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Heritability Estimates for Pinus ponderosa of the Inland Empire

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Abstract

Genetic variation in seven-year total height of ponderosa pine (*Pinus ponderosa* Laws.) was estimated. Seven test plantations provided different environmental conditions throughout the Northern Rocky Mountains. Each plantation contains randomized block plantings of 434 open pollinated families representing 93 wild stands selected within the Inland Empire. Two-way analyses of variance with proportional subclasses were performed both within and between plantations. Within each plantation families, blocks and the block x family interaction had significant ($\alpha = 0.01$) effects on the seven-year total height of the progeny. Between selected combinations of plantations significant differences ($\alpha = 0.01$) existed in total height due to family, site and the site x family interaction. Narrow-sense heritability estimates within and between plantations indicated substantial genetic variation. These estimates fall well within the range of other published reports and indicate that this species will respond favorably to selection.

Key words: Progeny test, Heritability, Pine, *Pinus ponderosa*, Juvenile tests, Forest genetics.

Zusammenfassung

Bei *Pinus ponderosa* Laws. wurde die genetische Variation der Gesamthöhe im Alter 7 geschätzt. Hierzu dienten 7 Versuchsflächen verschiedener Umweltbedingungen in den nördlichen Rocky Mountains. Jede Versuchsfläche enthält randomisierte Blocks mit 434 frei abgeblühten Familien als Nachkommenschaften aus 93 natürlichen Beständen, die im Inland Empire selektiert worden waren. Es wurden Zwei-Wege-Varianzanalysen mit proportionalen Unterklassen innerhalb und zwischen den Flächen durchgeführt. Innerhalb jeder Familie der Versuchsfläche zeigten die Block- und die Block x Familien-Interaktionen Signifikanzeffekte ($\alpha = 0{,}01$) in der Gesamthöhe der Nachkommenschaft. Zwischen ausgewählten Versuchsflächen-Kombinationen gab es signifikante Differenzen ($\alpha = 0{,}01$) in der Gesamthöhe, die auf die Familie, den Standort und deren Interaktionen zurückzuführen waren. Heritabilitäts-Schätzwerte im engeren Sinne innerhalb und zwischen Versuchsflächen zeigten eine wesentliche genetische Variation an. Diese Feststellungen passen zu anderen Veröffentlichungen und zeigen an, daß diese Species auf eine Selektion günstig reagiert.

Introduction

Previous studies have demonstrated that ponderosa pine is genetically variable for characteristics related to growth (Wells 1964; Squillace and Silen 1962, Callaham and Liddicoet 1961, Weidman 1939, and others), and early results from provenance research suggests that this variation is adaptive (Rehfeldt 1980a).

In this study we examined genetic variation in seven year total height for 434 selected families of ponderosa pine. The specific objectives were: 1) to describe patterns of genetic variation in seven year total height, and 2) to estimate narrow-sense heritabilities in tree height within and between sites.

Genetic variation of ponderosa pine in the northern Rocky Mountains is assumed to relate directly to the complex gradients associated with mountain topography. If so, genetic variation attributable to parent-tree location would best be described by a topocline. The assumption derives from the concept that for any area delimited in space and time, the range of environments can be represented by an average effect and deviations from that average. For plants within such an area, an analogous average genetic effect and deviations exist because adapted plant types occur in proportion to the environment (Levins 1969). If there is a gradient change in the environment at several adjacent locations, there should also be a gradual change in genotypes forming a cline (Levins 1963). Further, genetic variation among plants within locations along the same gradient can be expected to be proportional to the number of plants sampled within locations (Donovan *et al.* 1976).

Materials and Methods

Geographic Area

This study was conceived and implemented by the Inland Empire Tree Improvement Cooperative consisting of members from universities, industries and public agencies

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Table 1. — Description of Outplanting Sites.

Plantation	Elevation (ft)	Latitude	Longitude
Condon, Montana	3680	40°32'	113°42'
Lubrecht, Montana	4800	46°53'	113°30'
Rye Creek, Montana	6200	45°58'	113°54'
Wolf Creek, Montana	3250	48°18'	114°47'
Lone Mt., Idaho	2450	47°55'	116°49'
Tensed, Idaho	2849	47°10'	116°50'
Meadow Creek, Idaho	3320	45°54'	115°52'

located in the northwestern portion of the United States. Seed was collected from an area extending from the Canadian border south to the Salomon River and from the Okanagan River east to the Continental Divide (MADSEN and BLAKE 1977). Ninety-three wild stands of ponderosa pine were subjectively chosen on the basis of their above average growth performance. Within these selected wild stands, 434 phenotypically superior parent trees (families) were chosen. Open pollinated seed collections from these trees were made from 1968 through 1971. Seed from each maternal parent tree was kept separate from other seed lots and treated as a half-sib family. Some members of these half-sib families could be full-sibs, or even selfs, but to be conservative with respect to heritability estimates, a halb-sib relationship was assumed.

Field Methods

The common environment method was used to estimate genetic variation. Seven test locations representing a range of environmental conditions were selected *(Table 1)*. Seedlings were grown as bare root stock at the Coeur d'Alene Nursery, Idaho for one year before outplanting. First-year mortality was replaced with one-year-old container-grown stock. At each plantation location five blocks were established in a completely randomized block design. Depending on the space available at the location of the plantation, between 86 to 237 families (from a total of 434) were assigned at random to each block.

Each family was replicated four times by placing four seedlings in a ten-foot square spacing. Total height measurements (± 1 cm) were recorded for 1979.

Analyses

An analysis of variance (ANOVA) is appropriate for estimating variance components when an equal number of observations per subclass exists. However, with an unequal number of observations per subclass, regression techniques are employed if the imbalance is not severe, i.e., less than 30 (2%) missing observations. If a very severe imbalance exists, i.e., 200 or more (5%) missing observations, an alternative method is the ANOVA with a proportional number of randomly selected observations per subclass as discussed by BANCROFT (1968). For this study the general model of a two-way classification with unequal frequencies in the subclasses was adopted, namely:

$$Y_{ijk} = \mu + A_i + B_j + (AB)_{ij} + \varepsilon_{ijk}$$

where:

Y_{ijk} = seven year total height in cm
A_i = environment (site or block) effect ($i = 1, \ldots, a$) and $a = 2, 3, 4$ or 5
B_j = family effect ($j = 1, \ldots, b$) and $b = 86, 96, 118, 203, 204$ and 237
$(AB)_{ij}$ = interaction effect
ε_{ijk} = random error ($k = n_{ij}$)
$n_{ij} = nu_iv_j$ = number of proportional subsamples.
u_i = proportions between levels of factor A
v_j = proportions between levels of factor B
k = 1, 2, 3 or 4

Due to mortality, unequal numbers of observations existed in families and across environments. To achieve proportionality in these subclasses, observations were removed at random from the data bases prior to analysis.

To conduct F-tests for purposes of testing the equality of treatment means (main effects and the interaction) expected mean squares were calculated. Appropriate F-ratio denominators were fabricated using the Satterthwaite-Cochran (SC) approximation (BANCROFT 1968).

Two types of analyses were performed within each plantation. The first used complete block representation by sacrificing families with missing observations in one or more blocks. This resulted in 90% or more family representation at the Idaho plantations but only in 57% to 81% at the Montana sites. Therefore, additional analyses were made for the Montana plantations using 90% or more family representation. This required the elimination of data such that the maximum number of families was retained at the expense of blocks, i.e., blocks with poor survival were removed from the analyses.

The above analyses used proportional numbers of observations within each family, For each plantation, the elimination of seedlings was such that the number of seedlings remaining in each of the retained blocks was constant within each family. For example, if the number of seedlings for a family per block in blocks 1 through 5 respectively was 3, 2, 2, 3, 2, then random elimination of one seedling from block 1 and one seedling from block 4 "balanced" that particular family at that plantation, Another plantation, for example, might only use blocks 2, 4, and 5 in the analyses. If a family then had 3, 4 and 1 observations respectively in the three blocks, then random elimination of two seedlings in block 2 and three seedlings

Table 2. — Form of the analysis of variance and expected mean squares within plantations.

SOURCE OF VARIANCE	EXPECTED MEAN SQUARES[1]
A (Block)	$\sigma^2 + K_1 \sigma^2_{AB} + K_2 \sigma^2_A$
B (Family)	$\sigma^2 + K_3 \sigma^2_B$
AB (Block X Family)	$\sigma^2 + K_4 \sigma^2_{AB}$
Residual	σ^2

[1] Where:

	Rye Creek	Wolf Creek	Condon	Lubrecht	Meadow Creek	Tensed	Lone Mt.
K_1 =	0.3119	0.3051	0.3025	0.3031	0.1586	0.2903	0.2674
K_2 =	225.0000	213.0000	498.0000	395.0000	297.0000	480.0000	540.0000
K_3 =	5.6882	7.9511	5.3615	6.5060	17.0597	11.1044	12.3792
K_4 =	2.8441	1.9878	2.6758	2.1687	3.4119	2.2209	2.4758

Table 3. — Form of the analysis and variance and expected mean squares between plantations.

SOURCE OF VARIANCE	EXPECTED MEAN SQUARES[1]
A (Site)	$\sigma^2 + K_1 \sigma^2_{AB} + K_2 \sigma^2_A$
B (Family)	$\sigma^2 + K_3 \sigma^2_B$
AB (Site X Family)	$\sigma^2 + K_4 \sigma^2_{AB}$
Residual	σ^2

[1] where:

	Condon X Lubrecht	Condon X Lubrecht X Rye Creek	Condon X Lubrecht X Wolf Creek	Lone Mt. X Tensed	Lone Mt. X Tensed X Meadow
K_1 =	0.6272	0.6055	0.5419	0.3374	0.2413
K_2 =	2576.0000	1055.0000	1349.0000	3609.0000	1456.0000
K_3 =	25.2487	36.7810	34.2827	30.4528	45.4924
K_4 =	12.6244	12.2603	11.4276	15.2264	15.1641

in block 4 "balanced" that particular family at that plantation.

A two-way analysis of variance, using blocks and families as main effects, was computed separately for seven year total height at each of the seven plantations. Estimates of the "true" variation among sources were obtained as "components of variance" after the allowance for random variation (Snedecor and Cochran 1968). The form of the analysis of variance and expected mean squares *(Table 2)* follows the example of Wright (1963).

Two-way analyses of variance were computed for common families between plantations. Because the same number of blocks could not be maintained across sites for common families, blocks were collapsed and incorporated with the replicates. Thus, the number of sites was either 2 or 3, the number of common families varied, and the number of replicates became 9, 10, 11 . . . . . or 20. Five analyses were conducted using specific plantation combinations, namely those having the same families common across sites. The form of the analyses of variance and expected man squares *(Table 3)* also follows the example of Wright (1963).

Heritability Estimates

Only additive genetic variability can be estimated in an open pollinated progeny test such as this one. Therefore, heritability can only be estimated on a narrow-sense basis. Since vigor characteristics in trees appear primarily controlled by additive genes, estimating narrow-sense heritability is appropriate (Madsen and Blake 1977).

Heritability (h^2) equals the ratio of the total additive variance (σ^2_f) to the total phenotypic variance (σ^2_w).

The concept of heritability in a selection unit can be used as a practical measure because the denominator is the phenotypic variance of the unit (Hanson 1963).

Family height growth heritability estimates were computed for each plantation. From the analyses of variance at each plantation, variance components were used to calculate family heritability from the following equation:

$$h^2 = \frac{4\sigma^2_B}{\sigma^2_{error} + \sigma^2_{AB} + \sigma^2_B}$$

where:

σ^2_B = 1/4 additive genetic variance

σ^2_{AB} = interaction variance

σ^2_{error} = error variance

$\sigma^2_{error} + \sigma^2_{AB} + \sigma^2_B$ = total phenotypic variance

Two heritability estimates were calculated for each of the Montana plantations. The first one used all 5 blocks regardless of the number of families included. The second was based on balanced data achieved by eliminating entire blocks as necessary to have the same families represented in each block. Due to mortality and missing data, between 8.14% and 10.29% of the families were eliminated from the analysis of variance calculations and subsequent heritability estimates.

Table 4. — Degrees of freedom and calculated F-values by source of variation for 7-year height within each of seven plantations.

Source	Rye Creek df	Rye Creek "F"	Wolf Creek df	Wolf Creek "F"	Condon df	Condon "F"	Lubrecht df	Lubrecht "F"	Meadow df	Meadow "F"	Tensed df	Tensed "F"	Lone Mt. df	Lone Mt. "F"
A (Block)[1]	1	8.98*	2	1.01	1	1.56	2	4.63*	4	8.13*	4	1.96	4	5.13*
B (Family)[2]	78	2.06*	106	1.76*	185	2.28*	181	2.00*	86	4.46*	215	3.62*	217	3.40*
AB (Block X Family)	78	1.96*	318	1.25*	185	1.42*	362	1.41*	344	1.83*	860	2.15*	868	1.55*
A (Block)[1]	4	1.18	4	6.79*	4	47.77*	4	9.11*						
B (Family)[2]	49	1.88*	92	2.07*	89	2.68*	165	2.30*						
AB (Block X Family)	196	1.07*	368	1.35*	356	1.33*	660	1.28*						

[1] Calculations followed Satterthwaite-Cochran procedure (Bancroft 1968).
[2] Calculations followed the Standard procedure (Bancroft 1968.

* Statistically significant at the .01 level of probability.

Heritability estimates were computed for five combinations of plantations. Variance components from the analyses of variance were used to calculate family heritabilities. The same equation could be used for these estimates as were used to calculate heritabilities within plantations. The only difference is that for these analyses the interaction effect contains families across different sites whereas the previous one utilized families within a specific site. These calculations were simpler in the sense that if a family was not represented at a site, it was treated as though it was not common across the sites being compared.

Results and Discussion

Calculated F-values by source of variation resulted in significant differences between blocks, families and the block × family interaction at each location (*Table 4*). The calculations for family significance followed standard procedures, and the calculations for block significance followed the Satterthwaite-Cochran approximation procedure.

Almost all of the sources were statistically significant ($\alpha = 0.01$). There were four exceptions to this, all at the block level. Several explanations can be offered for them. First, the block source at Rye Creek using all five blocks in the analysis was confounded by the lack of observations at the family level. Only 57% of the families planted could be used for the analysis. Two other plantations, Condon and Wolf Creek, had nonsignificant F-values for the analysis using 90% or more of the families planted. These results were confounded by the lack of blocks in the ANOVA. Blocks in this analysis were eliminated to maintain families. The fourth nonsignificant F-value occurred at the Tensed plantation. Tensed was the most uniform planting site in this study. Apparently the design was not sensitive enough to detect the natural variability of the site.

The next step was an analysis of variance between sites. A minimum of two sites was required to show any variation at this level and the maximum number of families was retained.

Calculations for family F-tests of significance followed standard procedures and the calculations for site F-tests of significance followed the Satterthwaite-Cochran approximation procedure. The F-values calculated by source of variation resulted in significant differences between sites, families and the site × family interaction (*Table 5*).

All sources of variation were statistically significant ($\alpha = 0.01$). This is due to the large sample size and the degrees of freedom at the family level as related to the degrees of freedom at the site level.

Two narrow-sense heritability estimates were calculated at each Montana plantation from the variance components of the ANOVA. The first included 90% or more of the families planted regardless of the number of blocks required to achieve this percent. The second shows the effects of missing data on statistical results by sacrificing family observations to utilize the complete block representation. Only one set of heritability estimates was computed for each Idaho plantation (*Table 6*). Estimates apply only to the seven year total height. Complete block representation estimates ranged from .3064 to .5601 according to

Table 5. — Degrees of freedom and calculated F-values by source of variation for 7-year height between plantations.

Source	Condon X Lubrecht df	Condon X Lubrecht "F"	Condon X Lubrecht X Rye Creek df	Condon X Lubrecht X Rye Creek "F"	Condon X Lubrecht X Rye Creek df	Condon X Lubrecht X Rye Creek "F"	Lone Mt. X Tensed df	Lone Mt. X Tensed "F"	Lone Mt. X Tensed X Meadow Creek df	Lone Mt. X Tensed X Meadow Creek "F"
A (Site)[1]	1	2022.53*	2	988.54*	2	791.00*	1	10.18*	2	125.36*
B (Family)[2]	203	3.34*	85	4.89*	117	3.17*	236	4.80*	95	5.38*
AB (Site X Family)[2]	203	1.75*	170	1.74*	234	1.46*	236	2.28*	190	1.91*

[1] Calculations followed Satterthwaite-Cochran procedure (Bancroft 1968).
[2] Calculations followed the Standard procedure (Bancroft 1968).

* Statistically significant at the .01 level of probability.

Table 6. — Narrow-sense heritability estimates based on family means within each plantation as calculated from the ANOVA.[1]

PLANTATION NAME	NUMBER OF BLOCKS	% OF TOTAL NUMBER OF FAMILIES PLANTED	h^2
Rye Creek	2	92	.4903
Wolf Creek	4	91	.3143
Condon	2	91	.6830
Lubrecht	3	90	.4585
Meadow Creek	5	91	.5601
Tensed	5	91	.5374
Lone Mt.	5	92	.5491
Rye Creek	5	57	.3064
Wolf Creek	5	78	.3902
Condon	5	44	.5352
Lubrecht	5	81	.4378

[1] Calculations followed Wright (1921), Falconer (1960) and Namkoong (1979).

location. Heritability estimates using 90% or more of the families planted for this study ranged from .3134 to .6830 depending on the location. Previous estimates using open pollinated progeny data for ponderosa pine height growth range from .362 (Squillace and Silen 1962) and .392 (Callaham and Hasel 1961) to .625 (Madsen and Blake 1977). Family heritability estimates on eleven year height ranged from .37 to .53 (Rehfeldt 1980b).

Narrow-sense heritability estimates between plantations (sites) ranged from .2292 to .4133 depending on which combination of plantations was chosen *(Table 7)*. The heritability estimates appear higher for those sites that had better survival. The Lone Mt. X Tensed combination used two plantations with the best survival whereas the Condon X Lubrecht X Wolf Creek combination, with the lowest heritability estimate, utilized three plantations that suffered winter frost damage and had poorer survival. The surprisingly high heritability for the Condon X Lubrecht X Rye Creek combination, which also had the same types of damage, perhaps resulted from the smaller number of common families across the sites. Thus, estimates for this study, with one exception, fall well within the range of other published reports of heritability in ponderosa pine (Rehfeldt 1980b, Madsen and Blake 1977, Squillace and Silen 1962).

Table 7. — Narrow-sense heritability estimates between plantations as calculated from the ANOVA.[1]

Plantation Combinations	Number of Families Common Across Sites	h^2
Condon X Lubrecht	204	.3223
Condon X Lubrecht X Rye Creek	86	.3627
Condon X Lubrecht X Wolf Creek	118	.2292
Lone Mt. X Tensed	237	.4133
Lone Mt. X Tensed X Meadow Creek	96	.3329

[1] Calculations followed Wright (1921), Falconer (1960) and Namkoong (1979).

The results reported here represent early performance of progenies for which seed was maintained separately by maternal parent. Considerable variation in 7-year tree height was encountered within each planting site.

Summary and Conclusions

The objective of this study was to examine genetic variation in seven year total height and to estimate family heritabilities, within and between sites, for ponderosa pine in the Inland Empire.

The sample consisted of 434 open pollinated families from each of 93 wild stands. The families were planted at test plantations located throughout the range of ponderosa pine in the northern Rocky Mountains. Seven-year total height data were obtained from all families at each of the test plantations.

Analyses of variance within plantations and subsequent F-values showed that families, blocks and the block × family interaction have significant ($\alpha = 0.01$) effects on seven year total height. Family variation within each test plantation appears much greater than the variation due to block or the block × family interaction. Narrow-sense heritability estimates within plantations ranged from .3064 to .6830 depending on the site and the number of blocks used. The results clearly indicate substantial genetic variation and that ponderosa pine will respond favorably to selection.

Five analyses of variance between plantations and subsequent F-values showed that families, sites and the site × family interaction have significant ($\alpha = 0.01$) effects on seven year total height. At the Idaho plantations, family variation between sites appears greater than the other two sources of variation. However, the plantations in Montana show site variation to be greater than the variation due to family or due to site × family interaction.

From the ranking of family mean heights at each plantation it was found that specific families grew faster at specific sites. Significant genotype × environment interactions occurred within and between all of the test plantations, but trends were not apparent. The reason for this is the young age of the trees and associated large variation in height, However, time may show more distinct differences as seen in earlier studies (Conkle 1973 and Steinhoff 1970) in which early performance was not a good predictor of longterm growth. Substantial time could be saved in tree improvement if outstanding performers could be recognized early. However, until dependable juvenile-mature height growth correlations can be established in this material, the results of this study should be regarded as preliminary and used with caution.

In the meantime the use of local seed sources may be the safest procedure for planting ponderosa pine in the northern Rocky Mountains.

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Variation in growth and branching characteristics of Pinus attenuata

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Abstract

Seed of *Pinus attenuata* from natural stands in western North America was sown in Canberra in 1960. Seedlings from 39 seedlots were planted in 1961 at an altitude of 770 m in the Australian Capital Territory.

After 12 years growth the heights and diameters were weakly inversely correlated with latitude of seed source. There was also a weak inverse correlation between tree height and the altitude of seed source. Differences in growth and branch characteristics among the seed sources were substantial. While statistically significant, the phenotypic correlations among these traits were not strong. The most vigorous trees, which also displayed relatively fine branches, were from the Coast Ranges of California below altitudes of 1000 m. Subsequent infection by *Dothistroma* caused an appreciable loss of foliage, but some provenances were little affected and the ranking on growth was little changed at 20 years of age.

Key words: *Pinus attenuata*, knobcone pine, provenances, growth, branching, variation, *Dothistroma*.

Zusammenfassung

Im Jahre 1960 wurden Samen aus natürlichen Beständen von *Pinus attenuata* in Nordwest-Amerika in Canberra ausgesät. Im Jahre 1961 wurden die aus 39 Samenproben angezogenen Sämlinge in 770 m Höhe im Bereich der Hauptstadt Australiens ausgepflanzt. Nach 12 Jahren ergab sich eine schwach negative Korrelation zwischen Baumhöhe bzw. Baumdurchmesser und der geographischen Breite der Saatgutherkunft. Die Baumhöhe und die Höhe ü. NN der Saatgutherkunft waren ebenfalls schwach negativ korreliert. Es gab erhebliche Unterschiede im Wachstum und im Zweigcharakter zwischen den Herkünften. Trotz statistischer Signifikanz waren die phänotypischen Korrelationen unter diesen Merkmalen nicht streng. Die leisstungsstärksten Bäume, die auch verhältnismäßig feine Äste aufwiesen, stammen aus dem kalifornischen Küstengebirge aus Höhen unter 1000 m. Nachträglich auftretender *Dothistroma*-Befall bedingte einen bemerkenswerten Laubverlust, aber einige Provenienzen wurden wenig angegriffen, und die Klassifizierung nach der Wuchsleistung blieb im Alter 20 nur wenig verändert.

Résumé

On a semé à Canberra en 1960 des semences de *Pinus attenuata* pris dans des peuplements naturels de la région occidentale de l'Amérique du Nord. Les plantes résultant de 39 lots de semences ont été établies en 1961 à une élévation de 1.000 m au Territoire Capital australien.

Au bout de 12 années de croissance on a trouvé qu'il existait une corrélation faiblement inverse entre la hauteur et le diamètre des arbres et la latitude d'origine des semences. Les différences relatives à la croissance et aux caractéristiques qui existaient entre les provenances étaient importantes. Quoique statistiquement signifiantes, les corrélations phénotypiques entre ces traits n'étaient pas étroites. Les arbres les plus vigoureux, qui montraient également de relativement belles branches, provenaient de la Chaîne Littorale de Californie, d'élévations de moins de 1.000 m. L'attaque ultérieure de *Dothistroma* a entraîné une perte considérable de feuillage, mais quelques provenances demeuraient peu affectées et la classification selon la croissance ne s'était changée que peu à l'âge de 20 ans.

Introduction

The Californian closed-cone pines, *Pinus attenuata* Lemm., *P. radiata* D. Don and *P. muricata* D. Don, form a