Ecological Genetics of Ponderosa pine in the northern Rocky Mountains

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Introduction

A long-term genetic variation study of punderosa pine (Pinus *ponderosa* LAWS.) was begun at the University of Montana in 1974. Genetic variation in ponderosa pine has been previously examined in a number of range-wide and regional studies by SQUILLACE and SILEN (1962), WELLS (1964 a, 1964 b), CONKLE (1973), JENKINSON (1974), WANG and PATTEE (1974), and VAN DEUSEN (1974). The objectives of this regional study were: (1) to estimate the relative amounts of genetic variation within and between families, populations (or stands) and groups of populations from the same habitat type, and (2) to study the influence of single and combined environmental selection pressures on variation in seed weight and 14 seedling characters. The preliminary results, which are reported here, demonstrated a significant relationship between genetic variation in several ponderosa pine characters and certain environmental variables at the seed source. Patterns of variation were predominantly clinal. Also, a variance analysis indicated significant genetic differentiation within and between families, populations, and groups of populations from the same habitat type.

We tested a new concept in this study: the use of habitat types as an environmental selection parameter. Habitat typing, which originated in Finland (CAIANDER 1909), is a method of stratifying forest environments by using groups of understory species in combination with late successional overstory species as indicators (DAUBENMIRE and DAUBENMIRE 1968, PFISTER et al., 1974). Since a habitat type is the end result of plant succession, the climax or mature plant community reflects an integration of all the environmental factors affecting vegetation.

The standard approach to assessing seed source environments in geographic variation studies is to use regional weather patterns and assume that all trees in a region are subject to the same influences. While this approach often reveals significant climatic selection factors, the use of habitat types has a number of advantages. First, habitat types can reflect local climatic differences that regional weather patterns do not account for. Habitat types can also partially reflect plant competition factors and some soil variations. In short, habitat typing gives an index of a population's ecological niche. On a practical level, habitat types are on-the-ground, identifiable units that can easily be incorporated into seed zone delineations. In the northern Rocky Mountains nearly all foresters and forest technicians are now familiar with the current habitat typing systems. Utilizing habitat types along with traditional criteria, such as latitude, longitude, elevation, etc., may increase the accuracy of our seed zoning system.

Materials and Methods

Seed collections

From 1968 to 1971 open-pollinated seed was collected from each of 434 trees, above average in growth characteristics and form. These trees were selected from 93 wild stands in the northern Rocky Mountain-Inland Empire area — a region extending from the Canadian border south to the Salmon River in Idaho and from the Okanagan River in Washington east to the Continental Divide in Montana (Figure 1).

Cones were collected from one to seven trees (usually five) in each stand. The distance between selected trees varied: the minimum distance between parent trees was approximately 20 meters and the maximum was 400 meters, with an average of around 70 meters. The seedlot from each parent tree was kept separate and labeled with a family number.

A bulk stand seed collection from either squirrel caches or average phenotypic trees was also taken from 42 of the stands. Bulk stand collections from the other 51 stands consisted of pooled seed from the selected parent trees in those stands.

The cones were sent to the U.S. Forest Service Nursery in Coeur d'Alene, Idaho, where the seed was extracted, cleaned, and stored. After cleaning, 300 seeds per family were weighed to obtain an average farnily seed weight.

Experimental Design

The seeds were sown by family in a randomized complete block design at the Forest Service Nursery in Coeur d'Alene in May, 1972. There were 83 seeds from each family sown in each of three replicates. Seed were spaced approximately 4 cm apart within plots. Plot size was 15.2 cm X 91.4 cm with 15.2 cm between plots. Seeds from bulk stand collections were also sown in three replicates, but with 332 seeds in each plot. Plot size here was 61.0 cm X 91.4 cm. Seedlings were watered and fertilized the first year. The second year seedlings were watered only during a dry period in August. There was no root pruning. In April of the third growing season the seedlings were lifted and permanently transplanted into two seed orchards and eight test plantations.

In April 1975 an experiment was conducted in the School of Forestry greenhouse in Missoula to determine if seed weight affects gennination and early seedling growth. In this experiment 490 seeds from 49 families (representing 10 stands) were weighed and then grown for 8 weeks in containers. For each of the 49 families, 10 weighed seeds, plus another 90 unweighed seeds, were sown.

Measurement Methods

Seed weight and 14 seedling characters were chosen for measurement. Many of these characters have economic significance. All were thought to be valuable in assessing enviromental selection pressures. Seedling characters quantified were:

One year height
Two year height
Two year height adjusted for seed weight
Needle length
Needle number per fascicle
Root surface area
Root weight

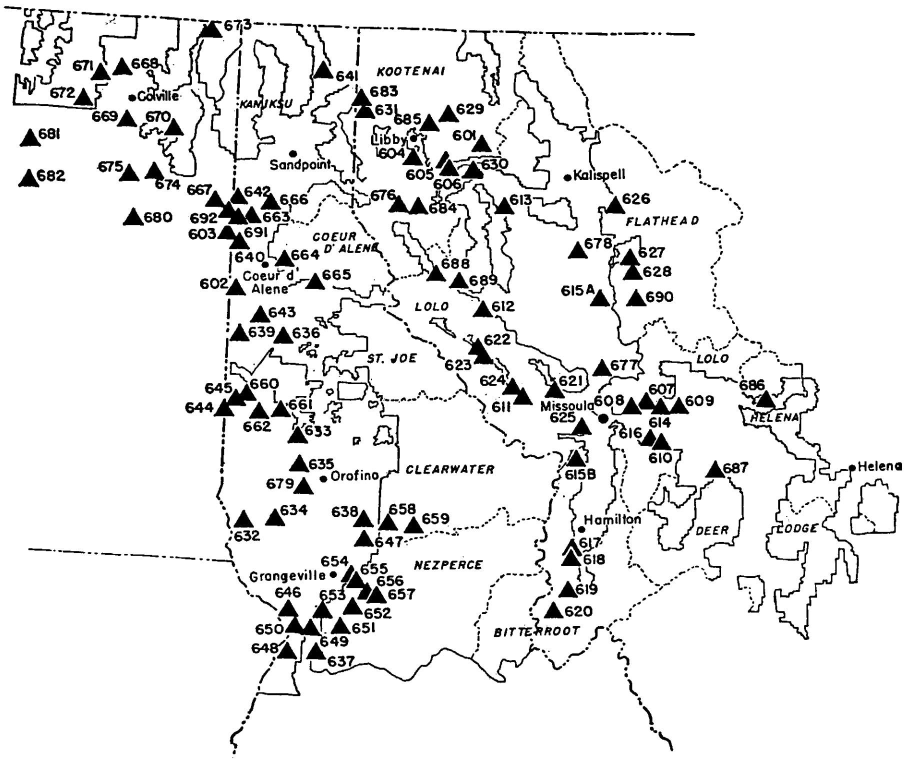

Figure 1. — Map of eastern Washington, northern Idaho, and western Montana illustrating the distribution of stands represented by open-pollinated collections.
(Two sites are given as points for orientation: Colville, Washington, lat. 48°31', long. W. 117°55' and Grangeville, Idaho, lat. 45°56', long. W. 116°08', Scale: 1 cm = 26,5 km.)

Shoot to root weight ratio
Root surface area to height ratio
Root surface area to root weight ratio
Total weight
Bud break
Lammas growth
Height growth cessation

Height of five randomly chosen seedlings per family per replicate was measured to the closest 5 mm. A different group of five randomly chosen seedlings in each family plot of the first replicate was used to record secondary needle length and number of needles per fascicle. Since family needle measurements were not taken in different replicates this character is treated only as a stand variable.

Initial correlation analysis demonstrated that average seed weight per family was significantly correlated with 1- and 2-year height growth averages per family. As a result of this correlation the greenhouse experiment was initiated to check the seed weight-early growth performance relationship on an individual basis. Since seed weight is influenced by seed source environment and by the stage in seed development at the time cones are collected, a source of error is inherent in the seed weight-influenced early height measurement. Seed weight effects have been found in a number of studies with ponderosa pine (Jenkinson 1975, Wang and Pattee 1974, Wells 1964 a, 1964 b). This source of error is comparable to the non-genetic seed source influences ("c" effects) which must also be dealt with in clonal evaluations (Libby and Jund 1962). To observe height growth differences without the effect of seed weight, a new variable was formed by a covariance adjustment. For this variable, average family height per replicate was adjusted in accordance with average family seed weight (Snedecor and Cochran 1968).

All of the other characters were measured on seedlings from the bulk stand collections. These measurements were averaged to yield a variable representative of the stand for use in regression analysis. The seedlings used for the root surface area measurements and for the shoot to root relationship measurements were obtained when the seedlings at Coeur d'Alene were lifted for outplanting. Phenology measurements were taken on bulk stand seedlings during their fourth growing season at the Lubrecht test plantation, Greenough, Montana.

Assessment of Seed Source Environment

As previously mentioned, the habitat type of each stand was used as an index of the seed source enviroment. The habitat type classification system was developed for eastern Washington and northern Idaho by Daubenmire and Daubenmire (1968) and modified for Montana by Pfister *et al.* (1974). All of the stands were visited and classified as to habitat type. To quantify these types in the regression analyses, a ranking system was developed for moisture and temperature relationships between habitat types, on a scale of 1 to 10, with 1 being either the driest or the warmest rating. Since 53 habitat types (excluding phases) were used in the rankings, a number of habitat types have equal temperature and/or mositure indices. Elevation, latitude, and longitude of each stand were also recorded as environmental-geographic parameters.

Analytic Procedures and Results

Variance Analysis

An analysis of variance for a hierarchical model of mixed effects was used to estimate variation within and between families, stands, and habitat type groupings *(Table 1).* Two-year height growth data, both adjusted and unadjusted for seed weight, were used in the analyses. Measurements of 180 of the 434 families were used in these analyses because of unequal numbers at two levels of the analyses — *i. e.*, there were unequal numbers of stands representing each habitat type and there were unequal numbers of fami-

Table 1. — Analysis of variance for 20—2 height, adjusted and unadjusted.

Source	DF	F-Value		Prob > F		Intraclass Correlation For 2-0 Ht. Unadjusted (% σ^2_T)	Expected Mean Squares
		Adj.	Unadj.	Adj.	Unadj.		
Rep	2	2.178	2.067	.1443	.1578	0.1	$\sigma^2_e + 5\,\sigma^2_{rxf} + 25\sigma^2_{rxs} + 100\sigma^2_{rxHT} + 900\sigma^2_r$
Hab. Type	8	2.976	3.488	.0158*	.0070**	7.7	$\sigma^2_e + 15\sigma^2_f + 75\sigma^2_s + 300\sigma^2_{HT}$
Stand (HT)	27	1.673	2.377	.0287*	.0008**	7.2	$\sigma^2_e + 15\sigma^2_f + 75\sigma^2_s$
Fam. (HT Stand)	144	8.233	8.164	.0001**	.0001**	23.0	$\sigma^2_e + 15\sigma^2_f$
Rep x HT	16	0.723	0.747	.7589	.7347	0.0	$\sigma^2_e + 5\sigma^2_{rxf} + 25\sigma^2_{rxs} + 100\sigma^2_{rxHT}$
Rep x Stand	54	1.284	1.246	.1020	.1309	1.1	$\sigma^2_e + 5\sigma^2_{rxf} + 25\sigma^2_{rxs}$
Rep x Fam.	288	2.274	2.287	.0001**	.0001**	12.4	$\sigma^2_e + 5\sigma^2_{rxf}$
Error (within Fam)	2160					48.5	σ^2_e
Total	2699						

* Significant at the 5 percent level.
** Significant at the 1 percent level.

lies representing each stand. Within the 180 families there were nine habitat types represented by four stands each, and each stand was represented by five families. In cases where there were more than four, five-family stands per habitat type, the four stands were chosen randomly.

These analyses showed that significant genetic variation in height growth exists both within stands and among habitat type groupings. A number of studies with seral tree species have shown significant within population (stand) variation for various characters (Kriebel 1964, Stern 1964, Squillace 1966, Wright 1963). The results of our study, in regard to height growth, support this generality. The significant variation among habitat types supports the use of this criterion as a selection parameter.

Tukey's method (Steele and Torrie 1960), a test of contrasts with an average sensitivity, was used to determine specific differences among habitat types. These tests demonstrate that the effects of habitat type environment on height growth result primarily from the low mean heights of seedlings from the three coolest habitat type groups represented, *i.e. Pseudotsuga menziesii/Calamagrostis rubescens, Pseudotsuga menziesii* or *Abies grandis/Xerophyllum tenax* and *Pseudotsuga menziesii/Vaccinium caespitosum.* This temperature gradient trend was apparent throughout all of the habitat types tested. *Pinus ponderosa/Symphoricarpos albus,* the "warmest" habitat type represented, had the greatest mean seedling height. Moisture relationships, however, appeared to have little influence on this character.

Intraclass correlations were computed to assess the relative contribution of each component in the analysis of variance to the total variance. Since individual seedling heights were not adjusted for seed weight influences, no meaningful within-family variation estimate could be made for adjusted 2-year height. Intraclass correlations, therefore, could only by computed for unadjusted height growth. Nearly half of the total variance in 2-year height growth was attributable to variation within families. Variation among families within stands was roughly three times larger than either variation among stands within habitat types or variation among habitat types. However, the relative variation within and among families and stands has been found to change significantly with development in at least one forest tree species, *i.e.,* Douglas-fir (Namkoong *et al.* 1972).

Regression Analysis

Patterns of genetic variation are normally viewed as being either continuous (clinal) or discontinuous (ecotypic). Continuous and discontinuous patterns are not qualitatively different. These patterns are a result of the adaptive strategies of the population, which, in turn are dependent upon niche distribution (in time and space), differences in selection pressures, and migration rates. In addition, different variation patterns along the same environmental gradient within the same species but for different characters are not uncommon (Stern and Roche 1974).

Identification of genetic variation patterns can be useful in delineating seed zone boundaries. There are some inconsistencies in pattern interpretation. For example, Langlet (1971) has presented a discussion on the ambiguity of the term "ecotype". Some of the problems in interpreting variation patterns have arisen because of inadequate sampling intensities; many of the problems, though, appear to be merely associated with individual interpretation of definitions. An effort was made in this study to classify genetic variation patterns by a statistical method involving linear and curvilinear regression data. The reasoning behind this method goes as follows: In cases where variation in characters linearly follows environmental gradients, the relationship is clinal; where variation in characters is related to changes in the environment but does not follow linear gradients, the relationship may be thought of as ecotypic; where variation varies indiscriminately with respect to changes in the environment, the variation is random. Often the non-linear relationship between the character and the environmenal gradient will be curvilinear, in which case a quadratic or cubic regression equation can describe the relationship.

In our analyses each stand character was tested as to its linear and curvilinear association with the five environmental and geographic gradients *(Table 2).* A suggested genetic variation pattern was assigned each character depending on

Table 2. — Patterns of genetic variation.

	Type Designation*				
	Elevation	Latitude	Longitude	Moisture	Temperature
			Stand Data		
2-0 Ht. Adj.	2	3	3	1	1
2-0 Ht. Unadj.	2	3	3	1	2
Seed Wt.	2	1	2	4	2
Root Surf. Area	1	1	1	1	4
Root Wt.	1	1	1	1	1
Shoot Wt./Root Wt.	1	1	1	1	1
Rsa/Ht.	3	2	1	1	1
Rsa/Root Wt.	1	1	1	1	1
Total Wt.	1	1	1	1	1
Bud Break	3	2	1	1	1
Ht. Growth Cess.	1	1	1	1	1
			Family Data		
2-0 Ht. Adj.	1	3	3	1	3
2-0 Ht. Unadj.	1	3	3	1	3
1-0 Ht. Unadj.	2	2	3	4	2
Seet Wt.	2	4	2	3	2

*Type Designation	Suggested Biological Relationships
1	Random (non-significant statistical relationships)
2	Clinal (linear relationship only)
3	Clinal-ecotypic (both linear and curvilinear relationships significant)
4	Predominantly ecotypic (linear non-significnat, curvilinear significant)

whether it was significantly associated with an environment-geographic gradient in a linear and/or a curvilinear relationship. A strong discontinuous break in a character might be difficult to measure by use of this technique. Plotting the data in such cases may demonstrate the relationship better than can a mathematical function.

Only a few characters that were not randomly occurring demonstrated a stronger curvilinear than linear variation pattern. Where curvilinear regression equations were stronger than the linear relationship, the linear relationship was still significant in all but three cases. Examples of what appears to be ecotypic variation were found with significantly larger root surface areas in the warm habitat types and with considerably larger seed weights in the drier habitat types.

Two correlation matrices were computed: one for the characters representative of the stands, and one for the family characters. Seed weight plus all the seedling characters exept occurrence of lammas growth and needle number per fascicle were correlated with the five environmental variables *(Tables 3, 4, 5,)*. The correlation matrices can be broken down into three components: correlations among characters, correlations of characters with the environmental factors, and correlations among environmental factors. These correlation matrices reveal only the linear relationships among variables. *Table 2*, as mentioned earlier, reveals the few relationships among characters and environmental factors that were only curvilinear in nature.

Correlations among characters were complicated because five different seedling samples were used for the measurements; *i.e.*, different samples were used for 1-year height, 2-year height, needle measurements, phenology measurements, root surface area, and shoot-to-root relationship measurements. As would be expected, several significant correlations among characters were found. For example, root weight should be correlated with root surface area and 1-year height growth is normally highly correlated with 2-year height growth. A few relationships, however, were surprising, such as a negative correlation between needle length and height growth and a positive correlation betwen needle length and root weight.

A number of characters were strongly related to environmental parameters at the seed source. The highest correlations were found with height growth and elevation, height growth and longitude, date of bud break and elevation, date of bud break and latitude, and seed weight and temperature.

Two characters — lammas growth and needle number per fascicle — could not be quantified properly for inclusion in the regression analyses. Hypergeometric analysis revealed that lammas growth and/or prolepsis was significantly associated with two seed source environmental variables: elevation and latitude. The elevation relationship was positive, with lammas growth more common in the high elevation sources (at the relatively high elevation Lubrecht test plantation). Lammas growth in the higher elevation sources was unexpected. Spring budbreak tended to occur later in these sources than in others — a trend associated with populations in areas having short growing seasons. A second flushing (lammas growth) in early fall would expose seedlings to frost damage in areas with short growing seasons. Of the 434 families sampled, 78 of them had one or more of the fascicles sampled with either more or less than three needles. Of these 78 families, 69 of them had one or more four-needle fascicles, five of them had one or more two-needle fascicles, two of them had a one-needle fascicle, and two of them had a five-needle fascicle. The occurrence of families with other than three-needle fascicles was randomly distributed, not following any environmental-geographic gradients. A check of the parent trees revealed that only one tree had other than all three needle fascicles. This was a tree in central Idaho that had about 20 percent two-needle fascicles.

Table 3. — Correlation coefficient matrix — stand data.

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)
1) 2-0 Ht. Adj.	1.000	.935**	-.260*	.275**	-.101	-.175	-.145	-.369**	.158	-.101	-.571**	.0713	-.147	.270**	.486**
2) 2-0 Ht. Unadj.		1.000	-.226*	.576**	-.046	-.087	-.087	-.379**	.127	-.040	-.602**	.001	-.261*	.214*	.497**
3) Needle Length			1.000	.002	.107	.221*	-.162	.061	-.194	.194	.039	-.054	.123	.057	-.057
4) Seed Wt.				1.000	.139	.173	.102	-.166	-.025	.127	-.341**	-.166	-.412**	-.072	.225*
5) Root Surface Area					1.000	.762**	.824**	.740**	-.514**	.789**	-.055	-.081	-.157	-.151	.085
6) Root Wt.						1.000	-.699**	.614**	-.735**	.958**	.036	-.129	-.143	-.080	.074
7) Shoot/Root Wt.							1.00	-.664**	.586**	-.490**	-.150	-.091	-.076	.178	.013
8) RSA/Ht.								1.00	-.397**	.503**	.322**	-.045	.077	-.272**	-.167
9) RSA/Root Wt.									1.00	-.697**	.040	.066	-.014	.043	-.072
10) Total Wt.										1.00	-.116	-.165	-.198	-.043	.105
11) Elevation											1.00	.176	.416**	-.593**	-.494**
12) Moisture												1.00	.697**	-.205	.090
13) Temperature													1.00	-.138	-.077
14) Latitude														1.00	.274**
15) Longitude															1.00

DF = 89

Tests: 5% > .207*
1% ≥ .269**

Table 4. — Correlation coefficient matrix — stand data.

	Growth Cess.	2-0 Ht. Unadj.	2-0 Ht. Adj.	Ndl. Lgth.	Seed Wt.	Root Surf. Area	Root Wt.	Shoot/ Root	RSA/ Ht.	RSA/ Rt.Wt.	Elev.	Moist.	Temp.	Lat.	Long.
Bud Break (Days After May 1)	.144	-.218	-.193	-.066	-.105	.094	.093	-.105	.248	-.072	.511**	.011	.276	-.535**	-.054
Growth Cessation (Days After August 1)		-.034	.071	-.063	-.119	.030	.015	.040	.016	.062	.209	.093	.042	-.195	-.063

DF = 37

Tests: 5% > .317
1% ≥ .408

Table 5. — Correlation coefficient matrix — Family data.

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
2-0 Ht	1.000	.918**	.811**	.397**	.000	-.185**	-.411**	.143**	.318**
2-0 Ht Adj		1.000	.686**	.006	.051	-.095*	-.373**	.182**	.308**
1-0 Ht			1.000	.459**	.050	-.167**	-.362**	.107*	.244**
Seed Wt.				1.000	-.104*	-.243**	-.179**	-.055	.091*
Moisture					1.000	.656**	.158**	-.218**	.086
Temperature						1.000	.449**	-.179**	-.081
Elevation							1.000	-.605**	-.479**
Latitude								1.000	.278**
Longitude									1.000

DF = 433

Tests: , 5% > .091*
1% ≥ .119**

An examination of correlations among environmental parameters yielded some important results in regard to interpretation of variation patterns. The correlation between temperature and elevation was, of course, expected. However, the negative correlations of elevation with latitude and longitude would not normally be found in a random sample. With these types of correlations, the reasons why characters are associated with certain environmental parameters become less clear. For example, how much of the variation in height growth is attributable to changes in elevation and how much is attributable to changes in longitude and latitude?

In cases in which characters were correlated with two or more environmental variables, a multiple regression analysis was made. Those environmental variables which made statistically significant improvements in each regression were used to compute multiple correlation coefficients (*Table 6*). The strongest relationship was found with 2-year

Table 6. — Multiple correlation coefficients.

Seedling Character	Number of Significant Linear Correlations With Environmental Variables	Strongest Multiple Correlation Coefficient (All Variables Must be Significant)
	Stand Data	
2-0 Ht. Adj.	3	.618 (elev + long)
2-0 Ht. Unadj.	3	.666 (elev + long + lat)
Seed Wt.	3	.455 (temp + long)
Root Surf. Area/Ht	3	.338 (elev only)
	Family Data	
2-0 Ht. Adj.	4	.401 (elev + long)
2-0 Ht. Unadj.	4	.453 (elev + long + lat)
1-0 Ht.	4	.389 (elev + lat)
Seed Wt.	4	.243 (temp only)

unadjusted height growth in which elevation, latitude, and longitude accounted for 44 percent of the variation ($r = .66$).

For the greenhouse experiment, correlation coefficients were computed to test the relationship between seed weight and germination, height growth, and total weight as measured at 8 weeks (*Table 7*). Results reveal the substantial influence of seed weight on early height growth and total seedling weight.

Table 7. — Seed weight experiment correlation coefficients.

Seed Weight:	Height	8 wk.	r = .602**
	Total Wt.	8 wk.	r = .630**
	Germination	8 wk.	r = .131

DF = 174
Tests: 5% ≥ .149*
1% ≥ .194**

A number of chlorotic seedlings were observed in the greenhouse experiment. ANDERSSON *et al.* (1974) demonstrated that albinism in *Picea abies* was controlled by a single recessive gene. Thus, only heterozygous trees can produce open-pollinated albino offspring. The highest within-family frequency of either totally chlorotic or chlorotic-cotyledon seedlings never exceeded 3 percent in the experiment. The 100-seedling samples of most families (44 of 49) had no chlorotic seedlings.

Two polymorphic characters observed in the greenhouse study were seed coat color and pattern. Both seed coat color and pattern exhibited distinct within- and between-stand variation.

Discussion

Results — based on the performance of two year old seedlings — indicate that genetic differentation of ponderosa pine is occurring on a local level in the region sampled. Environmental selection pressures apparently have a greater effect on populations than does rate of migration between populations. Several of the progeny-environment correlations reveal obvious adaptive relationships. This is not surprising considering the broad range of environmental conditions from which populations were sampled. Ponderosa pine families tested in this study came from the warm and dry steppe-forest transition sites on which ponderosa pine is climax, up through the moist sites dominated by western red cedar (*Thuja plicata* DONN.) and western hemlock (*Tsuga heterophylla* (RAF.) SARG.), to the relatively cool sites climaxed by Engelmann spruce (*Picea engelmannii* Parrg) and white spruce (*Picea glauca* (MOENCH) VOSS).

As previously mentioned, the significant effect of habitat type on height growth is a partial result of the lower mean heights of progeny from the cooler habitat types. REHFELDT (1974) found a similar pattern in Douglas-fir in the northern Rockies. We also observed a trend towards greater height growth in ponderosa pine from the warmer habitat types. Since habitats become progressively cooler with increase in elevation, a good correlation ($r = .60$) was found between mean stand height and stand elevation. Decreasing height growth with increase in seed source elevation is a common finding in forest tree genetic studies conducted on low- to mid-elevation test sites (WRIGHT 1976, HERMAN and LAVENDER 1968, CONKLE 1973, ROW and CHING 1973, REHFELDT 1974).

One population illustrated the effect of seed source habitat type on height growth regardless of elevation. This stand collection was from a warm and dry *Pinus ponderosa/Symphoricarpos albus* habitat type located at a high elevation (1255 m), south-aspect site in central Idaho. The mean 2-year height of this stand was very high, sixth highest in the entire study. This population followed the trend towards increased height growth in the warmer habitat types rather than the trend of decreased height growth with rise in elevation. Also, this population was characterized by a high mean root surface area, another trend associated with populations from warm habitat types. This observation is similar to one reported by REHFELDT (1974) in his Douglas-fir study which he found that populations from habitat types in low-elevation frost pockets behaved like populations from the cool, high-elevation habitat types.

Despite the number of examples demonstrating the selective influence of habitat types on certain characters (height growth, root surface area, seed weight, and bud break), there is also a significant amount of genetic variation in characters of populations from the same habitat type. To study this variation, stands from the following common habitat types were singled out for examination: *Pinus ponderosa/Symphoricarpos albus* (PP/SYAL), *Pseudotsuga menziesii/Symphoricarpos albus* (DF/SYAL), and *Abies grandis/Xerophyllum tenax* (GF/XETE). Each of these habitat types represents a very different ecological situation. The PP/SYAL habitat type is warm and relatively dry type usually occurring at low elevations. The DF/SYAL habitat type is probably one of the most common types in the northern Rockies. Usually it occurs at mid-elevations and is characterized by intermediate temperature and moisture regimes. The GF/XETE habitat type is almost always found at high elevations. This is a cool and relatively moist habitat type receiving a large amount of precipitation, mainly in the form of snow.

While the within-stand variation estimates for stands from all three habitat types were approximately equal, the coefficient of variation for 2-year adjusted height growth of DF/SYAL stands (.0839) was approximately twice that of the PP/SYAL stands (.0460) and the GF/XETE stands (.0394). Also, height growth of stands from the DF/SYAL habitat type was significantly correlated with elevation and longitude, whereas, height growth of stands from the GF/XETE habitat types was correlated with elevation only and height growth of stands from the PP/SYAL habitat type was not correlated with any enviromental-geographic gradient. These results suggest that habitat types represent an ecological niche — the amplitude of which is dependent upon the particular habitat type. That is, certain species combinations (habitat types) may come together only in a very narrow set of environmental circumstances (due to genetic variation of the species in the habitat type complex as well as lesser factors such as competition, fire history, insect outbreaks, etc.); other may come together over a broader set of conditions. The environmental selection pressures, then, will be more consistent or homogeneous for some habitat types. Thus, in populations from DF/SYAL habitat types, height growth was related to other environmental-geographic factors since the habitat type defined such a general niche that other criteria better measured the environmental selection pressures. The niche-variation model proposed here has been theoretically discussed by Mayr (1945), Li (1955), Maynard Smith (1962), and Levins (1962, 1963). A great deal of experimental evidence for a relationship between variation and width of niche exists (Townsend 1952, daCuna and Dobzhansky 1965, Van Valen 1965).

An examination of the correlation matrices reveals that many characters were not correlated with seed source environmental parameters. Also, where correlations were significant they were usually not strong. Along with these observations, the analysis of variance for height growth revealed that the majority of the variation in height growth was due to variation within and between families. These results are not suprising in view of discussions by Levins (1963, 1964) and Rehfeldt and Lester (1969) concerning systems of adaptation by pioneer and successionally advanced species. Pioneer species (as ponderosa pine very often is) must face a variable environment in time and sometimes in space. Pioneer species sacrifice high fitness for specific conditions for a high degree of flexibility or adaptability to a variety of environments. Thus, heterozygosity is important for pioneer species and genetic variation within populations should be substantial. This, of course, is a broad generality. For example, ponderosa pine often occurs as the only tree in climax communities. In such situations there will be a high correlation of environments between generations. The genetic structure of populations will vary depending on past history and the conditions of the given niche.

Delineation of seed zone boundaries on the basis of juvenile data presents a dilemma: if the zones are too broadly defined a net reduction in fitness of planting stock will result; if the zones are rigidly defined the scope of the tree improvement project must be very large in order to provide an adequate number of families per seed zone to select from. An example of this latter approach can be seen in the West Coast Douglas-fir cooperative tree improvement programs in which cooperators are asked to submit three open-pollinated Douglas-fir families per 1000 acres of forest ownership. Some 22,000 open-pollinated Douglas-fir families will be under testing by 1977 (Silen 1976).

Data from the present study indicate that a combination of elevation, latitude, longitude, and habitat type can be used to delineate most seed zones. Perhaps in some habitat types the other criteria will require less emphasis. Since eight test plantations were established on a variety of environments in this region, seed transfer rules can be modified as more information becomes available.

Although the within family σ^2 and within stand σ^2 accounted for 71.5 percent of the total σ^2 for 2 year height growth, the among stand σ^2 (within the same habitat type) was still significant. Actually, in the southern Idaho ponderosa pine tree improvement study the relative amount of among stand σ^2 is increasing with development and within stand σ^2 is decreasing (Wang and Pattee 1974). Thus, obtaining seed from the genetically superior natural stands will provide a good interim source of seed until the rouged seed orchards and test plantations come into seed production in approximately 15 years.

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Summary

Four hundred thirty-four open-pollinated ponderosa pine families from 93 stands in eastern Washington, northern Idaho and western Montana were grown in a replicated nursery test at Coeur d'Alene, Idaho for 2 years. In the spring of 1973 the seedlings were outplanted into eight test plantations and two seed orchards.

Seed weight and 14 seedling characters were scored at the nursery and at a Montana test plantation. The results indicate that ponderosa pine is a highly variable species and that the variation in a number of characters is significantly correlated with various environmental factors. Patterns of variation were predominantly clinal, although a few examples of ecotypic variation were found.

A new approach — the use of habitat types as an environmental selection parameter — was tested in this study. Habitat typing is a method of stratifying forest environments by using groups of understory species in combination with late successional overstory species as indicators. Environmental selection pressures, as measured by habitat type, were shown to affect variation in height growth, seed weight, and root surface area.

An analysis of variance of 2-year height growth revealed that 71.5 percent of the total variation was attributed to within and among family (within stand) variation. Significant variation in height growth was also found among stands having the same habitat type and among habitat type groupings. On the basis of this significant among stand variation, genetically superior natural stands will be used as an interim source of seed.

Key words: genetic variation, genecology, provenance, *Pinus ponderosa*, habitat type.

Zusammenfassung

434 Einzelbaum-Nachkommenschaften aus 93 natürlichen Vorkommen von *Pinus ponderosa* in den Staaten Ost-Washington, Nord-Idaho und West-Montana wurden nach der Anzucht in Coeur d'Alene, Idaho, in 8 Versuchsflächen und 2 Samenplantagen ausgepflanzt. Bei 300 der Nachkommenschaften war vor der Aussaat das Samengewicht festgestellt worden. Später wurden die Sämlinge auf Höhenwachstum, Nadellänge, Nadelzahl pro Kurztrieb, Wurzelgewicht usw., das heißt insgesamt 14 Merkmale hin untersucht. Die Ergebnisse zeigen, daß *Pinus ponderosa* als sehr variable Art anzusehen ist, wobei Herkunftsunterschiede stark hervortreten.

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An Intergrated Population of Abies grandis – Abies concolor in Central Idaho and its Relation to Decay[1])

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Introduction

Grand fir *(Abies grandis* [Dougl. ex. D. Don] Lindl.) and white or concolor fir *(Abies concolor* [Gordon and Glend.] Lindl. ex. Hildebr.) are two important and widely distributed true firs in the Western United States. Grand fir occurs primarily in the Pacific Northwest and in the Rocky Mountains from central Idaho to southern British Columbia. White fir grows in the southern Cascade, Sierra Nevada, and Rocky Mountains south of the range of grand fir (Little, 1971). The southern Rocky Mountains white fir is often referred to as *A. concolor* var. *concolor* and the Sierran to *A. concolor* var. *lowiana*. Presently grand fir and concolor fir are regarded as morphologically distinct *(Table 1)*. Between the undisputed ranges of grand fir and white fir lies an area in northeastern Oregon and west central Idaho supporting fir populations that are morphologically intermediate and not easily assigned to either species.

Several authors recognize *A. concolor* as occurring in these two regions (Davis, 1952 and Peck, 1961). Many disclaim its occurrence (McMinn and Maino, 1947; Fowells, 1965; and E. L. Little, personal communication, 1975).

These two species hybridize freely in areas of overlap in California and western Oregon (Hamrick and Libby, 1972). There are no reports, however, of verified hybrids occurring in the northern Rocky Mountains.

In central Idaho, south of the Salmon River (approximately 46° 30' N. Lat.) an intergraded population apparently exists between concolor fir and grand fir. Johnson (1966) recognized this morphological complex in west-central Idaho and tentatively interpreted it as an intergraded population of *A. concolor*, var. *lowiana*, *A. grandis* and trees which exhibited characteristics of both species. Daniels (1969) reported typical grand fir types, intermediate forms, and concolor-like individuals growing together near McCall, Idaho. He studied the phenotypic variability of the population and generally outlined its composition and extent using a hybrid index technique. Individuals in his

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