All Elevation Zones from 455 m to 1,585 m												
Replications[4]	3	0	393	619	95	1,685	515	17,780	6,817	893	0.0	8.9
Areas	1	28	3,561**[7]	7,913**	580*	22,738**	2,577**	86,262**	1,651	749*	5.2**	52.6*
Elevation zones within areas	13	818	103	325	69	881	235	3,539	1,649	119	0.5	9.3*
Stands within elev. & areas	18	157	80	182	90	536	138*	3,110*	1,599**	86	0.3	4.3
Trees within stands, elev., & areas	130	3,075	50**	141**	60**	343**	58**	1,755**	736*	71**	0.4**	4.1**
Experimental error[5]	471		7	18	18	63	38	707	577	43	0.1	1.7
Within plot[6]			12	52	6	19	6	143	139	10	0.1	0.9
Clearwater, St. Joe, Trestle, and Kaniksu but only 915 m, 1,065 m, and 1,220 m Elevation Zones												
Replications[4]	3		184	284	59	1,046	529	6,927	2,755	798	0.2	15.9
Areas	3	17	685**	2,003**	284	4,923*	601	20,599	170	849*	0.9	8.3
Elevation zones within areas	8	25	66	262	74	867	166	6,180	3,907	126	0.8	6.2
Stands within elev. & areas	11	31	23	144	118	427	83	2,995	1,502*	133**	0.7*	9.3*
Trees within stands, elev., & areas	92	28	55**	155**	65**	341**	46*	1,868**	722**	47	0.4**	4.6**
Experimental error[5]	334		10	19	14	65	34	640	471	39	0.1	1.6
Within plot[6]			2	7	6	19	6	143	139	10	0.1	0.9

[1]First-year height adjusted for seed weight and germination time effects.
[2]Does not include lammas growth in second year.
[3]Third-year height adjusted for first-year height differences.
[4]Only two replicates were used for analyses of cotyledon number and length, so degrees of freedom for replicates and error were reduced accordingly.
[5]Includes all interaction terms involving replication.
[6]Pooled estimate from 30 to 50 plots with 5 to 10 seedlings per plot.
[7]* and ** indicate significance at the 5 percent or 1 percent level, respectively.

Steinhoff, R. J.
1979. Variation in early growth of western white pine in north Idaho. USDA For. Serv. Res. Pap. INT-222, 22 p. Intermt. For. and Range Exp. Stn., Ogden, Utah 84401.

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Headquarters for the Intermountain Forest and Range Experiment Station are in Ogden, Utah. Field programs and research work units are maintained in:

- Billings, Montana
- Boise, Idaho
- Bozeman, Montana (in cooperation with Montana State University)
- Logan, Utah (in cooperation with Utah State University)
- Missoula, Montana (in cooperation with University of Montana)
- Moscow, Idaho (in cooperation with the University of Idaho)
- Provo, Utah (in cooperation with Brigham Young University)
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