

sis height/width, and a correlation of .94 with cone serotiny. The second principal component had a moderately large negative correlation with specific gravity (-.52), and a moderately large positive correlation with cone volume (.51), a result which was similar to that for the second principal component for the individual cone data. However, there was a difference between the two cases in that the second principal component for the location means also had a moderately large positive correlation with the ratio of cone width to cone length (.51). This suggested that this character was of more importance for distinguishing variation among locations than it was for distinguishing variation among individual cones. In terms of geographic regions, this second component separated the Rocky Mountain locations from the closed-cone coastal populations. The third principal component for the location data had a moderately large positive correlation with cone volume (.64) and relatively small correlation with specific gravity (.03), thus, it had essentially the same interpretation as for the principal components analysis of the individual cones, only the sign of the axis was reversed with respect to cone volume.

The fact that the first three principal components accounted for 94% of the variance suggested that there was probably not much distortion in representation of the data structure for the locations by a three dimensional stereo-

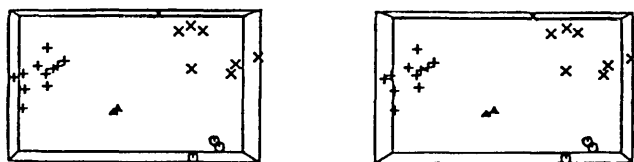


Fig. 3. — Stereogram of the 24 locations plotted on their first three principal components. Circles identify the populations with serotinous cones of the coastal region. Triangles identify the populations with non-serotinous cones of the coastal region. Plus signs identify the populations of the Sierra Nevada region. X's identify the populations of the Rocky Mountain region.

gram. However, it was considered desirable to investigate the extent of distortion due to reduction of dimensionality and possible non-linearity by an independent approach. The technique used was a correlation of matrices of resemblances between locations. One resemblance matrix being based on the full set of cone characters, while the other resemblance matrix was based only on the three first principal components. The correlation between the two sets of distances given by these two matrices was 0.993, indicating that the three dimensional stereogram provided a very accurate overall representation of the resemblances among locations.

The conclusion was that there appeared to be a strong group structure in the data, conforming to the geographic regions recognized by CRITCHFIELD (1957), with the addition that the closed-cone population from the coastal mountains of northwestern California was grouped with the closed-cone population from Mendocino.

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Genetic Structures and Expected Genetic Gains from Multitrait Selection in Wild Populations of Douglas fir and Sitka spruce

I. Genetic variation between and within populations

By Y. BIROT and C. CHRISTOPHE

Institut National de la Recherche Agronomique, Station
d'Amélioration des Arbres Forestiers, Ardon, 45160 Olivet,
France.

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Summary

The paper reports results from nursery stage till age 12 on genetic variation between and within populations of two major conifer species: Douglas Fir and Sitka Spruce. The research is based on provenance-progeny test established with the IUFRO seed collection achieved in the late sixties, with two levels of sampling: population and single tree within population. For Douglas Fir, 371 open-pollinated progenies from 26 populations are under test whereas these numbers are respectively for Sitka Spruce

of 292 and 21. Studied characteristics were mainly: growth phenology (bud set, flushing), form (branching, stem straightness).

Classical patterns of geographic variation were observed for both species. Genetic parameters (heritability, genetic correlations) varied from one population to another, especially for Douglas Fir, but also changed with the time. Additive effects were found surprisingly high for Sitka Spruce offering good prospects of future genetic gains. It is concluded that the genetic structure (between and wit-

hin populations) should be investigated as the background of any breeding strategy.

Key words: Douglas Fir, Sitka Spruce, provenance, heritability, genetic correlation, genetic variation.

Zusammenfassung

Es wird über Untersuchungsergebnisse zur genetischen Variation zwischen und innerhalb der Population von zwei Hauptkoniferenarten, Douglasie und Sitkafichte, vom Baumschulstadium bis zum Alter 12 berichtet. Die Untersuchung basiert auf einem Provenienznachkommenschaftstest, der mit der IUFRO-Sameneinsammlung in den späten 60er Jahren, auf zwei verschiedenen Versuchsebenen, d. h. der Einsammlung von Populationen und Einzelstammabsaaten durchgeführt wurde: Bei der Douglasie wurden 371 frei abgeblühte Nachkommenschaften von 26 Populationen getestet, entsprechend bei der Sitkafichte 292 und 21. Die untersuchten Hauptkriterien waren Wachstumsphänologie (Knospenansatz, Austrieb) und Form (Verzweigung, Geradschäftigkeit). Für beide Arten wurden klassische Schemata der geographischen Variation beobachtet: genetische Parameter (Heritabilität, genetische Korrelation) variierten von einer Population zur anderen, besonders bei der Douglasie, änderten sich aber auch im Verlauf der Entwicklung. Überraschenderweise waren additive Effekte bei der Sitkafichte sehr hoch, und boten gute Aussichten für zukünftige genetische Gewinne. Daraus wird gefolgert, daß die genetische Struktur (zwischen und innerhalb der Populationen) als Hintergrund jeder Züchtungsstrategie untersucht werden sollte.

1 — Introduction

Before embarking on a large scale breeding programme of a given tree species, it is of major interest for breeders to find out the main genetic patterns concerning the traits to be improved. Several questions have to be elucidated:

- 1) What is the extent of geographic variation and what populations should be taken as basic material for further improvement?
- 2) What is the genetic structure of a population? Is the pattern consistent from one population to another?
- 3) Are the genetic parameters (heritability, genetic correlations) favourable (or not) for the breeder's objective?
- 4) What is the stability of these patterns over the time and over environmental conditions?

When these main questions are answered, then it is possible on this background to set up a breeding strategy and to predict the genetic gains which can be achieved through selection.

If much research work tackled the question 1, less efforts have concerned the questions 2, 3 and 4, even for important species used in reforestation programme, as Douglas Fir and Sitka Spruce.

For Douglas Fir, the main results have been published by NAMKOONG *et al.* (1972), BIROT (1976), CHRISTOPHE and BIROT (1979), for Sitka Spruce, by FALKENHAGEN (1974, 1977) and GILLET (1981) but concerning a juvenile stage. Additional papers concern other species: Norway Spruce (VALANCE, 1979), White Spruce (YING and MORGENSTERN, 1979), Ponderosa Pine (NAMKOONG and CONKLE, 1976), Maritime Pine (KREMER, 1981), Calabrian Pine (ARBEZ and MILLIER, 1972).

Most of authors studied variation of *height growth*, while less attention has been paid to *adaptative traits* as flushing time, second flush (lamina shoot), growth cessation (bud set), or *form traits* (stem and branching characteristics).

With respect to the different topics pointed out above, the present paper is a contribution to a better understanding of the genetic structure of two important species: Douglas Fir and Sitka Spruce. The study is based on an unselected sampling as well at population level as at individual level (within population) taken from the seed collections carried out under IUFRO between 1966 and 1970. The results are reported in two different articles. The present one deals mainly with the genetic patterns between and within populations whereas the second one concerns the use of multitrait selection index method in these populations.

2 — Material and Methods

2.1 — Seed lots sampling

Seed collections throughout the natural range were achieved under IUFRO in 1966—67 for Douglas Fir and in 1970 for Sitka Spruce in order to investigate geographic variation. The collectors picked cones from unselected trees (therefore representative of the natural variation) distant from each other of about 100 m. Each population was represented by an average of 15 wind pollinated progenies (for details see BARNER, 1971 and FLETCHER, 1976). Cones were processed separately and seeds were stored as single progeny.

Among the different populations, 26 were selected in Douglas Fir (ranging from northern to southern (Washington) along the western foothill of Cascades Mountains) and 21 in Sitka Spruce (ranging from southern British Columbia to middle Oregon), according to the general knowledge available at that time on the geographic variation of both species and the most valuable seed sources for the practical french forestry. Informations on provenances location are given in *Table 1*.

2.2 — Experimental designs

The main informations about the experimental designs used and the test sites as well at nursery stage as at field stage are given in *Table 2*. The Douglas Fir experiment planted with a small spacing was systematically thinned (rate: $\frac{1}{2}$) 7 years after planting so that the natural genetic variation is maintained. Thus the maximum number of 48 trees per progeny dropped to an average of 24. For Sitka Spruce in the field, the fully randomized single tree plots were clustered into incomplete block of 80 trees, each progeny being represented by at least 50 trees in the whole experiment.

2.3 — Assessed traits

The list of assessed traits is given in *Table 3*; they can be related to:

- a) Growth: total height, height increment, girth, lamina shoot, length on leader.
- b) Phenology: flushing, bud set, lamina shoot frequency.
- c) Form: forking, stem sinuosity, branching. For Sitka Spruce, the number of "minor" branches (i.e. branches appeared on internodes) was counted at age 8.
- d) Others: needle colour in Sitka Spruce (age 4).

2.4 — Data processing; variance analysis

Let X_{ijk} be the vector of performances on individual of block k from the progeny j from the provenance i . The general linear model can be written as a multivariate mixed model as below.

$$X_{ijk} = \mu + B_k + P_i + F_{ij} + W_{ijk} \quad (1)$$

Table 1. — Location of provenances.

	Name of the provenance	I.U.F.R.O. N°	State	Latitude (North)	Longitude (West)	Elevation (m)	Number of progenies
DOUGLAS FIR	Diablo-Dam	1046 (1)	W	48°43'	121°07'	420	15
	Concrete	1047	W	48°39'	121°43'	470	15
	Bacon Point	1049	W	48°36'	121°23'	500	13
	Marblemount	1050	W	48°35'	121°24'	120	15
	Sedro-Woolley	1051	W	48°32'	122°19'	60	15
	Darrington	1053	W	48°16'	121°38'	150	15
	Arlington	1054	W	48°13'	122°04'	90	14
	Sloan Creek	1056	W	48°05'	121°18'	650	14
	Granite Falls	1057	W	48°05'	122°02'	610	11
	Perry Creek	1059	W	48°03'	121°28'	120	15
	Gold Bar	1063	W	47°52'	121°39'	120	14
	Skykomish	1067	W	47°42'	121°20'	300	15
	North Bend	1069	W	47°28'	121°45'	150	15
	Denny Creek	1070	W	47°24'	121°32'	550	14
	Chester Morse Lake	1072	W	47°22'	121°40'	600	15
	Enumclaw	1075	W	47°16'	121°56'	240	15
	Parkway	1079	W	47°02'	122°44'	790	15
	Yelm	1080	W	47°01'	122°44'	60	14
	Alder Lake	1081	W	46°34'	122°17'	420	14
	Packwood I	1083	W	46°34'	121°40'	650	14
Packwood II	1084	W	46°34'	121°42'	300	14	
Randle	1088	W	46°33'	122°03'	330	13	
Castle Rock	1088	W	46°19'	122°52'	150	15	
Cougar	1090	W	46°05'	122°18'	500	14	
Yale	1091	W	46°00'	122°22'	120	14	
Prindle	1095	W	45°37'	122°06'	450	14	
SITKA SPRUCE	Bellingham	3001	W	48°45'	122°38'	15-30	12
	Port Angeles	3002	W	48°09'	123°44'	105	17
	Forks	3003	W	48°04'	124°18'	120-150	17
	Kalaloch	3004	W	47°42'	124°25'	30	14
	Brinnon	3005	W	47°42'	122°53'	3	18
	Shelton	3006	W	47°21'	123°09'	6	15
	Humtulsips	3007	W	47°14'	123°57'	150	16
	Hoquiam	3008	W	47°05'	124°03'	6	15
	Raymond	3009	W	46°41'	123°52'	15-30	15
	Naselle	3010	W	46°22'	123°47'	0-15	16
	Astoria	3011	O	46°12'	123°58'	0-15	15
	Mecanicum	3012	O	45°49'	123°46'	45	11
	Tillamook	3013	O	45°20'	123°53'	90-120	16
	Newport	3014	O	44°42'	124°04'	15-30	4
	Big Qualicum	3062	BC-VI	49°23'	124°37'	0	20
	Haney	3063	BC-HL	49°14'	122°36'	90-300	11
Vedder	3064	BC-HL	49°07'	121°56'	30	9 (2)	
Port Renfrew	3065	BC-VI	48°35'	124°24'	2	15	
Muir Creek	3066	BC-VI	48°23'	123°52'	0	15	
Stilliguamish	3067	W	48°07'	121°45'	300-360	16 (2)	
Blenheim	3073	BC-VI	48°54'	124°57'	180-240	5 (2)	

W = Washington, O = Oregon, BC = British Columbia } ML = main land
 VI = Vancouver island
 (1): In all figures and tables for Douglas Fir, numbers of provenances are cited without the prefix "10".
 (2): Because of their relatively poor performances at nursery stage the provenances 3064, 3067 and 3073 were dropped for the field stage.

with: μ = grand mean
 B_k = fixed block effects with $1 \leq k \leq K$
 P_i = provenance effects with $1 \leq i \leq I$
 F_{ij} = progeny within provenance i effects with $1 \leq j \leq J_i$
 W_{ijk} = residual

The estimates of genetic parameters arising from this model will be considered as valid only in our experimental conditions. According to the model (2), it was necessary to verify the homogeneity of variance — covariance matrices within populations. A one-way multivariate analysis was

Values of K, I, J_i are given for both species in Table 4.

Table 2. — Information on experimental designs.

Let Σ be a variance — covariance matrix; the random effects P_i, F_{ij}, W_{ijk} are assumed to be multinormal variates being respectively distributed as $(O, \Sigma_p), (O, \Sigma_f)$ and (O, Σ_w) with the usual assumptions about the linear model.

Location	DOUGLAS FIR			SITKA SPRUCE		
	Nursery	Field		Nursery	Field	
Name	Nancy	Cendrieux		Orléans	Loqueffret	
Region	Lorraine	Périgord		Centre	Brittany	
Latitude	48°47'	45°02'		47°55'	48°22'25"	
Longitude	6°18'E	0°50 E		01°52'E	3°48'36" W	
Elevation	240	220m		150	250m	
Annual rainfall (mm)	700	850		600	1000	
Basic material	artific.	Alluvial		alluvial	granite	
Design						
Year of planting		1971 autumn			1977 spring	
Seedling age at planting		4			4	
Spacing at planting (m)		2 x 1,5			3 x 1,5	
		Nursery	Before thinning	After	Nursery	Field
Mean number of trees per progeny	48				200	50
Plot size (number of trees/plot)	1	1	1	1	40	1
Max. number of trees per block (incomplete block)	260	280	140	11680	80	

For both species and for most of traits, block effects were significant. Since our objective was to compare genetic patterns within and between populations as well as to predict genetic gains in a given environment, it was decided to adjust the individual performances according to block effects and then to use a complete random model. Adjustment was as follows:

$$Y_{ijk} = X_{ijk} - \hat{B}_k$$

where \hat{B}_k is the estimate of B_k .

Subsequently, the nested model as below was performed, with the same symbols as above:

$$Y_{ijk} = \mu + P_i + F_{ij} + W_{ijk} \quad (2)$$

Table 3. — List of assessed traits (age is given from seed) — (Nursery stage was till age 4 for Douglas fir and Sitka spruce).

Traits	Species and age (years) of assessment	Unit or code	
		Sitka spruce	Douglas-Fir
Total height	TH 3, 4, 7, 8	1,2,6,7,8,10 ^x ,11 ^x ,12 ^x	cm
Height increment	HI 8 th year	6, 12 ^x	cm
Girth	G	12 ^x	cm
Flushing	FLU 4	2, 9	number of days or degree x days
Bud set	BS 4, 8		days after January 1st
Lamma shoot frequency	LSF 4,8		%
Lamma shoot length	LSL 8		cm
Needle colour	NCD 4		score (1=blue to 3=green)
Minor branches number	MBR 8		
Branch angle	BRA	12 ^x	score 1 to 5 (1=acute to 5=right)
Forking (or ramicorn)	FDR	12 ^x	number of defects : 0 to 5 (1)
"Bayonet" defect	BAY	12 ^x	score 0 to 5 (according to the intensity of the defect)
Stem sinuosity	SIN	12 ^x	score 1 to 5 (from straight to crooked)

*: The Douglas-Fir experiment has been systematically thinned at age 11 (rate 1/2) but the measurement of TH 10, 11, 12 were taken at age 12 so the assessments after age 9 concern an average of 24 individuals per progeny instead of 48 individuals at the beginning.

(1): The variable was transformed as 0 if the score < 3, as 1 if the the score is ≥ 3.

performed for each provenance i according to the random linear model:

$$Y_{ijk} = \mu_i + F_{ij} + W_{ijk} \quad (3)$$

where F_{ij} and W_{ijk} are multinomial variates respectively distributed as $(O, \sum F_i)$ and $(O, \sum W_i)$.

The estimations of all parameters were obtained according to the HENDERSON's model (SEARLE, 1971) with the computational procedures AMANCE (BACHACOU *et al.* 1981).

Table 4. — Experimental design.

	DOUGLAS FIR		SITKA SPRUCE	
	Nursery	Field	Nursery	Field
Number of reps or blocs (K)	48	48	5	148
Number of provenances (I)	26	26	21	18
Number of progenies per provenance (J_i)	$11 \leq J_i \leq 15$	1d	$4 \leq J_i \leq 20$	1d
Total number of progenies ($= \sum J_i$)	371	1d	292	262

Table 5. — Variance components (% of total variation) and individual heritability.

Traits	SITKA SPRUCE				DOUGLAS-FIR			
	σ_p^2 %	σ_f^2 %	σ_w^2 %	h^2	σ_p^2 %	σ_f^2 %	σ_w^2 %	h^2
TH 1					9.2	13.6	77.2	.60
2					9.4	10.6	80.0	.46
3	9.0	12.0	79.0	.52				
4	8.0	12.0	80.0	.53				
6					14.9	7.0	78.9	.33
7	8.7	7.6	83.7	.33				
8	12.5	9.2	78.3	.42	14.3	5.8	79.9	.27
10					15.6	6.2	78.8	.29
12					16.1	6.8	75.1	.33
G 12					16.2	6.4	77.4	.31
FLU 2					16.5	16.1	65.4	.84
4	5.0	8.0	87.0	.34				
9					19.1	19.1	61.8	.85
NCD 4		8.0	92.0	.30				
BS 4	13.0	12.0	75.0	.53				
8	10.3	7.8	82.0	.35				
LSF 4	0.2	2.0	97.8	.06				
8	11.9	8.9	79.2	.40				
MBR 8	7.7	6.8	85.5	.29				
BRA 12					↑.4	12.1	86.5	.49
SIN 12					1.5	9.1	85.4	.39

σ_p^2 = provenance
 σ_f^2 = progeny within provenance
 σ_w^2 = residual

3 — Genetic Variation

The results presented below will successively deal with the following points: components of total variation (provenance-progeny-individual), geographic variation (= provenance variation), within provenance variations (= between and within progenies). A comparison between populations of the latter will allow a comparative study of genetic parameters (heritability, additive genetic correlations).

3.1 — Components of total variation

According to the model (2) performed over all populations, the proportion of each component (σ_p^2 , σ_f^2 , σ_w^2) ver-

Table 6. — Coefficients of correlation of variance components between traits.

	TH 6		TH 8		TH 10		TH 12		G 12		FLU 9		SIN 12		BRA 12
TH 8	1.00		.92		.84										
TH 10	.89	1.00	.97		.89										
TH 12	.99	.99	1.00		.98										
G 12	.96	.96	.96	1.00	.96										
FLU 9	.37	.43	.43	.40	.27	1.00									
SIN 12	.89	.87	.87	.89	.78	.13	1.00								
BRA 12	.11	.19	.13	.10	.08	-.15	-.07	1.00							
	.15	.15	.14	.11	.17	-.07	-.07	.05	1.00						
	.16	.13	.08	.06	.23	.03	.23	.03	.23	1.00					
	-.14	-.13	-.12	-.12	-.04	.19	-.46	.19	-.46	.05	1.00				
	-.03	-.05	-.05	-.04	.00	.05	-.17	.05	-.17	.05	-.17	1.00			

A- DOUGLAS FIR : Field stage

	TH 4		TH 8		TH 7		TH 7		LSL 8		LSL 8		MBR 8		MBR 8
FLU 4	.18		.89		.97		.91		.83		.83		.87		.87
NCD 4	.42	.13	.20		.53		.53		.60		.53		.60		.53
BS 4	.80	.13	.78		.83		.83		.87		.87		.87		.87
LSF 4	.60	.11	.02		.30		.31		.96		.89		.96		.89
(1)	-.18	-.02	.09		-.19		.00		.52		.44		.52		.44
	-.02	.00	-.12		-.19		.00		.19		.00		.19		.00

Nursery stage

B-SITKA SPRUCE

first line : provenance level
 second line: progeny within provenance level
 third line : individual (= residual) level

(1) In fact, the variable used is the frequency of individual without lamma shoot.

sus the total variation σ_t^2 was estimated for all traits; these values are given in Table 5. The mean values of intrapopulation heritability h^2 estimated by pooling all populations as the ratio $4 \hat{\sigma}_t^2 / \hat{\sigma}_f^2 + \hat{\sigma}_w^2$ are listed in the Table 5 too. Coefficients of correlation between traits at different levels (provenance-progeny-individual) are given in Table 6.

For Douglas Fir, the following figures were observed:

For total height at nursery stage the variation between progenies within provenance (σ_f^2) was of the same magnitude as the variation between provenances (σ_p^2) but at field stage, σ_p^2 was 2.5 times higher than σ_f^2 . At any stage the relative part of the residual variation (σ_w^2) was rather high (75 % to 80 %) as usually in this type of experiment. A sharp decrease with age of heritability values from juvenile stage to age 6 and then a stable level around .3 were noticeable.

For flushing time (in the field) the variation between provenances and between progenies within provenance was of the same magnitude (19 %); whereas the residual was only 62 %. This trait is really under strict additive genetic control ($h^2 = .95$) allowing good prospects of high genetic gains.

For stem form traits (sinuosity, branch-angle, forking) differences between progenies within provenance turned out as significant in the overall analysis. However for forking, this was due to only 8 populations: for the 18 others, progeny effects were insignificant. Consequently this trait was dropped out of the present study. Sinuosity and branch angle seem to be sensitive to environmental (or not controlled) effects: the relative proportion of residual variation was higher (85 %) whereas the part of the provenance variation was very-small (1.5 %). Due to rather high magnitude of the variation between progenies (respectively 12 % and 9 % for branch angle and sinuosity), heritability values of these traits were rather high (respectively .5 and .4). Such values and a large range of phenotypic variation enable the tree breeder to efficiently select.

At both level, provenance and progeny within provenance, correlations between flushing time (lateness) and height growth were rather weak (.4 and .3) but favourable. Correlations between sinuosity and total height as well as correlation between sinuosity and flushing were very low at progeny level (respectively $p = .1$ and $p = -.1$). By contrast, the correlations at provenance level between growth and sinuosity were highly unfavourable (.89), while flushing time and sinuosity were uncorrelated (.13).

Due to these correlations, selection of provenances at once vigorous, late flushing and with good stem characteristic seems to be quite impossible. But the within population selection might be of greatest interest. In this case, the multitrait selection procedure seems to be appropriate: increasing height growth and lateness of flushing with maintaining sinuosity and branch angle at the initial level appears to be feasible.

Correlations (at progeny and provenance levels) between all traits of vigour reached high values (at least .85). Between total height at age 2 (nursery) and age 12 (field), the correlation of progeny means was still good: .5, in spite of modifications in environmental conditions.

For Sitka Spruce, the same trend of relative decreasing with the time of σ_f^2 compared to σ_p^2 for height growth was noticeable. Heritability of total height (.4) was

higher than for Douglas Fir (.3). Conversely, flushing time showed much less variation between progenies ($\sigma_f^2 = 8 \%$) and also between provenances ($\sigma_p^2 = 5 \%$) so that the proportion of residual was high (87 %). Therefore the heritability level is surprisingly low for this trait ($h^2 = .3$). Some biases could be expected from the high temperatures of spring 1976: at provenance level, differences in flushing time did not exceed 3 days. Bud set, lamma shoots and minor branches number (age 8) had heritabilities of .3, .4. At age 8, correlations (at progeny level) of height growth with lamma shoots, minor branch number and bud set time, were all positive (.5, .6). Besides that, correlation (progeny level) between bud set time and lamma shoot frequency was very high (.9); minor branches number was also strongly correlated to bud set time (lateness) and lamma shoot frequency (.8). Therefore selecting for height growth and against late bud set, for less lamma shoots and for less minor branches (= less knotiness) will obviously be difficult.

A one-way variance analysis performed on progeny means data (the controlled factor being the provenance) showed that the correlations at progeny means between age 4 (nursery) and age 8 (field) were only of .47 for total height and .48 for bud set time. Only 2 progenies among the 30 most vigorous progenies at nursery stage were among the 30 most vigorous progenies at 4 years later in the field.

Table 7. — Provenances performances (F_p and F_p : provenance and progeny within provenances effects).

A - SITKA SPRUCE							
Prov.	TH 4(cm)	FLU 4(days)	BS 4(days)	TH 8(cm)	BS 8(days)	LSF 8	MBR 8
3001	xx 32.4	xx 111.6	xx 209.3	xx 192	xx 239	xx 26	xx 1.1
3002	xx 32.6	xx 112.5	xx 206.1	xx 190	xx 240	xx 19	xx .8
3003	xx 34.4	xx 111.9	xx 214.5	xx 205	xx 245	xx 30	xx 1.3
3004	xx 33.8	xx 113.3	xx 209.2	xx 203	xx 245	xx 34	xx 1.8
3005	xx 33.2	xx 112.1	xx 225.2	xx 189	xx 245	xx 24	xx 1.0
3006	xx 34.8	xx 111.8	xx 221.6	xx 197	xx 241	18	.8
3007	xx 36.1	xx 113.2	xx 220.3	xx 201	xx 244	xx 19	xx 1.2
3008	xx 38.4	xx 112.3	xx 237.0	xx 212	xx 249	xx 41	xx 2.1
3009	xx 37.2	xx 112.4	xx 227.5	xx 216	xx 251	xx 52	xx 2.7
3010	xx 37.5	xx 111.2	xx 226.8	xx 209	xx 248	x 41	xx 2.1
3011	xx 39.6	xx 111.2	xx 231.7	xx 226	xx 249	xx 50	xx 2.9
3012	xx 36.5	xx 110.9	xx 232.4	xx 215	xx 249	xx 49	xx 2.8
3013	xx 41.2	xx 113.0	xx 235.4	xx 225	xx 252	xx 56	xx 3.2
3014	42.6	xx 112.6	xx 232.4	x 245	xx 254	61	3.4
3062	xx 31.4	xx 110.4	xx 197.9	xx 188	xx 236	xx 16	xx .6
3063	xx 31.7	xx 111.3	xx 214.4	xx 183	xx 240	xx 23	1.0
3064	xx 31.5	xx 111.4	xx 208.5	---	---	---	---
3065	xx 33.3	xx 111.2	xx 218.7	xx 195	xx 242	xx 25	xx 1.1
3066	xx 39.4	xx 111.1	xx 225.9	xx 223	xx 248	xx 44	xx 2.8
3067	xx 31.3	xx 111.6	xx 201.4	---	---	---	---
3073	xx 35.1	xx 112.4	xx 202.3	---	---	---	---
Grand mean	35.4	111.8	228.4	269	245	35	1.8
F_p	xx 8.7	xx 8.8	xx 14.8	xx 17.3	xx 16.9	xx 12.2	xx 13.4
F_f	xx 10.8	xx 6.9	xx 10.9	xx 5.8	xx 4.8	xx 4.0	xx 4.1

B - DOUGLAS-FIR.					
Prov.	TH 12	FLU 9	FOR 12	SIN 12	BRA 12
1046	xx 529	xx 6.5	.56	x 1.99	xx 3.07
1047	652	xx 11.7	.59	xx 2.13	xx 3.04
1049	xx 619	xx 9.0	xx .55	xx 2.28	xx 3.05
1050	xx 633	xx 7.1	.76	xx 2.32	xx 2.97
1051	x 694	xx 10.3	.65	xx 2.61	xx 3.01
1053	x 674	xx 14.0	.56	xx 2.32	xx 2.99
1054	xx 683	xx 12.7	.61	xx 2.45	xx 3.06
1056	xx 689	xx 9.7	.52	1.97	xx 2.87
1057	xx 698	xx 13.7	.59	2.43	3.01
1059	xx 574	xx 10.1	.49	xx 1.95	xx 2.98
1063	x 655	xx 8.1	x .68	xx 2.44	xx 2.96
1067	xx 663	xx 12.2	.39	xx 2.12	xx 2.90
1069	x 643	xx 8.8	.86	xx 2.30	xx 2.96
1070	xx 626	xx 11.6	xx .56	xx 2.09	xx 2.98
1072	xx 612	12.2	xx .43	xx 2.04	xx 3.13
1075	xx 692	xx 11.8	xx .68	xx 2.47	xx 3.01
1079	xx 567	xx 11.1	.45	x 2.06	xx 2.91
1080	653	xx 7.7	.70	2.39	xx 3.09
1081	x 627	xx 9.9	.53	x 2.23	xx 3.05
1083	x 601	7.9	x .59	xx 2.11	2.92
1084	xx 608	xx 7.2	.69	2.09	xx 3.00
1085	666	xx 8.8	.61	xx 2.40	xx 2.70
1086	xx 677	xx 8.0	.58	xx 2.40	xx 2.99
1090	xx 639	xx 9.1	.47	xx 2.24	xx 2.88
1091	664	xx 8.6	x .63	xx 2.25	xx 2.99
1095	xx 629	xx 8.5	xx .57	xx 1.99	xx 3.12
Grand mean	637	9.9	.59	2.23	2.99
F_p	xx 24.7	xx 13.2	xx 2.9	xx 6.7	x 1.9
F_f	xx 2.7	xx 6.7	1.5	xx 2.9	xx 3.5

NB: xx, x significant respectively at 5% and 1%

Table 8. — Within progeny variance and correlations for different traits.

Traits		DOUGLAS-FIR			SITKA SPRUCE			
		MINI	MAXI	MEAN	Traits	MINI	MAXI	MEAN
σ_w^2	TH 12	4800	8300	6600	TH 8	950	1347	1139
	FLU 9	11	16	13	BS 8	131	224	178
	G 12	15	26	21	M.BR 8	3	16	8.5
	SIN 12	--	--	--	LSF 8	133.10 ⁻³	227.10 ⁻³	198.10 ⁻³
ρ_w	TH 12/FLU 9	-.12	.17	.02	TH 8-BS 8	.11	.26	.17
	SIN 12/FLU 9	-.18	.03	-.07	TH 8-M.BR 8	.14	.28	.20
	SIN 12/TH 12	-.04	.19	.10	TH 8-LSF 8	.16	.29	.23

3.2 — Geographic variation

According to the model (2) the provenances effects were estimated and listed in Table 7 whereas coefficients of correlation between traits at provenance level are given in Table 6 as already noticed.

In Douglas Fir, the variation of height growth between provenances was relatively large: at age 12 the best provenance Granite Falls (1057, mean height: 7m) outgrew the poorest Diablo Dam (1046, 5.30 m) of 32 % and the grand mean of 9 %. The classical clinal pattern of height growth decrease with increasing the elevation of seed source is clear. Flushing time was also variable from 6.5 days for the earlier provenance Diablo Dam (1046) to 14 days for the latest: Darrington (1053). Variability of form traits is more difficult to evaluate because of the type of measurements (qualitative score). Nevertheless, forking⁽¹⁾ and sinuosity revealed real variation between provenances: 1067 exhibited 39 % of forked trees versus 1050 with 76 % of forked trees; for sinuosity, mean score was 2.23 varying from 1.95 (1059) to 2.61 (1051).

Due to favourable correlations between total height and flushing time, the selection of provenances simultaneously

late flushing and fast growing appears to be feasible, for example: Darrington (1053), Arlington (1054), Granite Falls (1057), Enumclaw (1075). Beside that, these populations are of high interest since they turn out as very stable over a large range of environmental conditions, not only in France but also in Western Europe.

For Sitka Spruce, height growth showed the usual clinal pattern of latitudinal variation; total height decreases with increasing latitude of seed source. However the provenance Muir Creek (3066) from the extreme south of Vancouver Island (milder climatic conditions) had a better growth than expected from its latitude. The relative difference between the best (Newport, 3014) and the poorest (Haney, 3063) was 34 % at age 8; it was about the same in nursery (age 4). The coefficient of correlation between provenances means for total height age 4 (nursery) and 8 (field) was as high as .93**. Flushing time in nursery was extremely influenced by the hot temperature of spring 1976 as already mentioned. Bud set time followed a clinal variation as noticed by many authors, southern populations being later than northern populations with an exception again for Muir Creek. Bud set was later at age 8

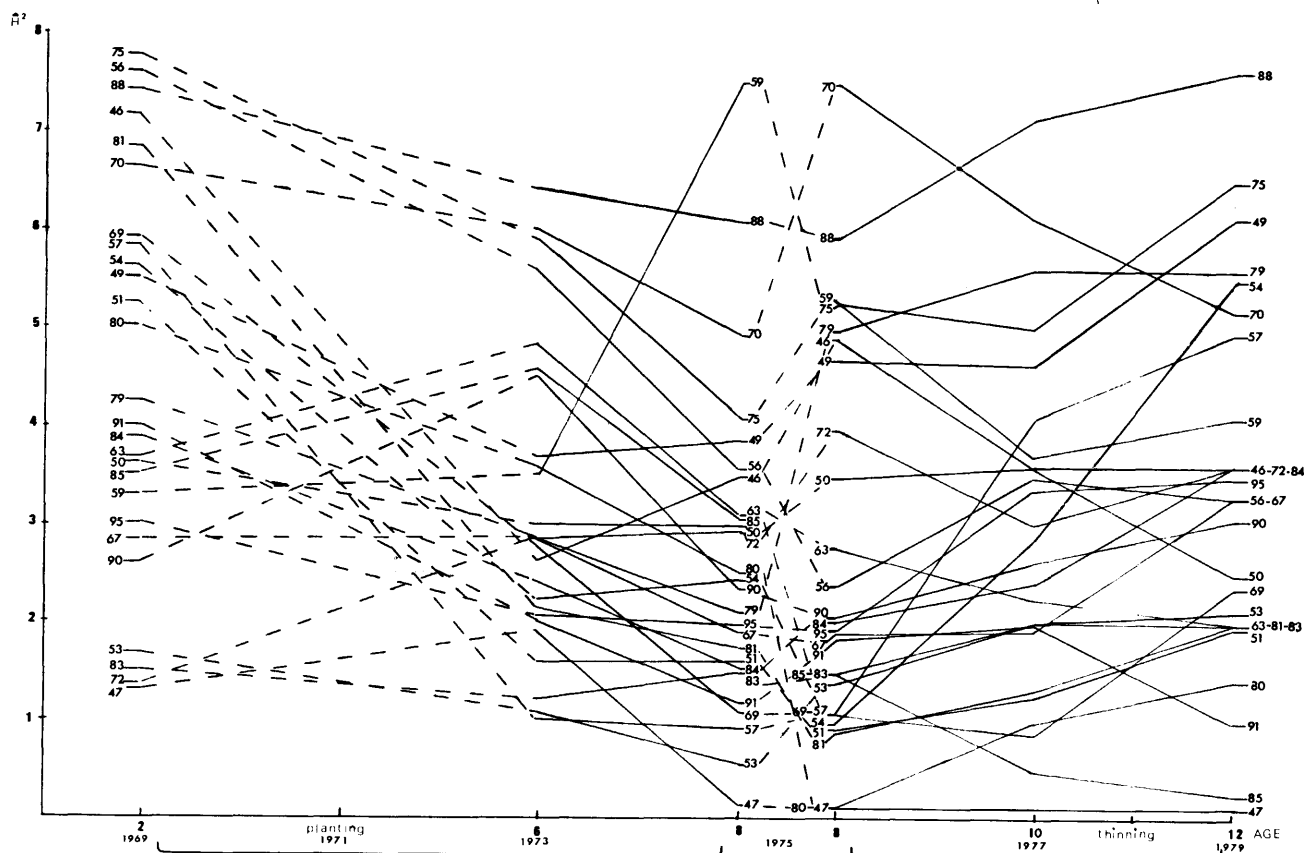


Fig. 1. — Estimates of h² values of total height at different ages.

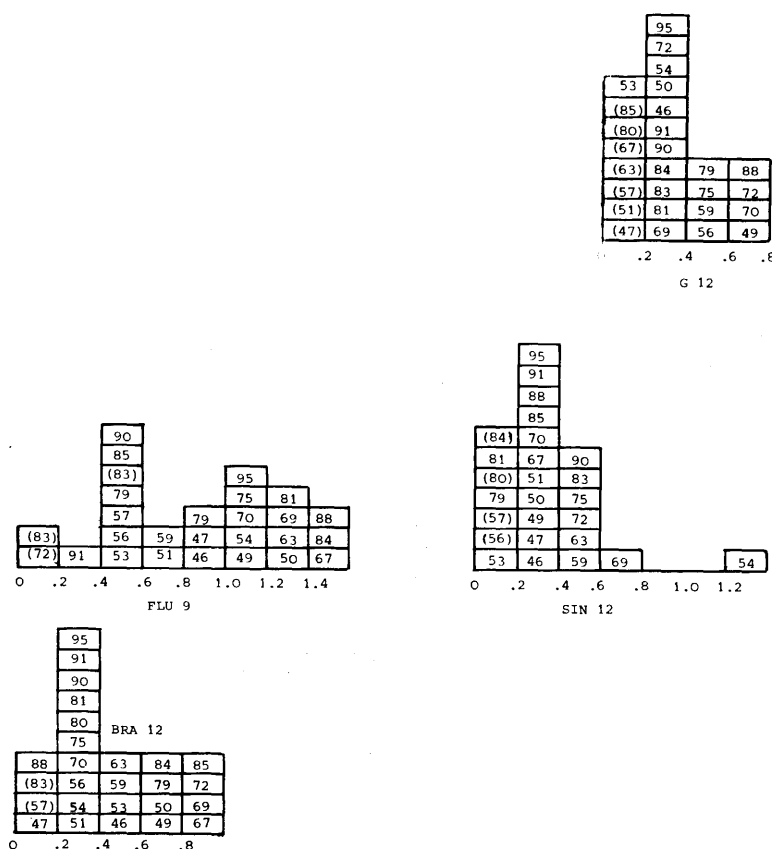


Fig. 2. — Douglas Fir — Distribution of heritability estimates.

than at age 4 (due to different climatic conditions), however the ranking of provenances for total height was consistent ($r_{TH8, TH4} = .87^{**}$). Differences between provenances in bud set time were as high as 29 days (age 4) and 18 days (age 8) for the 18 provenances assessed at both stages. Correlation at provenance level for total height and bud set time at age 8 was $.83^{**}$ (see Table 6). Therefore selecting provenances for early bud setting (with respect to the risk of fall frost) would lead to decrease the vigour. Lammas shoot frequency and minor branches number were strictly correlated $r = .98$; both traits showing a clinal variation with latitude.

3.3 — Within provenance variations: comparison between provenances

Arising from model (3) used in each provenance i , the within progeny (i.e. individual) variance ($\sigma_{w_i}^2$), the between progeny variance ($\sigma_{f_i}^2$) as well as "within" (p_{w_i}) and "between" (genetic) (p_{f_i}) coefficients of correlation between the different traits have been estimated. The estimates at individual level are listed in Table 8. For both species the homogeneity of all within-progeny parameters variances σ_w^2 and correlations (p_w) can be proved. Conversely, the genetic parameters (p_f and h^2) showed larger variation between provenances.

In Douglas Fir the heritability of each trait was computed for each provenance (Fig. 1 and Fig. 2). The variations with age of heritability of total height are given in Fig. 1. It can be easily seen that the range of values is roughly the same at age 2 as at age 12 (from 0 to .77). The general trend of decrease between age 2 and age 6, and even age 8, is likely due to the transplanting shock assumed to be severe when planting tall seedlings (4 years

(¹) it is reminded that forking defect includes also ramicorn branch.

old) and also due to the more important environmental variation in field than in nursery.

These facts, joint to increasing competition effects between age 6 to 8, increased the residual variance (σ_w^2) and so reduced the part of genetic variation. For the provenances 1063, 1072, 1085 and 1090, a slight increase of heritability of height growth was noticeable from age 2 to age 6, however because of the wide confidence intervals of h^2 , this difference is non significant. Between age 6 and 8, the provenance 1059 showed a strong increase of heritability; this fact is not surprising due to the strong heterogeneity of this provenance (CHRISTOPHE and BIROT, 1979).

Due to the thinning, heritability at age 8, 10 and 12 has been estimated on the half part of seedlings as earlier, so that the estimation is less accurate (wider confidence interval). Except for three provenances (1070, 1050, 1091), the slight increase for h^2 between age 10 to 12 must be mentioned. For age 8, estimates of h^2 were calculated first from all planted trees and second from half number of trees (remaining after thinning). Differences between both values will be discussed further.

Generally one may notice a certain stability over the time of the ranking of some provenances for total height heritability at high level (1088, 1075, 1049, 1070), middle level (1072, 1090, 1095, 1050) or low level (1053, 1083, 1047).

Heritability of girth was also around .3 on average. It was over .4 in 8 populations among the 26, whereas it was insignificant ($\sigma_f^2 \cong 0$) for 7 populations. Heritability of girth was not significantly inferior to total height heritability, as expected because of competition effects are usually stronger for girth than for height.

Estimates of heritability of flushing were very high, very often exceeding 1.0 (12 populations) except in 2 populations (1072 and 1083). Heritability of branch angle was

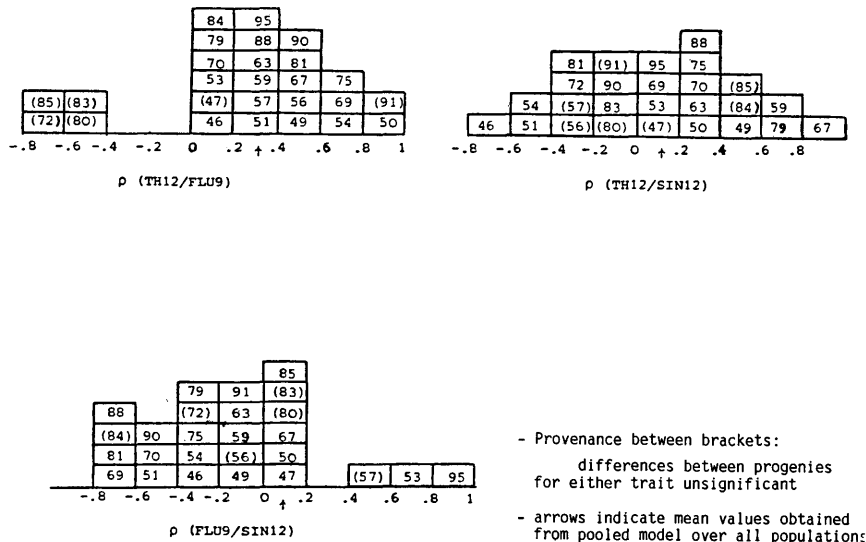


Fig. 3. — Douglas Fir — Estimates within population of additive genetic correlations.

substantial: 12 populations had values exceeding .4, whereas heritability of sinuosity was slightly lower (only 8 populations over .4). Among them, 1054 (Arlington) had an heritability of 1.2 but at the same time was on average among the most crooked provenances.

Correlations of progeny (within provenance) means for total height at age 2 (nursery) and 12 (field) are given in Fig. 3. Fortunately, all coefficients were positive, but in some populations as 1054 Arlington, the correlation was weak, whereas it was high in others (1090). For 15 populations the coefficient of correlation was over .4.

Additive genetic correlations are given in the same Figure. For all traits, estimates from pooled model (2) are similar to the means of estimates from model (3) for each population. For flushing and total height (age 12), 6 populations were rejected because of lack of additive genetic variability for height (1047, 1080, 1085, 1091) or for flushing (1072, 1083), while 15 exhibited correlations over .2; there

were only significant positive coefficients, ranged from zero (1053, 1079) to .8 (1050). These results are promising with respect to the efficiency of selection on both traits. For total height and sinuosity, the magnitude of genetic correlations was very wide, ranging from $-.6$ (1046, 1054) to .8 (1067). This situation is quite embarrassing for the tree breeder; among the 26 provenances, 9 had a coefficient of correlation over .2 (thus unfavourable), whereas 7 were rejected because of lack of variability of either trait; 5 only had correlations below $-.2$. In some populations (1067, 1079, 1059, 1049), a compromise between growth and straightness will be difficult to find. Moreover the trees are still young and it is necessary to reevaluate this correlation when older. Between flushing and sinuosity, the additive genetic correlation had a wide magnitude ranging from $-.7$ (favourable) to .8 (unfavourable). But among the 26 provenances, only 2 (1053, 1095) had correlation over .2, whereas 10 were below $-.2$ and 6 were rejected because

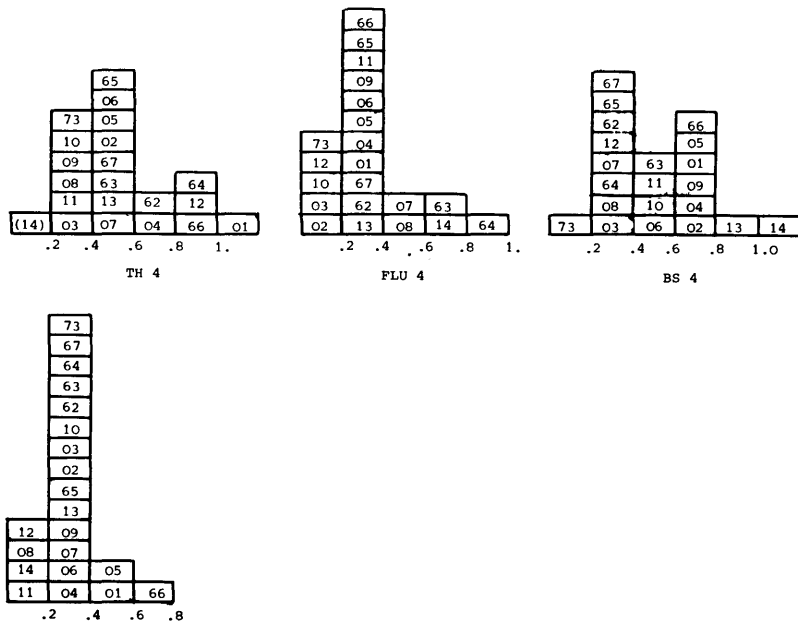


Fig. 4. — Sitka spruce — Individual heritability of different traits for each provenance in nursery.

of lack of variability for either trait. However the most crooked provenances had a favourable genetic correlation either between TH12—SIN12 (1054, 1051) or between FLU9—SIN12 (1075, 1088) or both. These results are not really unfavourable for the selection: on the average, it will be possible to improve lateness of flushing and growth without increasing stem sinuosity, even into provenances with bad stem form (see CHRISTOPHE, BIROT, 1983).

All these results stress the point that there are real variations in genetic parameters among wild populations sampled throughout the natural range of Douglas Fir. Estimates obtained for a given population in one site can not be extrapolated to other populations, even in the same site. Therefore it is of major interest to select populations not only on their performances in average, but also for their "good" genetic parameters (high value of h^2 , favourable additive genetic correlations).

Sitka Spruce: Distribution of individual heritability values (for each provenance and for each trait) are given in Fig. 4 and 5 respectively at nursery stage and field stage. For most traits h^2 ranges from 0 to .8. For height growth between age 4 and age 8, heritability values within provenances were correlated $r = .78$; on the average heritability values at age 8 were smaller than at age 4 as already mentioned. For flushing at nursery stage heritability values ranged from .1 to .9, but only 5 provenances had values over .4. However, the first three provenances with the highest heritability comprised 11 progenies or less so that one may expect either sampling error or a wide confidence interval. The hot temperatures of 1976 have certainly reduced the variation for flushing time although at provenance level even in normal conditions the variation seem to be limited (BURLEY, 1966; GILLET, 1981; KLEINSCHMIT and SAUER, 1976; KLEINSCHMIT, 1978; KRANENBORG and KRIEK, 1979; KRAUS and LINES, 1976; LACAZE, 1970; MAGNESEN, 1976; O'DRISCOLL, 1976 and 1978): the difference between the extreme progeny means (the latest and the earliest) was only 8 days. Needle colour had an heritability less variable, probably because of the difficulty of evaluating this trait. Bud set, minor branch number and lamma shoot length (8 years) had intermediate values around .3, .4. One must keep in mind that the confidence limits of the heritability estimates presented here, may be wide.

Additive genetic correlation between all traits varied also between provenances (Fig. 6) but all were slightly or

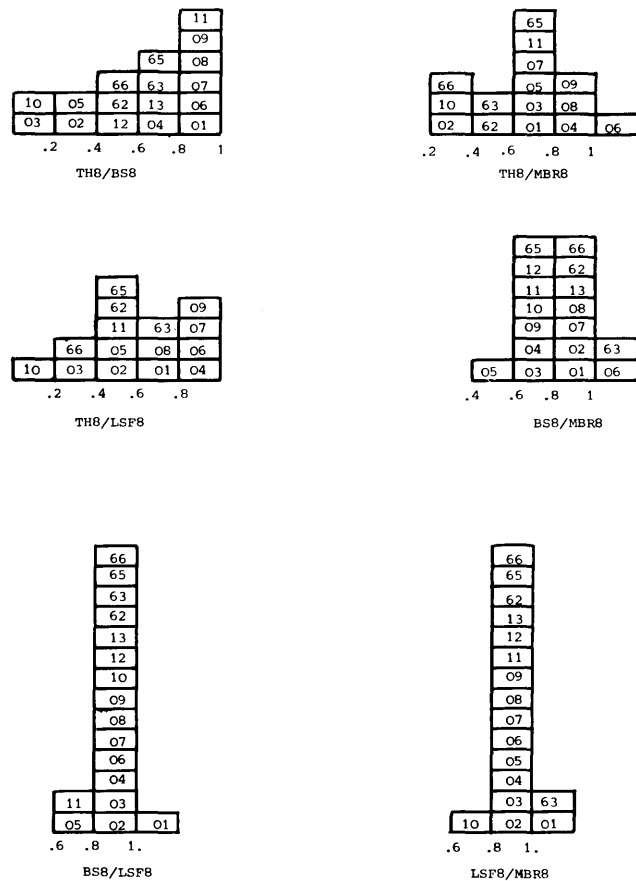


Fig. 6. — *Sitka spruce* (field stage) — Distribution of genetic additive correlations in each population.

strongly positive. Late bud setting, lamma shoot length, minor branch number were positively correlated with height growth. Therefore selection for improving growth with reducing bud setting, lamma shoot and number of internodal branches appears really difficult in most of populations.

4 — Discussion and Conclusion

1. One important result concerns *Sitka Spruce*. With this species the estimates of the relative importance of additive effects for height growth versus the total variation show higher values than those expected from the published

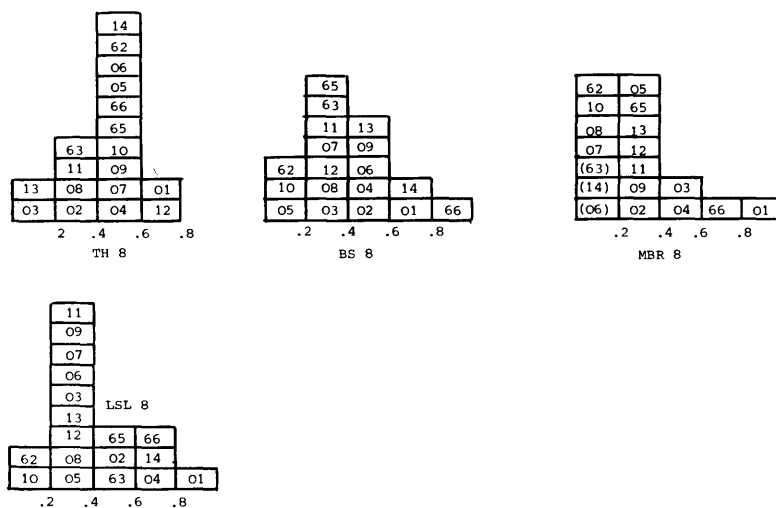


Fig. 5. — *Sitka spruce*: Individual heritability of different traits for each provenance in the field (provenance number in brackets indicates $\sigma_i^2 \geq 0$).

papers (SAMUEL *et al.*, 1972; SAMUEL and JOHNSTONE, 1979) and especially FALKENHAGEN (1974, 1977) who used partly the same seed collection. This result is really encouraging and offers good prospects for future selection.

2. Using open-pollinated progenies is criticizable if the panmictic regime is not verified. REHFELDT (1978) showed for Douglas Fir that open-pollinated seed progenies are worthwhile for estimating the breeding value of mother trees. It is likely that the assumption that all offsprings of one mother tree are half-sibs is not true, some of them being full-sibs. Consequently heritability values ($h^2 = 4 \cdot \frac{\sigma_f^2}{\sigma_f^2 + \sigma_w^2}$) could be overestimated. Another remark is that open-pollinated material would be of poor value for breeding purpose with respect to inbreeding; offsprings, even from different mothers, could have a common father. The probability of this event can be certainly decreased by collecting cones a good flowering year and on trees sufficiently distant from each other.

3. The precision of estimates is also to be discussed. It is clear that the most unprecise estimates concern for each provenance the variances-covariances matrix at progeny level. The mean number of 15 progenies in a population is probably rather low. The within progeny sampling is questionable too. At age 8, two estimations of heritability of total height were performed, the first on all trees of each progeny (i.e. from 20 to 48), the second on the trees being left after thinning (about 1/2 but ranging from 10 to 27 trees per progeny). Some discrepancies between both estimations can be observed (*Fig. 1*) especially in certain provenances (1070, 1079, 1059, 1080). Detailed investigations have shown that systematic thinning was in fact non homogeneous. In provenance 1070 the worst progeny before thinning was much worse after thinning, whereas the best progeny became better after thinning. Consequently σ_f^2 was increased of 40 % whereas σ_w^2 remained the same, thus heritability was increased. This is due to a relative heavier thinning of the tallest trees for the former progeny, and to an heavier thinning of the poorest trees for the latter.

4. An interesting point is the evolution with age of components of total variation. FRANKLIN (1979), using data from Douglas Fir. (NAMKOONG *et al.*, 1972) and Ponderosa Pine (NAMKOONG and CONKLE, 1976) tests showed phase changes relative to the expression of additive genetic variance. He described a model permitting the comparison of the magnitude of genetic versus environmental variances in height growth.

Under the model, stand development was divided into juvenile-genotypic, mature-genotypic and codominance-suppression phases. Data on Loblolly and Slash Pines were fitted to the model too. The results presented here as well for Douglas Fir as for Sitka Spruce follow the same pattern in the juvenile-genotypic phase with a general decrease of heritability of height. For both species we would be now at the beginning of mature-genotype phase with an increase of heritability. There is indeed a slight trend of increasing heritability on the average. One may notice that in some Douglas Fir provenances, there is a sharp increase of height heritability between age 8 and 12, and this concerns mainly vigorous populations (1057, 1054, 1075, 1089); this results would be in agreement with the FRANKLIN's assumption about competition effects. In the Douglas Fir, competition effects are likely since the spacing was close (2×1.5) till age 11.

The general pattern of decrease then increase of height heritability have also been described in *Pinus nigra* from 2 years to 10 years after planting (ARBEZ and MILLIER, 1972) and *Pinus pinaster* (KREMER, 1981).

In different provenances of Norway Spruce (15 provenances represented each by 10 progenies), VALLANCE (1980) found the mean figure of variation: continuous increase of heritability of height up to 10 years after planting. In this case, the spacing was very close: 1.4×1.4 m. However YING and MORGENSTERN (1979) did not find clear pattern of variation of height heritability in White Spruce between age 11 and 22.

Using very close spacing for the progeny test as suggested by FRANKLIN rises the question of the competition effects on the genetic parameters. On one hand, it is clear that σ_w^2 is increased, but on another hand, differences between initially fast and slow growing families would be augmented (thus, increase of σ_f^2), especially with a single tree plot progeny test where there is intergenotypic competition. Moreover, that stresses the point of early selection: such an approach would allow to select trees for initial growth rather than for final growth, which could probably be selected in progeny test with wide spacing.

5. It could appear as inconsistent to say on one hand that there are differences among provenances in the genetic variance-covariance matrices, and on another hand to pool all provenances and to make computation overall populations. As a matter of fact, one may imagine a distribution of population with a grand mean and a variance, but with populations statistically different when compared two by two. We are exactly in that situation. Finally some differences between provenances in genetic parameters were observed, and this is important to know in order to adapt the breeding strategy to populations or group of populations. This result stresses the point that preliminary investigations on genetic parameters and their variation between populations are necessary before setting up a breeding strategy.

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Amount and Distribution of Isozyme Variation in Ponderosa pine from Eastern Montana

By J. H. WOODS¹⁾, G. M. BLAKE²⁾ and F. W. ALLENDORF³⁾

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Summary

Pinus ponderosa seeds from 50 trees in each of six small isolated stands located within a nine kilometer radius of Colstrip, Montana, were examined at 23 isozyme loci. Megagametophyte and embryo tissue from each seed were screened separately. Measures of genetic diversity showed no significant differences between male and female components within or between stands. The average proportion of heterozygous loci per embryo (H_e) was not significantly different between stands. For all stands combined, H_e was 0.012. Genotype proportions did not deviate from expected Hardy-Weinberg proportions.

Nearly 99 % of the genetic diversity resided within individual stands, with a significant 1.5 % due to differences between stands. Genetic distance between stands is not correlated with geographic distance. Considering the natural fire history of the stands, it is suggested that there is a great deal of gene flow into a stand during its early stage of development.

Key words: isozyme analysis, *Pinus ponderosa*, gene flow, population differentiation, heterozygosity, forest genetics.

¹⁾ School of Forestry, University of Montana, Missoula, Montana 59812, USA

currently with: Cowichan Lake Research Station, British Columbia Ministry of Forests

²⁾ School of Forestry, University of Montana, Missoula, Montana 59812

³⁾ Department of Zoology, University of Montana, Missoula, Montana 59812

direct correspondence to: JACK H. WOODS, Cowichan Lake Research Station, British Columbia Ministry of Forests, Mesachie Lake P.O., British Columbia. VOR 2NO, Canada

Zusammenfassung

An Samen von *Pinus ponderosa* var. *scopulorum* ENGELM. von 50 Bäumen aus je sechs kleinen isolierten Beständen innerhalb eines Radius von 9 Kilometern um Colstrip, Montana, wurden 23 Isoenzym-Loci untersucht. Megagametophyten und Embryogewebe von jedem Samen wurden getrennt untersucht. Eine Bestimmung der genetischen Verschiedenheit hat keine wichtigen Unterschiede zwischen männlichen und weiblichen Bestandteilen innerhalb von Beständen oder zwischen Beständen gezeigt. Der durchschnittliche Anteil an heterozygoten Loci je Embryo (H_e) war zwischen Beständen nicht signifikant verschieden. Für alle Bestände kombiniert, war der durchschnittliche H_e -Wert 0.012. Die Verteilung der Genotypen wich nicht von der erwarteten Hardy-Weinberg-Verteilung ab.

Fast 99 % der genetischen Verschiedenheit für die 23 Loci sind innerhalb jedes einzelnen Bestandes zu finden, mit einer signifikanten, 1,5 %igen Differenz zwischen den Beständen. Die genetische Entfernung zwischen Beständen ist nicht mit der geographischen Entfernung korreliert. Wenn man die natürliche Waldbrand-Geschichte der Bestände betrachtet, ist anzunehmen, daß es in der Frühentwicklung eines Bestandes einen starken Genfluß gibt.

Introduction

The use of electrophoretic techniques to study isozyme variation in coniferous species has become widespread in recent years. Wind-pollinated conifers generally show a great deal of genetic variability (HAMRICK *et al.*, 1981), and less population differentiation than trees that are pollinated by other means (BROWN and MORAN, 1981). Many studies have investigated the distribution of isozyme variability in conifers over a broad geographic range (LUND-