Geographic Variation of early growth and frost resistance in Douglas-fir*)

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1. Introduction

In the years, 1962 and 1963, Klaus STERN — then a member of the Schmalenbeck institute of forest genetics — initiated a provenance study in Douglas-fir. The aim of this study was to test the early performance of provenances in a poor site known for its risk of late frost. In addition, another new aspect of the study was to compare seed lots of the northwestern part of the distribution range with southern lots. The latter has rarely been included in one of the numerous previous studies in Europe (cf. SCHOBER 1963). However, more recent studies do not neglect the southern part of the distribution range (cf.. BIROT 1972).

Recently, HERRMANN (1973), STEPHAN (1973) and STERN et al. (1974) reported on the field results of this study. The present publication is based on newly-collected data and on further statistical analyses run after additional computational checks were made on the previously presented data.

2. Material and Methods

The design of the field tests has been described in detail by HERRMANN (1973) and by STERN et al. (1974). Only a few informations on the material may interest here: *Figure* 1 shows the geographic origins represented in the three tests. Experiment no. 3 contains 74 different provenances. Seven of these were repeated to give the 81 provenances required for a lattice design. However, this particular condition of the layout was neglected and the design treated as one in complete randomized blocks. A subset of 56 of these provenances forms experiment no. 4. Finally, experiment no. 5 is one year younger and is comprised of more lots from the southern part of the distribution range of the species. The three field tests are located in the same area in Northwest Gerrnany.

There are four replications in each of the three tests; 16 trees were planted per plot. As a rule, all traits were observed in the individual trees. Details of character assessment were also reported by STERN et al. (1974). A rating system was applied for both winter frost damage (0 corresponding to no damage, 5 to most severe damage) and late frost damage (percentage of shoots killed). Winter frost damage observed in the field may have two causal components: damage induced by low temperatures occurring early in winter and/or damage induced by frost drought. These phenomena could not be discriminated in this study. It was believed that the degree of damage in these instances was a better indicator of the tolerance of the provenances than the percentage of affected trees. In addition to scoring the degree of winter frost damage, the killing of the terminal bud was noted for every tree. The numbers of such trees were asssessed in summer if the terminal bud had not flushed and were converted to percentages of the surviving trees. The other trait yielding percentages was mortality, both of these traits were subjected to statistical analysis without transformation. For all the statistical analyses run with both original and transformed data there was no major difference in either test statistics or relative magnitude of error variation. The statistical treatment used was the unweighted analysis of plot means or provenance means.

Originally, STERN subdivided the area covered by the sampling into 8 regions. In the present study this number was reduced to 4 in order to attain greater simplicity and to have more samples within the individual regions. The group membership of the provenances is shown in figure 1. Region 1 consists of 31 seed lots that represent Oregon and Washington west of 120° longitude, and Vancouver Island. Region 2 is represented by lots from Washington and Oregon east of 120° longitude, Idaho Montana, and two lots from Alberta. Provenances from Colorado and Utah were combined to form region 3 while the origins that constitute region 4 are from Arizona and New Mexico. A single provenance is from Mexico (region 4) at 25° latitude; the northernmost lot came from British Columbia (region 1) at 52° latitude.

HERRMANN (1973) listed the number of trees sampled in seed collection and indicated that generally the seed of very few trees enter a seed lot. The entries of experiment 5 consisted of only single tree progenies.

The line of demarcation between the coastal form, Pseudotsuga menziesii var. menziesii, and the Rocky Mountain form, P. menziesii var. *glauca* (BEISSN.) FRANCO (cf. CHINC and HERMANN 1973) was recognized by letting all P. menziesii var. menziesii origins represent region 1.

3. Results and Discussion

3.1 Variation of provenance means between regions

A statistical model was used to test the significance of differences between these four regions and to estimate the variation among those regional means relative to the variation arnong provenances of the same regions. The sum of squares between all provenances was broken up so that the two mean squares and variance components could be estimated. *Table* 1 summarizes the analyses of variance of the various observations of tree height, frost damage and mortality. With only one exception the differences among the regions are significant. In all traits other than mortality these differences were responsible for the greater part of the variation among all provenances. This result is unexpected since the small numbers of individual seed trees could have been responsible for more variance unexplained by the applied statistical model.

The prevailing of the between-regions component is most pronounced in winter frost and tree height. In the loss of the terminal bud and late frost little consistency is found in these estimates over years. Only in mortality do the regions explain a moderate percentage of the total variance. The differentiation among provenances immediately after planting was low and increased only slightly since then.

Due to less exposure of experiment no. 5 only minor differences in frost damage and mortality occurred. This experiment was also remarkable in that almost half of the

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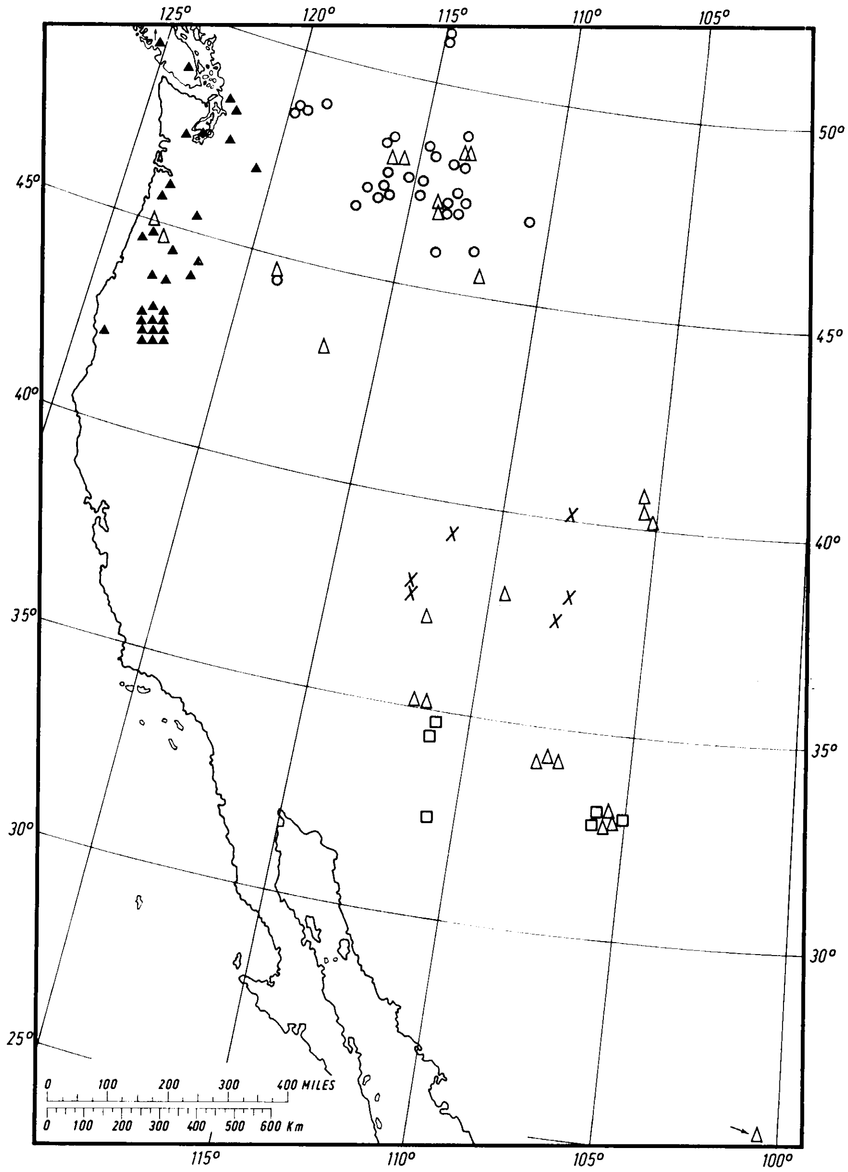

Figure 1. — Geographic location of the places of origin of 99 provenances. The 25 origins denoted by △ are planted in experiment no. 5. The other 74 are denoted by different symbols according to the region they were assigned to: ▲ region 1, ○ region 2, × region 3, and □ region 4. — The locations of some of the origins are only approximate since they possess virtually the same position but differ in elevation only. In drawing this figure, map 80-W of LITTLE (1971) was used.

traits did not reveal important provenance variation within regions.

The means computed for the regions are given in *table 2.* In the two larger tests the provenances from region 1 suffered most by winter frost in the terminal buds and the other parts of the trees. Second were the trees with the southernmost origins, while the other two regions were affected to a lesser extent. These results could not be observed in late frost as the date in spring when the causal frost occurred is unknown. It can only be inferred from other tests that some individual lots may have escaped the frost due to their particular phenology, or for some other reason. The damage by late frost is however no indicator of early flushing. The variation in mortality is mainly due to the loss of considerable percentages of the planted trees in some provenances from region 1. The mortality percentage does not increase regularly due to errors in counting.

The effect of atmospheric conditions on the experimental trees in the field cannot directly be compared with the response to treatments in potted young trees or cut-off branches in the growth chamber. The latter method of testing the potential value of provenances has well- known advantages. The results presented in the present paper neither required simulation of actual conditions nor subjecting the trees to an artificial environment. The decision to study field tests exclusively was made in order to obtain data on frost damage, height growth and mortality in the same trees simultaneously so that practical conclusions could be drawn. The reported provenance means have to be seen from this angle.

In experiment 5, region 1 is represented by two lots originating from west of the Cascade ridge. These two progenies are among the fastest growers up to the age of 11 years. In the other tests there was no such difference between regions 1 and 4 (the other region where height growth is above average).

Table 1. — Summary of the analyses of variance run for the individual traits and field tests. The entries are variance components, expressed as percentages of their sums. Asterisks refer to 5,1 and .1 per cent level of significance.

Experiment number		3			4			5		
source of variation		regions	provenances	error	regions	provenances	error	regions	provenances	error
d.f.		3	70	219	3	52	165	3	21	96
trait	age[1])									
tree	6	52***	36***	12	59***	31***	10	65***	22***	12
height	8	44***	41***	15	39***	42***	19	60***	24***	16
	11				35***	38***	26	61***	23***	16
winter	7	80***	6***	14	80***	5***	15	61***	3	36
frost	8	76***	8***	16	77***	6***	17	53***	7***	40
	9	83***	6***	11	73***	9***	19	45***	31***	24
terminal	7	11***	7*	82	65***	3*	32	32***	0	68
bud	8	19***	9*	73	28***	0	72	25***	3	73
	9	62***	8***	30	62***	2	37	24***	27***	49
late	7	46***	23***	31	56***	14***	30	44***	6*	49
frost	8	62***	4*	34	18***	4	78	38***	5*	57
	9	72***	13***	15	55***	8***	36	28***	1	71
mortality	6	18***	22***	60	12**	21	67	0	0	100
per cent	7	8*	27***	65	13**	17	70	3	3	94
	8	10**	28***	61	5*	12	83	2	0	98
	9	28***	27***	45	6*	9*	85	2	11*	87
	11				3	14**	83	2	17**	81
	12	17***	30***	53						

[1]) Experiment no. 5 was initiated 1 year later.

Table 2. — Regional means for the traits assessed in the three field experiments.

Experiment number		3				4				5			
Region		1	2	3	4	1	2	3	4	1	2	3	4
number of provenances		31	31	6	6	21	24	6	5	2	9	5	9
trait	age[1])												
tree	6	63	39	42	67	81	45	49	78	70	40	33	47
height	8	91	63	55	100	126	87	76	133	142	91	67	97
	11					215	157	118	212	300	220	142	205
winter-	7	2.9	.6	.7	1.5	2.0	.1	.1	.3	1.1	.1	.1	.1
frost	8	1.9	.6	1.0	1.2	2.1	.5	1.1	1.0	1.1	.0	.4	.4
	9	2.5	.6	1.0	1.2	1.6	.4	.7	1.0	1.2	.1	.3	.7
terminal	7	93	88	96	96	67	19	38	50	40	15	23	32
bud	8	16	17	35	27	18	6	16	10	6	4	13	13
	9	96	65	87	94	46	8	32	61	6	2	6	11
late	7	6.4	4.8	5.5	6.6	2.7	.9	1.3	2.2	1.0	.2	.3	.5
frost	8	1.1	.4	2.3	2.8	.1	.1	.1	.2	.0	.1	.2	.3
	9	7.4	3.5	4.7	5.2	2.3	.3	.5	1.9	.2	.0	.2	.3
mortality	6	8	3	3	1	7	3	2	3	2	1	1	1
%	7	13	11	5	4	8	4	3	4	2	1	2	1
	8	13	9	4	5	9	6	3	4	2	1	2	2
	9	25	12	6	8	9	6	4	4	2	1	2	3
	11					8	7	4	4	4	1	3	3
	12	26	15	10	13								

[1]) Experiment no. 5 was initiated 1 year later.

At the age of 8 years the 13 provenances west of the Cascade ridge within region 1 averaged 103 cm, the 18 eastern provenances only 82 cm; this difference was highly significant, and confirming the results of numerous experiences made in central Europe and elsewhere. Significant differences might exist among contagious parts of other regions (cf. Kung and Wright 1972). However, one has to keep in mind the quantitative information contained in table 1.

In winter frost damage during the winter of 1967/68 (when the most severe damage at all occured), the western group averaged 3.05 and the eastern group 2.79. This difference was found not to be significant.

The difference reported above for height growth has to be observed in the light of the large difference in elevation. The western group had an average elevation of only 240 m above sea level while the group from east of the Cascade ridge averaged 970 m. This allows us to attempt to explain the variation among provenances by means of regression on geographic origin data and on some climatic data.

3.2 *Regression analyses*

From a practical point of view, the above analysis-of-variance model (where the effect of the regions conventionally was regarded to be a random effect) in conjunction with the following regression approach is essential. Only the existence of some regional or other pattern facilitates the search for parts of the distribution range where the most desirable provenances for follow-up studies or direct use in silviculture are to be expected.

For 71 provenances planted in experiment no. 3 data on 7 such variables was available, i.e.

1) degree of latitude (LA)
2) degree of longitude (LO)
3) elevation above sea level (EL)

The remaining four climatic data were taken from maps produced as overlays by LITTLE (1971); these are

4) precipitation effectiveness (P-E index, PE)
5) length of the growing season in days (DA)
6) precipitation or rainfall (PR)
7) plant hardiness (according to average annual minimum temperatures, HA).

One may doubt whether the latter group of data is appropriate in provenance research, since it is certainly a crude method to use these maps where the lack of detail is obligatory. However, one must not forget that the precise information on the geographic origin (though it can easily be directly applied in locating desirable seed sources) is only a replacement. Adaptation to a large extent must be due to the direct effect of climatic factors, thus making the geographic-data approach necessarily indirect.

The 7 variables listed above were used as variables, x_1 through x_7 of a regression model. This model was augmented by variables x_3 through x_{14} representing the squares of the variables in the former group. In order to obtain a good estimate of the maximum degree of determination the 21 cross-products among x_1 through x_7 were entered as variables x_{15} through x_{35}. The longitude of the origin was included also as a cubic term (x_{36}) since this was suggested by the result of differences among the western and eastern part of region 1. Finally, three orthogonal contrasts (x_{37} through x_{39}) among the four regions should provide for variation among the regions that was unexplained by regression on the quantitative data. The last three variables should provide a means to (a) estimate the effect of the regions in comparison to the quantitative data alone, and (b) to study the additional fit due to including the regional membership after various subsets of quantitative variables have been accounted for. For instance, *figure 1* suggests that latitude, longitude and their product may describe the region membership of an origin. Another question is whether these variables yield the same degree of determination if one attempts to explain the variation among provenances derived from these regions. Regression models were fitted to the provenance means in all of the 16 traits assessed in experiment no. 3.

To avoid confusion by discussing only selected results the essential parts of *tables 3 and 4* are first summarized. *Table 3* lists the regressor variables that entered the complete model (0) and 23 partial models. The degrees of determination (R^2) of these various models are reported in *table 4*. Normality tests were made only after fitting the complete models. They generally did not yield deviations in the distribution of the residuals from normal distribution. However, an a priori risk of one chance significance still exists. The following points summarize the results:

1) There are no striking differences in the fit of the complete models. Estimates of R^2 are similar for the measurements of height growth and winter frost but vary considerably for the other frost data. Mortality in 1968 (age 7) displays an interruption of the general trend which was due to regarding a few too many trees as dead or missing (mortalities are estimated on the basis of only 64 trees).

2) Models (1), (2) and (3) are the simple linear regressions on variables that are conventially used to describe the geographic variation pattern. Besides the (positive) relation between winter frost damage and longitude there is not much to observe. In the late frost data, there is however a notable variation observations in the three successive years. Regressing the provenance means on all three variables simultaneously in model (10) means a large increase in R^2. In the winter frost data the degrees of de-

Table 3. — Variables that entered the regression models.

Model	d.f.	1 LA	2 LO	3 EL	4 PE	5 DA	6 PR	7 HA	8 LA**2	9 LO**2	10 EL**2	11 PE**2	12 DA**2	13 PR**2	14 HA**2	15 LA*LO	16 LA*EL	17 LA*PE	18 LA*DA	19 LA*PR	20 LA*HA	21 LO*EL	22 LO*PE	23 LO*DA	24 LO*PR	25 LO*HA	26 EL*PE	27 EL*DA	28 EL*PR	29 EL*HA	30 PE*DA	31 PE*PR	32 PE*HA	33 DA*PR	34 DA*HA	35 PR*HA	36 LO**3	37 REG.1	38 REG.2	39 REG.3
(0)	39	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
(1)	1	×																																						
(2)	1		×																																					
(3)	1			×																																				
(4)	1				×																																			
(5)	1					×																																		
(6)	1						×																																	
(7)	1							×																																
(8)	7	×	×	×	×	×	×	×																																
(9)	4				×	×	×	×																																
(10)	3	×	×	×																																				
(11)	6	×	×	×					×	×	×																													
(12)	9	×	×	×					×	×	×					×	×					×																		
(13)	3																																					×	×	×
(14)	14	×	×	×	×	×	×	×	×	×	×	×	×	×	×																									
(15)	28	×	×	×	×	×	×	×								×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×				
(16)	28								×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×				
(17)	35	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×				
(18)	36	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×			
(19)	10	×	×	×	×	×	×	×																														×	×	×
(20)	17	×	×	×	×	×	×	×	×	×	×	×	×	×	×																							×	×	×
(21)	31	×	×	×	×	×	×	×								×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×		×	×	×
(22)	31								×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×		×	×	×
(23)	38	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×		×	×	×

Table 4. — Degrees of determination (R^2, multiplied by 1,000) estimated in the various models listed in *table 3*. Least significant estimates ($\alpha = 0.05$) are entered in the bottom line.

Trait	age	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
		Model no.																							
tree height	6	885	58	124	187	221	437	295	524	683	596	580	694	742	479	807	857	865	874	874	699	825	863	876	885
	8	880	23	107	226	245	434	287	467	668	569	553	644	694	402	785	842	845	865	865	675	809	853	862	879
winter frost	7	948	11	522	338	273	207	362	689	802	730	780	809	824	852	855	908	910	922	923	872	908	933	937	948
	8	929	64	450	195	147	164	294	660	818	709	812	829	840	803	860	898	894	913	913	857	888	917	909	927
	9	946	37	505	213	160	78	297	574	828	689	800	828	839	863	870	901	901	917	919	899	910	940	938	945
terminal bud	7	637	164	1	9	0	0	4	63	267	145	210	214	237	233	356	545	550	587	593	336	391	592	572	635
	8	764	235	132	285	183	68	142	66	430	207	338	398	420	336	484	629	660	721	721	490	553	660	687	760
	9	905	230	155	21	70	141	134	486	693	519	660	702	709	742	771	790	793	818	827	787	823	887	872	902
late frost	7	792	161	76	25	77	80	62	328	507	382	434	456	513	497	602	703	689	724	724	574	643	766	739	792
	8	918	730	87	190	37	46	10	53	750	201	738	792	801	767	820	899	885	912	913	804	826	907	892	918
	9	912	59	333	132	165	83	223	511	673	592	625	698	716	735	797	839	847	870	876	764	826	895	890	911
mortality	6	601	7	199	67	10	1	54	73	265	170	233	261	306	261	296	523	489	553	585	341	357	547	549	581
	7	513	44	118	55	0	23	5	6	219	86	141	176	232	139	267	466	457	496	506	253	290	476	476	500
	8	605	14	158	78	0	8	21	38	273	149	164	210	246	176	289	544	547	577	593	307	333	558	570	596
	9	783	0	295	112	1	13	26	119	567	377	358	462	489	350	604	743	750	768	776	610	641	758	763	775
	12	784	0	205	90	0	25	13	63	53	293	254	397	441	239	557	723	749	763	780	552	596	736	765	775
$R^2_{0.05}$		669	52	52	52	52	52	52	52	186	127	105	168	222	105	306	519	519	616	629	240	355	561	561	656

termination already approach those of the full model.

3) Minor increases in R^2 following augmentation by the squares of the geographic variables in model (11) and their cross-products in model (12) show that the essential information is already contained in the three original variables of model (10).

4) Under the following models the prediction of the provenance means was based solely on the climatic data. Models (4), (5), (6) and (7) have all low estimates of R^2 like models (1), (2), and (3). The exception again is winter frost damage that could be predicted from HA alone with degrees of determination of about .6.

In model (9) the four climatic data are combined resulting in R^2 in the average being only slightly smaller than in the respective geographic data model (10). This indicates that the use of such maps has not a priori to be disapproved of.

5) Model (8) combines models (9) and (10) and it contains the seven original variables. R^2 is around .5 and is much superior to either (9) or (10).

6) Adding the squares of variables x_1 through x_7 leads to model (14) which in the average increases R^2 by .1. This is due mainly to curvilinearity with regard to the climatic variables. The increase in R^2 is most striking in the group of observations on mortality.

The further extension of the model by the 21 cross-products clearly increases the degree of determination (it averages .1 more in model (17)). The accounting for the cubic term x_{36} in model (18) just appears not to be worthwile.

7) Neglecting all informations on the origins except the fact that they are located in one of the four regions simply means putting the analyses of variance of the foregoing chapter another way. Model (13) has only three variables but the average R^2-value is only about .1 smaller than the value after fitting the former model (14) which contains as many as 14 variables. *Table 5* shows two examples of standard deviations after the fitting of these two models, both are close to the order of magnitude required for practical application.

8) Fitting the contrasts among regions in addition to model (8) is about as efficient as fitting them in addition to model (14). Models (19) and (20) also have similar R^2-values.

Fitting models (15) and (16) yielded the following information: Tests for reduction of fit after omitting the linear and square components of the seven basic variables indicated that the presence of the cross-products makes them dispensable. Even in the absence of the regions from the model, these cross-products apparently express the interaction of climatic factors that possibly have an impact on the genetic variation pattern.

9) The reduction of unexplained variation, due to fitting the regional in addition to the seven basic variables with or without certain transformations, i.e. models (14) through (17), was not significant. Models (20) through (23) have only slightly larger estimates of R^2. The better fit of model (19)

Table 5. — Standard deviations about regression.

Trait	age	mean	model (13)		model (14)	
			standard dev.	R^2	standard dev.	R^2
damage by winter frost	8	1.65	.47	.803	.50	.860
height growth	8	77 cm	19 cm	.402	13 cm	.785

relative to model (13) was however significant in some traits such as height growth. This clearly is an indication that the climatic variation within the regions does have impact on some traits. Also, the elevations of origins within a region shows considerable variation (cf. the average elevation of origins in region 1 west and east of the Cascade ridge).

3.3 *Consistency of regressions among regions*

In describing the variation pattern among stand or single tree progenies by regression on geographic data an implicit assumption is the validity of this regression in all parts of the distribution range.

The general experience with regressions of height growth on elevation is a decrease in tree height with increasing elevation. This is true for almost any study of this kind provided that the experimental site has lower elevation than most of the origins. However, the question in the present study is whether a given elevation is representative of a particular set of environmental factors regardless of the geographic position. In region 1, elevations range from 20 m to about 1,500 m above sea level; in region 2, they range from 610 m to 1,980 m; finally in region 4 the range is between 1,680 m and 2,640 m. Can we expect that regressions are parallel among samples having such different average elevations, and does an increase in elevation represent the same change in environmental factors in the northwestern part of the distribution range as 10 degrees of latitude further south?

Figure 2 shows the provenance means in some selected traits plotted against the elevation of the origin. The provenances represented are the 74 entries of experiment no. 3 that were also used in the regression studies of the foregoing paragraph. The symbols used in these plots are the same as in *figure 1*. For convenience elevation was selected as an "independent" variable (latitude or any of the climatic variables might have served just as well for demonstration).

Under ideal conditions the general regression lines for winter frost damage on elevation (with degrees of determination of approximately .25) could be elongated from close to sea level up to 2,600 m above sea level. The plots in *figure 2* at first do not reveal this condition. There are not even parallel regression lines with varying distance to the axis in the various regions. The variation among the regions is such that regions 1 and 2 hardly overlap at 7, 8, and 9 year of age. The data on late frost damage does not show a clear relationship and the pattern of differentiation among and within the regions varies greatly from year to year.

The last two plots of *figure 2* referring to height growth show the regression lines themselves. In the first two regions these regressions were significant. In regions 3 and 4 the positive slopes were not always significantly different from zero. They were however always significantly different from the negative slopes in regions 1 and 2. This is one of the cases of heterogeneity among the individual slopes within the separate regions. High-elevation provenances from the southern part of the distribution range thus are not inferior in early height growth, instead, they grow faster than the low-elevation sources. WRIGHT *et al.* (1971) did not detect any elevational trends in height growth.

This may be difficult to interpret biologically but one safe statement may be made: elevation as such cannot truly be representative of a set of environmental factors. The regression on elevation thus cannot be regarded as an estimate of an absolute relationship but has to take account of other factors such as the geographic latitude and/or region. This regression does not measure an elevational cline since the samples were not taken along a transect minimizing the simultaneous effects of other correlated environmental variables. MORGENSTERN (1969) has presented the results of such a designed sampling in another context.

Practically, the heterogeneity of regressions has a twofold impact. First, it means a lower estimate of the degree of determination or reduced efficiency of description and prediction. Secondly, predictions possess low validity in spite of a given estimate of determination. The uncritical application of a statistical formalism may distort the true relations, whereas a more detailed study of these regressions may show that a considerable part of the regression sums of squares is due to the heterogeneity among regions.

A large number of such regression analyses (GULLIKSEN and WILKS 1950) were run in order to find out whether the various traits measured have any peculiarities in this respect. A maximum of three regressores could be used owing to the small number of sources within regions 3 and 4. The determination generally was rather low and there was an erratic pattern among traits (dependent variables) and combinations of regressor variables with regard to a detectable heterogeneity.

3.4 *Combined analysis of two parallel tests*

As stated above, experiment no. 4 contains 56 out of the 74 sources of experiment no. 3. This set of 56 provenances was planted in two locations containing four replications each. The set of provenances in this rudimentary series of field trials is identical with the one in experiment 4 (representation of the regions is given in table 2). The combined analysis of these data may yield some further information on the reliability of conclusions drawn from experiments with small plots. *Table 6* summarizes this information.

After computing the averages over the two locations there still exists a wide range of variation among the provenance means. The difference in height growth between the shortest and the tallest provenance is still more than 1 m at the age of 8 years. The similarity of the means estimated in the two locations is measured by correlation coefficients above .9 and low percentages of the variance components due to interaction between all provenances (regions disregarded) and planting sites. A large amount of interaction variance in this case should decrease the correlations between means in the two tests. The research findings on winter frost damage are similar in that the correlation is close and the interaction variance, though significant as in all other instances, is small. The two locations have a similar macroclimate and a similar regime of soil factors responsible for provenance differentiation in tree height and winter frost damage. Hence they may be regarded as additional replications of the same environment.

The situation is different in the other traits. Despite a wide range in the percentage of trees with terminal buds killed by winter frost there is much more interaction. In two of the three years during the observation period the variance between sources is not significant, the correlation being very low. It has to be kept in mind that $r = .31$ means that one experiment yields less than 10 per cent of the information on provenance means estimated in the other experiment. It seems that this particular aspect of frost damage is greatly influenced by the "local" environment.

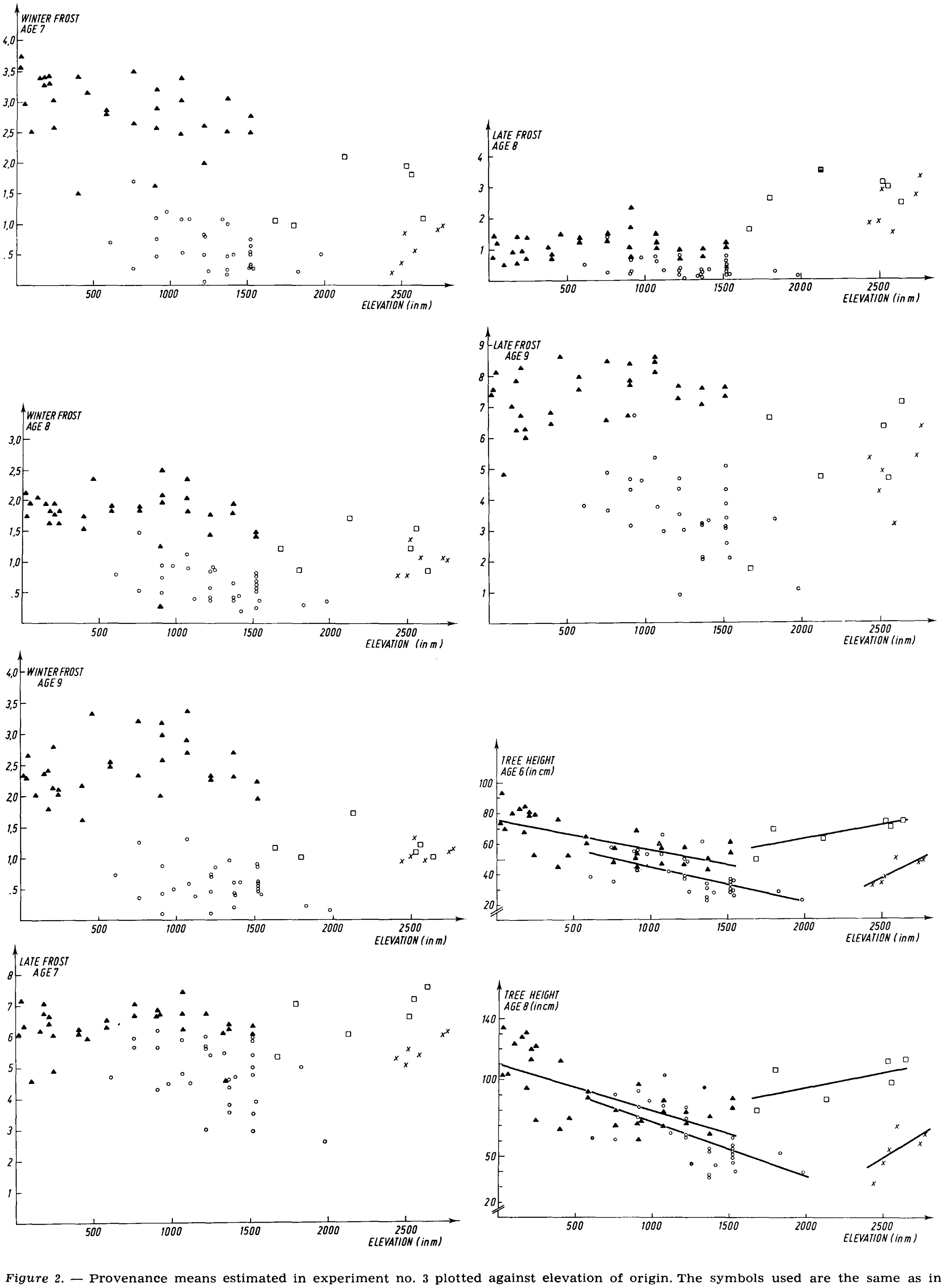

Figure 2. — Provenance means estimated in experiment no. 3 plotted against elevation of origin. The symbols used are the same as in fig. 1, i.e. ▲ for provenances from region 1, ◯ region 2, × region 3 and □ region 4.

Table 6. — Summary of information from combined analyses of experiments no. 3 and 4. The variance components are expressed as percentages of their respective sums.

Trait	age	range of provenance means min.	max.	correlation coefficient 54 d.f.	variance components provenances 55 d.f.	interaction 55 d.f.	error 330 d.f.
tree	6	25	101	.95***	85***	3***	13
height (cm)	8	48	163	.94***	78***	2*	20
winter	7	.1	3.4	.94***	80***	2*	18
frost	8	.2	2.4	.94***	75***	2*	23
	9	.2	2.7	.91***	72***	9***	20
terminal	7	40	89	.31*	10	42***	48
bud	8	7	36	.04	2	20***	79
	9	27	86	.78***	51***	6*	44
late	7	1.9	5.6	.73***	52***	10***	38
frost	8	.1	1.9	.42**	6	54***	41
	9	.6	5.9	.80***	54***	18***	28
mortality	6	0	15	.14	7	22***	72
	7	1	24	.04	2	23***	75
	8	1	23	.13	5	19***	76
	9	1	33	.26*	10	22***	68

The same is true with late frost damage: the response of the provenances to late frost is peculiar to a given plantation and a given year.

Though mortality shows a wide range from practically zero up to one fifth (age 8) and to one third (age 9), a large portion of variance is due to pooled error. Furthermore, the means in the two locations have little relationship with each other. However, due to the large experimental error involved, it can not be decided at this point whether differential mortality in the two tests is the consequence of the provenances getting adapted to the "local" conditions.

The existence of interactions reduces the general validity of the regression approach to locate the "best" provenances. Such predictions have then to be detailed to possibly small parts of the area where the species is to be grown in the future.

3.5 *Correlations among the provenance means of various traits assessed*

The regression approach taken above has some more practical disadvantages. Means of a given trait computed for each year allow detailed inferences but do not indicate the variation pattern of the average scores over a sample of successive years. However, this can be determined with additional computations. A more severe problem is the separate analysis of the various traits that may be closely correlated. In experiments far outside the natural range the correlations among the traits gain importance. The structure of the data in the present study prevents a multivariate analysis that would allow some further genetic interpretation of the multiple observations.

The correlations are more closely examined in a correlation matrix *(table 7)* which was estimated from the 74 provenance means in experiment no. 3. Another observation of winter frost damage was based on a plot-wise assessment made by Stern after the winter following planting.

The correlations among the two height measurements is almost complete. This coefficient was expected to be the largest since the 8-year height of trees, to a large portion, consists of the 6-year height. Besides errors of measurement the correlation is reduced only by differential mortality and differential height increment. Frost damage did not necessarily lead to loss of the leader. Another group of traits with close intercorrelations are the mortality assessments. The difference to unity in these coefficients is due only to minor errors of counting and to differential loss of trees in the intermittent periods. Typically, the correlations among successive years are stronger than if there are two years intervals.

In the three other groups of traits, the correlations estimate the similarity in response to the annually renewed atmospheric effects. The winter frost data are very closely correlated. Only the earliest assessment is an exception which may reflect some response to transplanting or late effects of the nursery where the planting stock was raised without replication. The negative sign of these coefficients is most remarkable. The various assessments of the loss of the terminal bud and damage due to spring frost are only loosely correlated and show considerable variation in magnitude. This could be inferred from the actual nature of these damages and from other aspects of the experimental results reported above.

There is no clear pattern of correlations between the three groups of data on frost damage. The coefficents between winterfrost and late frost have the same sign if one disregards the results of the earliest assessment of winter frost. Thus it is usually the same provenances that suffer, to a similar extent, from both winter and spring frosts. The loss of the terminal bud in some years is correlated to late frost and winter frost, in other years it is not. This is in line with the large experimental error of this trait which therefore looses much of its biological significance.

The data on winter frost damage are very loosely correlated to observations reported by Gerhold (1965) on provenances included in both his and the present tests. A trait like winter frost damage may have been obscured by snow. If there are provenances with height growth below the thickness of the snow cover they should have suffered less from winter frost. The plot diagrams of the provenance means in these traits studied on a display terminal did not indicate such a condition. The same was true for the correlation with Gerhold's data.

The most recent mortality data show the closest correlations with the frost damage data so that sensitivity to frost offers itself as a cause of mortality. A clear interpretation, however, is not possible since it is unknown whether it really was the most sensitive trees that died. The correlation among the means should change due to the mor-

Table 7. — Correlations among provenance means in experiment no. 3 (72 d.f.)

trait	age	tree height	winter-frost				terminal bud			late frost			mortality		
		8	5	7	8	9	7	8	9	7	8	9	7	8	9
tree height	6	.98	—.07	.75	.66	.57	.23	—.32	.60	.62	.39	.62	—.18	—.08	.01
	8		—.15	.67	.56	.46	.14	—.43	.50	.55	.27	.53	—.21	—.13	—.06
winter frost	5			—.20	—.11	—.14	.08	.45	.08	—.02	.54	—.17	—.25	—.25	—.18
	7				.91	.91	.34	—.20	.72	.64	.28	.83	.19	.33	.50
	8					.95	.46	.02	.82	.67	.43	.85	.18	.32	.57
	9						.43	—.04	.82	.69	.35	.91	.26	.41	.65
terminal bud	7							.38	.55	.56	.53	.49	.14	.21	.32
	8								.11	.02	.47	—.08	.11	.11	.15
	9									.82	.62	.87	.11	.21	.37
late frost	7										.55	.83	.00	.15	.28
	8											.44	—.21	—.14	.03
	9												.14	.29	.49
mortality	7													.92	.76
	8														.83

tality itself. A further explanation of this is made in the following section.

Finally, height growth and mortality are uncorrelated. The moderate positive correlations among height growth and frost damage may be interpreted in two ways: either the faster the growth of a provenance the more liable it is to frost or, conversely, the more sensitive a provenance the faster its growth in spite of its sensitivity. The results of this study indicate that the latter is a reasonable explanation of this condition. A causal interpretation of the relations among height growth, mortality and frost damage are possible only if the records of the single trees are studied in detail. However, this has little to do with the present problem of provenance variation. It must be remembered that many such correlations are due to the fact that the provenances that enter such an experiment rarely can be looked upon as a random sample of subpopulations in the strict sense of the word. Correlations then may be a consequence of conditions peculiar to a nonrandom sample. Stern and Roche (1974, loco citato p. 114 ff.) discuss genetic theories on the basis of such correlations among quantitative characters in provenance studies.

3.6 *Environmental correlations*

A matter that does have some bearing on the experimental procedure and on the interpretation of the results is the environmental correlations among the traits. They were estimated from experiment no. 3 with 218 degrees of freedom after computing the error deviations of the plot means. Rather than reporting the complete correlation matrix only an outline is presented. *Table 8* gives the coefficient averages for the various groups of measurements. The largest coefficients occur on the main diagonal. The correlation between the two measurements of height growth ist .86, the average of the 10 correlation coefficients among the 5 assessments of mortality is .60; these coefficients were expected to be large since both height growth and mortality are cumulative processes. The incidence of a certain degree of winter frost damage in a given plot in a given year is however almost independent of the conditions in other years. This independence is even more pronounced with the loss of the terminal bud, where the average coefficient is only .05. This means that the plots as parts of the test site do not show the tendency to be more liable to frost in successive years. In other words, the sole causative agents appear to be the effects of the provenance (which at this point was corrected for) and the weather conditions that are common to all parts of the test site. In addition, trees having suffered from winter frost or having lost their terminal bud are not necessarily preconditioned to be damaged the following year. Late frost, however, does appear to be influenced by features of the individual plots like the occurrence of grass cover or minor variations in the level of the soil surface. The average of the three coefficients among the three successive measurements is slightly larger and equals .31. In this study coefficients bearing different signs did not compensate each other, but the averages of the absolute values of the coefficients are similar.

Correlations between groups of measurements are all rather weak except between late frost and the two other forms of frost damage. The present analysis does not allow decisions whether these correlations are due to mutual conditioning or other causes. Height growth and mortality show little correlation with any of the other measurements so that reduced height growth or increased mortality are hardly the consequence of frost damage.

Table 8. — Summary of error correlations.

	tree height	winter frost	terminal bud	late frost	mortality
tree height	.86	—.05	—.13	—.02	—.19
winter frost		.19	.11	.32	.05
terminal bud			.05	.23	.05
late frost				.31	—.01
mortality					.60

The results of the correlation analyses suggest that observing frost damage in a sample of years yields additional information on the behavior of the provenances. This is also true with winter frost since in other parts of central Europe there existed cases of severe winter frost leading to loss of essential parts of the experimental material. This risk has to be studied before provenances or groups of provenances can be recommended for mass-growing.

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Summary

Traits observed in tree field tests were growth, damage by winter frost and late frost, loss of the terminal bud, and mortality. Data on the various types of frost damage were collected during three successive years. The provenances represented four geographic regions.

Analyses of variance yielded estimates of variance components between regions and between provenances within regions. The former components were mostly significant and larger than the latter.

Three geographic and four climatic data of the origins contained less information on the provenances than their region membership. Simple analysis of variance thus was superior to a multiple regression model in describing the variation pattern of all provenance means.

Regressions of provenance means on both geographic and climatic data within regions were mostly not significant. The greater part of the estimates of regression coefficients were not consistent among regions.

Two field tests having 56 provenances in common gave similar results on tree height and winter frost damage. Results on mortality were uncorrelated. The correlations of terminal bud loss and late frost damage varied greatly from year to year.

In some traits the correlations among provenance means computed in three subsequent years varied greatly. It can be inferred that repeating observations of frost damage over a sample of years considerably increases the amount of information on provenances. The correlations between the three observations of late frost damage had a moderate environmental component. The closest correlations occurred between tree height, mortality and frost damage.

Key words: Pseudotsuga menziesii (Mirb.) Franco, Field tests, Provenances, Analyses of variance, Growth, Frost damage, Mortality.

Zusammenfassung

In drei Herkunftsversuchen mit Douglasie wurden das Höhenwachstum, Schäden durch Winter- und Spätfrost, der Verlust der Gipfelknospe im Winter sowie die Mortalität beobachtet. Frostschäden wurden während dreier aufeinanderfolgender Jahre aufgenommen.

Varianzanalysen erbrachten Schätzungen von Varianzkomponenten für Unterschiede zwischen Regionen des Verbreitungsgebiets und zwischen Beständen innerhalb der Regionen. Erstere waren meist signifikant und größer als die letzteren.

Die Regionszugehörigkeit enthielt mehr Information über die Herkünfte als drei geographische und vier klimatische Angaben über die Herkunftsorte. Zur statistischen Beschreibung des Variationsmusters zwischen allen Herkünften eignete sich daher die einfache Varianzanalyse besser als ein multiples Regressionsmodell.

Regressionen der Herkunftsmittel auf geographische und klimatische Angaben der Herkunftsorte innerhalb einzelner Regionen waren im allgemeinen nicht signifikant. Der Großteil dieser Regressionskoeffizienten war zudem regionsweise verschieden.

Zwei Feldversuche mit 56 gemeinsamen Herkünften erbrachten ähnliche Ergebnisse über Höhenwachstum und Winterfrostschäden. Die Ergebnisse über die Mortalität waren unkorreliert.

Bei einigen Merkmalen wechselten die Korrelationen zwischen den jährlich erhobenen Mittelwerten sehr. Man muß den Schluß ziehen, daß die mehrfache Aufnahme der Frostschäden in aufeinanderfolgenden Jahren einen erheblichen Informationszuwachs über die Herkunftsmittel bedeutet. Die Korrelationen zwischen den Spätfrostschäden in drei Jahren hatten eine spürbare Umweltkomponente. Die engsten Korrelationen bestanden zwischen Höhenwachstum, Winterfrostschaden und Mortalität.

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