

Genetic variation within and between populations of Douglas fir

By C. CHRISTOPHE and Y. BIROT

Station d'Amélioration des Arbres Forestiers,
I.N.R.A., Centre de Recherches Forestières d'Orléans,
Ardon, 45160 Olivet, France

(Received January / November 1979)

Summary

The paper deals with results (at 8 years from the seed) from a provenance-progeny test including 26 populations of Douglas Fir (each of them being represented by 11 to 15 wind-pollinated progenies) sampled throughout the western foothill of Cascades Mountain in the State of Washington. Attention was concentrated on phenological (flushing, flowering) and growth traits.

Considerable variation between means of population (even within a short distance) is emphasized. For height growth clinal variation with elevation and longitude was pointed out.

Genetic patterns varied from a population to another. These discrepancies would be large enough to justify different strategies of selection, especially according to heritabilities and genetic additive correlations.

On the average, decreasing heritability for height growth with age was noticeable. Further investigations are necessary to elucidate the evolution with age of this parameter.

For breeding purposes, the interest of using as base population provenances with medium performances but with favourable parameters (high heritability, positive genetic correlation between flushing and height growth) instead of provenances with good mean performances but with less variation is discussed.

Finally, the question of multiple provenance seed orchard is raised. Because of variation in genetic parameters between populations, basic research on estimation of new genetic parameters resulting from crossings between populations is suggested.

Key words: Douglas Fir, provenance, genetic variation, heritability, genetic correlation, progeny test.

Résumé

Un test de provenances-descendances de Douglas comporte 26 provenances de la région du Piémont Ouest de la Chaîne des Cascades de l'Etat de Washington. Chaque provenance est représentée par 11 à 15 descendances maternelles. Les résultats présentés concernent des critères phénologiques et de vigueur: ils mettent en évidence d'importantes différences entre moyennes de provenances, même pour des provenances peu éloignées. Une variation clinale avec l'altitude et la longitude est détectée pour la croissance en hauteur.

Les paramètres génétiques varient d'une provenance à l'autre. Ces différences de comportement justifieraient différentes stratégies de sélection, prenant en compte les héritabilités et les corrélations génétiques additives.

En moyenne, on note une diminution de l'héritabilité de la hauteur avec l'âge. Il est nécessaire de poursuivre les mesures afin de vérifier cette tendance.

Dans les stratégies d'amélioration, on souligne l'intérêt de populations de base de performances moyennes mais avec des paramètres favorables (héritabilités élevées, fortes corrélations génétiques entre tardiveté du débournement et vigueur) par rapport à des populations de performances élevées mais moins variables ou avec des paramètres moins favorables.

Le problème des vergers à graines multiprovenances est abordé: il nécessite la mise en place de recherches fonda-

mentales afin d'estimer de nouveaux paramètres génétiques permettant la prévision de gains génétiques à partir de croisements entre individus appartenant à des populations différentes.

Zusammenfassung

Eine Nachkommenschaftsprüfung mit 26 Douglasienprovenienzen aus den westlichen Vorbergen der Kaskaden im Staate Washington wurde in Frankreich angelegt und nach 8 Jahren ausgewertet.

Jede Herkunft ist mit 11 bis 15 mütterlichen Nachkommenschaften vertreten. Die vorliegenden Ergebnisse betreffen vor allem das phänologische Verhalten und das Wachstum. Es zeigen sich wesentliche Unterschiede zwischen den Mittelwerten der Herkünfte und zwar auch bei geographisch nicht sehr weit voneinander entfernten Herkünften. Beim Höhenwachstum konnte eine klinale Variation mit der Seehöhe und der geographischen Länge festgestellt werden.

Die genetischen Parameter zwischen den Herkünften variieren sehr stark. Diese Unterschiede würden verschiedene Züchtungsstrategien rechtfertigen, die die Heritabilitäten und die additiven genetischen Korrelationen berücksichtigen.

Die Heritabilität des Höhenwachstums nimmt im Mittel mit zunehmendem Alter ab; die Beobachtungen müssen jedoch noch über mehrere Jahre weitergeführt werden, um diese Tendenz zu überprüfen.

Bezüglich der Züchtungsstrategien ist hervorzuheben, daß es besser erscheint, Ausgangspopulationen von mittlerer Leistung aber mit vorteilhaften Parametern (hohe Heritabilität, hohe genetische Korrelation zwischen Spätreifen und Wüchsigkeit) auszuwählen, als Populationen mit hohen Leistungen aber mit geringer Variabilität oder mit wenig vorteilhaften Parametern.

Abschließend wird auf das Problem der Samenplantagen mit Herkunftsgemischen eingegangen. Es erscheint dabei notwendig vorerst grundlegende Untersuchungen durchzuführen, um die neuen genetischen Parameter der Kreuzungen zwischen Individuen verschiedener Populationen zu schätzen, die dann eine Vorhersage des genetischen Gewinnes ermöglichen.

1. Introduction

The study of genetic variation in forest tree species is often thought in terms of emphasizing differences in mean characteristics between populations. This approach is especially interesting in genecology and in practical silviculture (selection of suitable seed sources for a given area). For a major tree species like Douglas Fir, many references dealing with this subject have been published, some of them being already quite old.

Studies on genetic variability within a population, and on the variation of this variability between populations, are also very important. On one hand, they may better describe — or explain — the "between populations" variations. This point is interesting, for example, in population genetics studies. On the other hand, they may supply very helpful guidelines to tree breeders, because of a better knowledge on the genetic structure of the populations and

Table 1. — Location of the provenances
(State of Washington)

Name of the provenance	N°	Latitude (North)	Longitude (West)	Elevation (m)	Number of progenies
Diablo-dam	1046	48° 43'	121° 07'	420	15
Concrete	1047	48° 39'	121° 43'	470	15
Bacon-point	1049	48° 36'	121° 23'	500	13
Marblemount	1050	48° 35'	121° 24'	120	15
Sedro-woolley	1051	48° 32'	122° 19'	60	15
Darrington	1053	48° 16'	121° 38'	150	15
Arlington	1054	48° 13'	122° 04'	90	14
Sloan creek	1056	48° 05'	121° 18'	650	14
Granite falls	1057	48° 05'	122° 02'	90	11
Perry creek	1059	48° 03'	121° 28'	610	15
Gold bar	1063	47° 51'	121° 39'	120	14
Skykomish	1067	47° 42'	121° 20'	300	15
North bend	1069	47° 28'	121° 45'	150	15
Denny creek	1070	47° 24'	121° 32'	550	14
Chester morse lake	1072	47° 22'	121° 40'	600	15
Enumclaw	1075	47° 16'	121° 56'	240	15
Parkway	1079	47° 02'	121° 34'	790	15
Yelm	1080	47° 01'	122° 44'	60	14
Alder lake	1081	46° 48'	122° 17'	420	14
Packwood I	1083	46° 34'	121° 40'	650	14
Packwood II	1084	46° 34'	121° 42'	300	14
Randle	1085	46° 33'	122° 03'	330	13
Castle rock	1088	46° 19'	122° 52'	150	15
Cougar	1090	46° 05'	122° 18'	500	14
Yale	1091	46° 00'	122° 22'	120	14
Prindle	1095	45° 37'	122° 08'	450	14

on the genetic patterns within populations (heritability, genetic correlation, etc. . .). Two complementary ways can be used for this purpose:

a) Studies on the distribution of allelic variation in natural populations by means of biochemical genetic markers. Recent experiments based on isozymes have been done on Douglas Fir by MUHS (1974), BERGMANN (1975), YANG *et al.* (1977).

b) Studies, in different populations, of the genetic variation of different traits within populations: morphology, phenology, physiology. These are mainly based on progeny testing with material unbiased by selection and collected from natural populations. They deal with the concepts of quantitative genetics. This type of study has been undertaken on Douglas Fir by SILEN (1964), NAMKOONG *et al.* (1972), REHFELDT (1974, a and b), BIROT (1976), KVESTICH (1976), SZIKLAI (1978). The suitability of using wind-pollinated progenies for this purpose has been discussed previously. In Douglas Fir, this material has proved reliable, as far as the progeny mean and within progeny variance are concerned (REHFELDT, 1978).

The present paper is mainly devoted to inter- and intra-population genetic variation in Douglas Fir. The sampled populations were restricted to the area of the Western foothill of the Cascade Range in the State of Washington, which turned out to be of high genetic quality in most provenance tests established especially in Northwestern Europe.

2. Material and Methods

2.1 — Provenance sampling

26 provenances were selected among the populations sampled by IUFRO throughout the natural range of Douglas Fir. Detailed informations on this material have been given by BIROT (1974, 1976). In each provenance, 11 to 15 wind pollinated progenies were collected from dominant but unselected trees, located about 100 m from each other in order to avoid coancestry. Afterwards the seeds from these progenies were processed separately. Location of provenances is given in table 1.

2.2 — Experimental design

After raising in the nursery near Nancy, the progeny test was planted out with 4-years-old seedlings during the 1971 fall in Cendrieux (Department of Dordogne, Southwest of France: latitude 45° 02' N, longitude 0° 50' E, elevation 220 m); spacing was 2 × 1.5 m. 370 progenies were distributed in single-tree plots in 48 complete blocks (or reps). Because of mortality and missing data, the number of individuals per progeny is now about 35. This number can be considered as reliable for the present estimations.

2.3 — Statistical model

The linear model used in the provenance-progeny test was as follows:

$$Y_{ijk} = \mu + P_i + F_{ij} + B_k + (PB)_{ik} + W_{ijk} \quad (1)$$

where: μ = general mean
 P_i = provenance effect ($1 \leq i \leq 26$)
 F_{ij} = effect of progeny j within provenance i ($1 \leq j \leq n_i$ with $11 \leq n_i \leq 15$)
 B_k = block effect ($1 \leq k \leq 48$)
 $(PB)_{ik}$ = block × provenance interaction
 W_{ijk} = residue, $N(0, \sigma_w^2)$

In order to study environmental effects on provenances and on different traits, we used a reduced model with fixed effects as follows:

$$Y_{ijk} = \mu + P_i + B_k + (PB)_{ik} + W_{ijk} \quad (2)$$

Afterwards, the goal was to emphasize the different genetic levels of variation (provenance, progeny, individual) and consequently the individual phenotypic values adjusted to block effects were used, with the following model:

$$X_{ijk} = \mu + P_i + F_{ij} + E_{ijk} \quad (3)$$

Therefore total phenotypic variation was obviously reduced. This fact must be kept in mind in the analysis of the results.

Using model (3) implies assumptions of equality of residual variance within each progeny (ij), and equality of variance between progeny means, in the different provenances.

In order to check these assumptions, the one way variance analysis was performed for each provenance:

$$X_{ijk} = \mu_i + F_{ij} + \Sigma_{ijk} \quad (4)$$

Investigations on variations between populations and between progenies within populations, were achieved by analysis of variances according to models (3) and (4) considered as models with fixed effects.

Estimation of genetic parameters, taking into account three levels of variation (provenance, progeny, individual) were performed considering models (3) and (4) as models with random effects.

2.4 — Assessed traits

1 — *Total height* was assessed 2, 3, 4 years after planting. Afterwards the height increments of the 3rd and 4th year were computed.

2 — *Flushing* of the fifth year (1976) was assessed by periodical observations (every second or third day). One individual was considered as flushed, when the first terminal bud of the branches belonging to the 1975 whorl broke up. It has been previously shown that correlation between flushing time of the terminal bud on branches and the terminal bud on the leader shoot is rather high. 13 observations took place within a period of 35 days. Afterwards flushing time was expressed in number of days, and in number of degree \times days (temperature sum). Both variables are obviously highly correlated.

3 — *Number of male and female flowers* of the fifth year after planting were observed. The variable used in this paper is only for each sex, presence or absence (1 or 0) of flowers.

All traits were assessed on all trees in the experiment, i. e. about on 17.000 trees.

2.5 — Preliminary studies

a) Three years after planting, the experiment was damaged by late spring frost. Damage on lateral shoots was assessed.

In the earliest flushing population (1046), the frequency of damaged trees was 78%, whereas it was only 20% in the latest flushing populations (1053, 1057). For provenance means, the coefficient of correlation between earliness in flushing and frost damages was .97**. Once more this result stresses the interest of selecting "late" populations. Within each provenance, significant differences between progenies in frost damages were noted; on the average, correlation between frost damages and earliness was .81**. This value was more or less the same within each provenance except for 1072 (late flushing population) where the correlation did not differ from zero. Between individuals within progeny, coefficient of correlation was only .35** on the average. This value was about the same in the different populations.

Because of these damages, total height and height increment of that year were not taken into account as variables in this study.

b) Block effects were significant for all traits, even for flushing which is normally less affected than growth traits. The reason is that the trial is established on the slope of a valley. Blocks located at the top were earlier flushing, whereas blocks located at the bottom of the valley were later flushing, because of the accumulation of cold air;

Table 2. — Correlation of block means between traits

	Total height 2 years	Total height 4 years	Height increment 4th year	Flushing (lateness)
Total height 4 years	.91			
Height increment 4th year	.52	.82		
Flushing (lateness)	-.02	-.35	-.79	
Spring frost resistance (3rd year)	-.15	-.39	-.58	.60

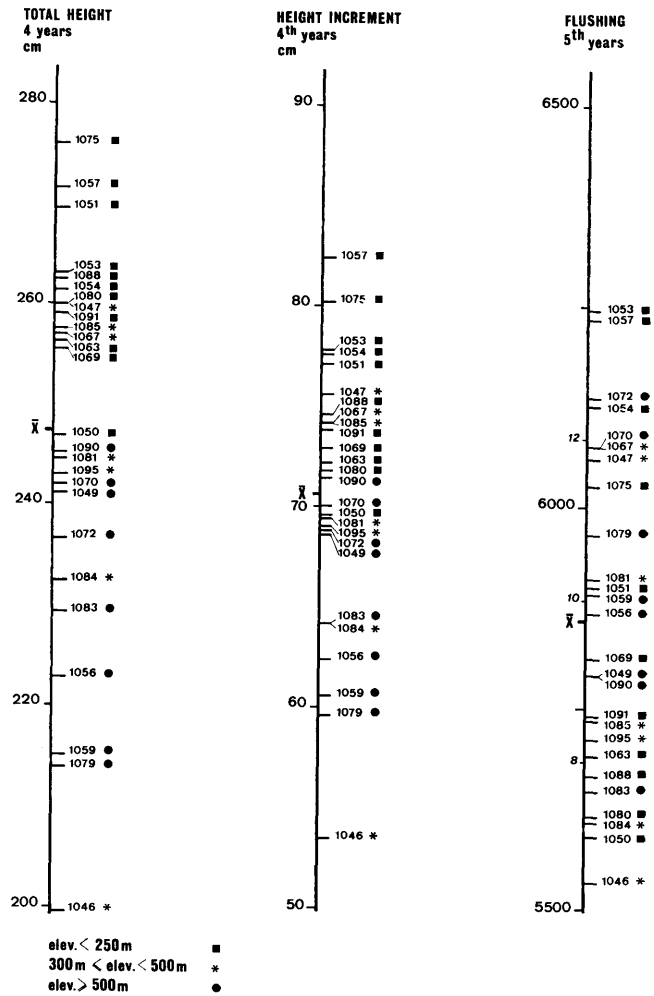


Figure 1. — Ranking of populations for height (4 years after planting), height increment (4th year) and flushing (5th year). (Flushing is expressed in number of degree \times days, values in italic are in number of days).

therefore the required temperature sum is reached earlier at the top than at the bottom. Consequently frost resistance was better at the bottom than at the top in his particular year where the frost occurred very late (see table 2).

Paradoxically there were negative correlations between height growth and flushing, because the late flushing blocks located at the bottom of valley are also slower growing. This moderate growth could be due to poorer soil conditions.

3. Results

3.1 — Variation between populations

Ranking of populations for total height (4 years), height increment of 4th year and flushing of 5th year is given in figure 1. Provenance effects were highly significant for all traits.

As pointed out by many authors, elevation of seed source has a marked effect on height growth. Seed sources below 300 m were top ranking for this trait whereas seed sources over 500 m were inferior to the general mean.

Flushing time was independent on elevation of seed source (and also on latitude). By contrast, HERMANN and LAVENDER (1968) found close positive correlation between lateness in flushing and elevation, for provenances from a smaller area in Oregon, but ranging from 800 to 1600 m in elevation.

Table 3. — Correlation between traits (provenance means)

	Total height 2 years (after planting)	Height increment 4th year	Total height 4 years	Flushing	Female flowers
Height increment 4th year (after planting)	.95**				
Total height 4 years (after planting)	.997**	.97**			
Flushing 5th year	.29	.49**	.33		
Female flowers 5th year	.47*	.41*	.46*	-.10	
Male flowers 5th year	.38*	.51**	.42*	.70**	.32

The coefficients of correlation (see table 3) of provenance means between lateness in flushing and height growth were weak but with a positive trend. Therefore selection of vigorous and late flushing populations appears to be possible.

Compared to the results from nursery stage (BIROR, 1976), ranking of provenances for flushing was very stable: correlation $r = .97^{**}$ between 2—0 seedlings in the nursery located near Nancy, and flushing of fifth year in the field. For total height (2 years and 8 years from the seed), correlation was $r = .82^{**}$ (see fig. 2). The behaviour of 3 provenances only, seemed to be the reason for this weaker correlation: 1091 was more vigorous at nursery stage, whereas 1053 and 1057 were faster growing in the field (see fig. 2). In spite of zero correlation between the weight of 1000 seeds and total height (2 years) of the means of the 26 provenances, it was remarkable that 1091 had the heaviest seeds (12,34 g) whereas 1053 and 1057 had the lightest (respectively 10,3 g and 9,14 g).

From these results, early selection of population for flushing and height growth appears to be feasible. For height growth, it is at least possible to eliminate seed sources located over 500 m in elevation, as the material is introduced at low or middle elevations in France.

In spite of ecological differences between Dordogne area (dry summer) compared to other zones (more abundant

rainfall during the growing season) where Douglas Fir is usually grown in France or in Europe, one must notice that the good sources as 1054 (Arlington), 1053 (Darrington), 1057 (Granite Falls), 1075 (Enumclaw) remain more or less the same in both types of conditions. The stability of this material seems to be very good.

As pointed out earlier by SORENSEN (1967), important variations occur on relatively short distances. Such a pattern was found in our experiment: for example, provenance 1050 (Marblemount) and 1053 (Darrington) are separated by only 35 km and grow in the same general ecological conditions (especially same elevation). The results showed that the former was very early flushing and fairly growing, whereas the latter was very late flushing and fast growing. Migration (genes flow) rather than natural selection is assumed to explain such differences.

Significant differences between provenances in flowering (male and female) were noticeable (see table 4) in spite of a slight abundance of flowers on average because of young age of the trees (9 years from the seed). There was no correlation between male and female flower production, but a trend of positive correlation between flowering (male or female) and vigour (see table 3). There was no correlation between flushing (lateness) and frequency of individuals bearing female flowers, but the correlation was strongly positive between flushing and the frequency of individuals bearing male flowers. Within provenances (between progenies), this close relationship was found only in the provenance n° 1075 (Enumclaw). Within the other populations, both traits were independent of each other.

These results confirm previous findings on the interest of Douglas Fir provenance selection for practical silviculture. The relative phenotypic difference between provenances 1057 (Granite Falls) and 1046 (Diablo Dam) is 37% for total height, 55% for 5th year height increment, 108% for flushing time (expressed in number of days).

Subsequently, using 3 nested genetic levels (provenance, progeny, individual), attention will be concentrated on the

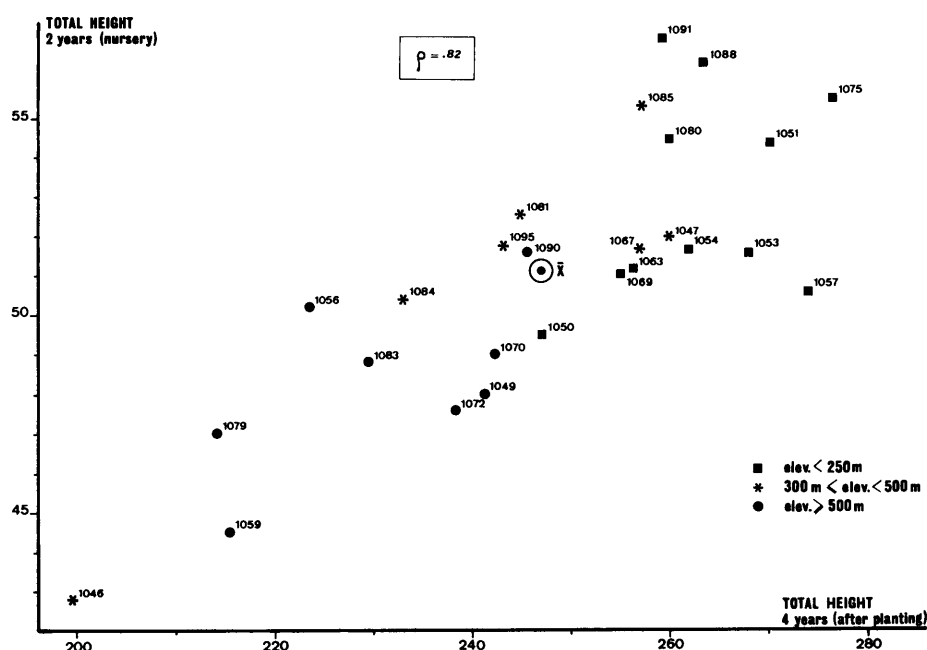


Figure 2. — Correlation of provenance means between total height (2 years in nursery) and total height (4 years after planting).

Table 4. — Frequency (%) of individuals bearing flowers (5th year)

	Male	Female
Maximum	32 (1075)	16 (1063)
Minimum	8 (1083)	4 (1046)
Average	18	9

(Number of provenance between brackets)

parameters of variability (variances and correlation) and on their variation according to provenance.

3.2 — Variation within population; comparison between populations

Model (4) (i. e. one way variance analysis) was used for each provenance:

$$\begin{aligned} \text{total variance} &= \text{variance between progenies} + \\ &(\text{or covariance}) \quad (\text{or covariance}) \\ &+ \text{variance within progeny} \\ &(\text{or covariance}) \end{aligned}$$

Computation was performed through the computer programme UNFAL designed by the Biometrics Division in Nancy.

3.2.1. — Variance of flushing and height growth

Maximal, minimal and mean values of total and residual (within) variances for each trait are given in table 5.

Ratio $\frac{\sigma^2 \max_i}{\sum_{i=1}^{26} \sigma^2_i}$, computed for each trait, was not found superior to .05 for "total" variance and .04 for "within" (residual) variance. Therefore and according to HARTLEY's tables (PEARSON, 1954) variances were considered as the same in the different provenances. Consequently a "mean" value of variance may be used, either that arising from model (4), or from model (3) (see table 5).

In general, there was no correlation between variance and provenance mean for a given trait. However for the "within" variances of flushing, a previous finding of BIROR (1974) was confirmed: in the early flushing provenances, σ^2_w increases with the lateness of the provenance mean. This pattern could probably be partly explained by experimental biases. At the first assessment of flushing, a high

proportion of individuals would be flushed in these early provenances; consequently the histogram of flushing could be truncated on its left side, and the individual variation within provenance would be reduced. This assumption was checked on the earliest progeny of the provenance 1046: 60% of the trees were flushed at the first assessment.

3.2.2 — Correlation between flushing and vigour

— For all 26 provenances, the "within" correlations were insignificant. On the average they were of .03 between flushing and height increment (4th year), and .04 between flushing and total height (4th year).

— The "between" (progeny means) correlations showed variations (Fig. 3) according to provenance: for flushing and height increment (4th year) they ranged from $-.21$ (NS) to $.70^{**}$ (8 were significant), and for flushing and total height they ranged from $-.42$ (NS) to $.55^{**}$ (only one provenance showed a significant correlation). This discrepancy could perhaps be explained by frost damages which occurred during the third year after planting, more markedly on early provenances. Because of reduced growth, vigorous and early provenances like 1069, 1091, 1063, 1051 and 1090, with a positive correlation between height increment (4th year) and flushing, had no correlation between flushing and total height (4th year). Therefore it is suggested to pay more attention to correlation between flushing and height increment rather than to correlation between flushing and total height.

Among the 8 provenances having positive correlation between height increment and flushing, 7 are located below 300 m in elevation and are vigorous. Only one, 1059 (Perry Creek), is located at higher elevation (610 m) and is slow growing. In fact, this provenance seems to include two different groups of progenies, as shown by values of variance between means of progeny, and by histogram means of progeny for height growth: the first group is fast growing whereas the second group is slow growing. Different reasons could explain this heterogeneity: tree sampling in forest, inbreeding, etc. . . Subsequently, provenance 1059 will be dropped.

Most important for the tree breeder is that there are no negative correlations at progeny level between flushing (lateness) and vigour for any provenance. This allows him to select, either for both traits (multiple trait selection) especially in provenance with null or slight correlation, or

Table 5. — Comparison of variances

	Total height 4 years (cm) (after planting)	Height increment 4th year (cm)	Flushing 5th year (* × days)
"Total" variance			
maxi	2613 (1059)	508 (1063)	21.10 ⁴ (1081)
mini	1923 (1091)	328 (1053)	13.10 ⁴ (1046)
mean (1)	2228	409	16.10 ⁴
(2)	2352	423	16.10 ⁴
"Within" variance			
maxi	2404 (1063)	462 (1063)	15.10 ⁴ (1070)
mini	1750 (1088)	352 (1080)	10.10 ⁴ (1050)
mean (1)	2086	389	12.10 ⁴
(2)	2186	399	12.10 ⁴

NB — mean (1) has been computed as the arithmetic mean of "total" or "within" variances

— mean (2) was computed by using the nested analysis of variance [model (3)] computer programme HIERA designed by the Biometrics Division in Nancy.

— between brackets: identification of provenances.

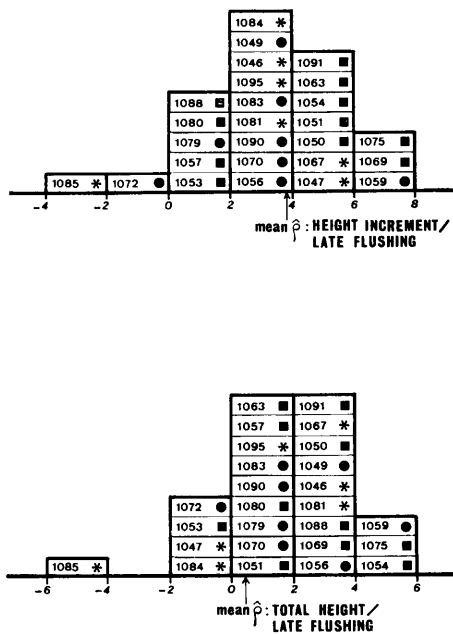


Figure 3. — Correlation between flushing and vigour : for each provenance correlation "between" (progeny means).

for one trait in the provenances with positive correlation. In the latter group already having a good level of vigour, selection should be concentrated on flushing and indirect gain would be obtained on the second trait.

However from a statistical point of view, chi-square test performed on the transformed variable z of coefficient of correlation: $z = \frac{1}{2} \text{Log} \frac{1+r}{1-r}$ leads to the conclusion that correlation between progeny means is not significantly different in the different provenances. On average the values were .17 between flushing and total height, .37 between flushing and height increment.

3.2.3. — Correlation between nursery (Nancy) and field test performances (Dordogne, Southwestern France) of progeny means

Two main factors are supposed to contribute to this correlation: juvenile \times mature relationships and genotype (progeny) \times site interaction. Obviously, there was no possibility in our study to separate effects of these two factors.

Concerning $G \times E$ interactions, CAMPBELL (1972) emphasized strong interaction for height growth between two sites for 54 Douglas Fir full sib families (4 years from the seed), 2 years after planting. Conversely, SORENSEN (1973) on 18 young Douglas Fir (3 years) half-sib families did not reveal any interaction in spite of the fact that the material was grown on two contrasted soil types.

As far as juvenile mature correlation is concerned, NAMKOONG *et al.* (1972) stressed changing in ranking of progenies, 10 years after planting.

In our experiment, different patterns in nursery \times field test relationships were noted according to provenances and traits.

For total height, assessed at 2 years in the nursery, and 6 years later (= 4 years after transplanting), correlation of progeny means (Fig. 4) was significant for 21 provenances among the 26 tested (on the average $r = .66^{**}$); for 8 provenances it was superior to $.70^{**}$.

Among the 5 provenances with $r \approx 0$, four did not exhibit significant differences between progenies in the field, but one (1091) did. Within this provenance, one progeny seemed to be strongly interacting: it was the fastest growing in the nursery whereas it was the slowest in the field (fig. 2). The reason for the reduction of growth in the field is perhaps the strong spring frost damages (99% of trees damaged) which occurred in this progeny in the third year in the field, because of its very early flushing. The behaviour of this particular progeny would be the reason for the poor correlation for provenance 1091.

For flushing (degree \times days), which is normally a stable trait, correlations between nursery and field test performances are much higher, except for 3 provenances (1083, 1072, 1051) where differences between progenies were slight.

On the average, the correlation was $.72^{**}$ for the other provenances. A dissymetrical distribution was observed (correlation was superior to $.70^{**}$ for 16 provenances).

In conclusion, because of some modifications in ranking after transfer of progenies from one place to another, early selection seems to be rather difficult to achieve, at least for growth traits.

3.3 — Genetic components of variation

From now on models 3 and 4 will be used as random effects models. In a first step, respective contributions of provenance, progeny, individual will be studied, then variation of genetic parameters between provenances will be investigated. One must keep in mind, that block effects

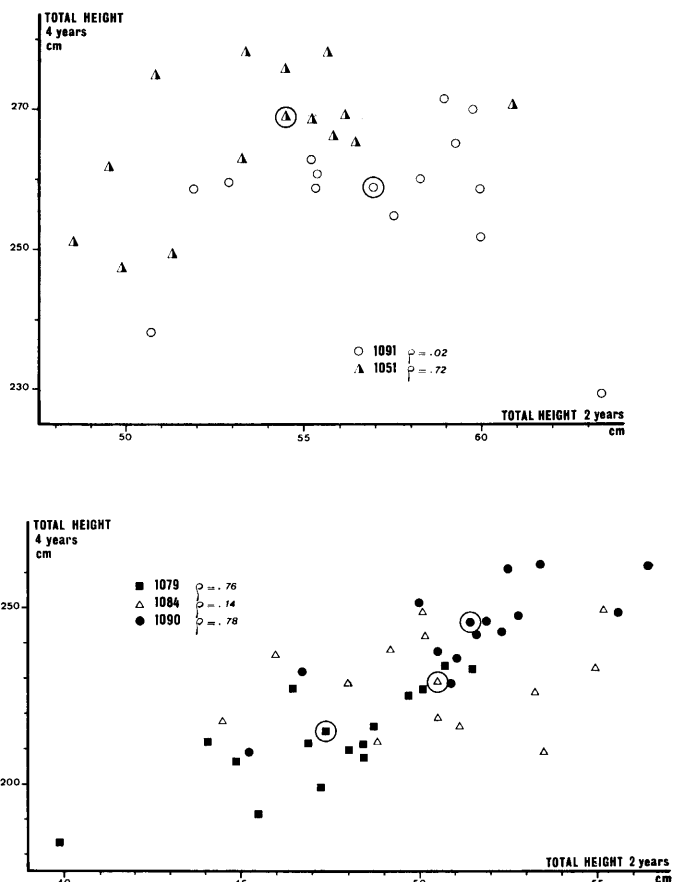


Figure 4. — Correlation of progeny means between height 2 years in nursery and height 4 years after planting (provenance mean in circle).

Table 6. — Components of variances for the different traits

	Total height 2 years (after planting)	Total height 4 years (after planting)	Height increment 4th year	Flushing 5th year	Flowers 5th year	
					Male	Female
σ^2_P	99	335	40	39.10 ³		
σ^2_{P/σ^2_T}	13	13 (9.4)	9	20 (17)	1.7	1.3
$\sigma^2_{D/P}$	54	166	24	39.10 ³		
$\sigma^2_{D/P/\sigma^2_T}$	7	6 (10.6)	5	19 (18)	5.3	3.7
σ^2_w	597	2186	399	124.10 ³		
σ^2_w/σ^2_T	80	81 (80)	86	61 (65)	93	95

Values between brackets indicate the corresponding percentage at nursery stage (BIROT, 1976). Values in italic and straight types are respectively variance and percentage of total variance.

have been removed from the model; therefore the total phenotypic variance is reduced.

3.3.1. — Partitioning of variance

Nested analysis of variance (HIERA computer programme) was performed for estimating the elements of the total variance according to the following equation:

$$\sigma^2_T = \sigma^2_P + \sigma^2_{D/P} + \sigma^2_w$$

total variance prove-nance progeny within provenance individual within progeny

Results are given in relative value of the total variance in table 6 for the different traits.

For *total height* the proportion of residual variance was important and about the same as in the nursery (this variance still includes 3/4 of additive genetic variance). The proportion of the variance due to progeny effect decreased from 10.6% in the nursery to 6% in the field, whereas the proportion of variance due to provenance effect increased from 9.4% to 13%. This reduction of the relative importance of the variation between progenies from 2 years to 8 years (from the seed) is of real importance for the tree breeder. This is probably due to remaining effects of transplanting shock affecting the progeny means. This point should be elucidated by further assessments and investigations.

As mentioned previously, this fact was stressed by NAM-KOONG *et al.* (1972) but over a longer period.

Studying the IUFRO Douglas Fir seed collection, but with provenances ranging from Northern California to South of B.C. along the Cascades Range, KVESTICH (1976) showed that the variation of total height (6 years from the seed) between provenance was about 25% both sides of the mean, whereas the variation between progenies (within provenance) was a little slighter.

For *flushing*, the proportions of variance due to provenance and progeny were slightly increasing from nursery to field stage. The relative part of residual variance was small (60%).

3.3.2. — Genetic interpretation of the different components

The genetic model can be written as follows:

$$Y_{ijk} = G_i + g_{ijk} + w_{ijk} \quad (5)$$

In this equation, Y_{ijk} is the phenotype resulting from the following components:

- G_i : genetic mean effect of provenance i
- g_{ijk} : additive genetic value of the k_{th} individual of the j_{th} progeny of the provenance i
- residual value (w_{ijk}) which includes non additive genetic effects and other indeterminate effects.

By comparison of model (5) with the statistical model (3), it appears that the covariance between relatives (half-sibs HS) may be written as follows:

$$\text{cov HS} = \text{cov } Y_{ijk} Y_{ijk} = \sigma^2_P + \sigma^2_{D/P} \quad \text{according to equation (3)}$$

$$= \sigma^2_G + \frac{1}{4} \sigma^2_g \quad \text{according to equation (5)}$$

Moreover, for each provenance, the following genetic model can be written

$$Y_{ijk} = g_{ijk} + W'_{ijk} \quad (6)$$

This equation is to be compared to statistical model (4). Within each provenance i :

$$\text{cov HS}_{(i)} = \sigma^2_{f(i)} = \frac{1}{4} \sigma^2_{g(i)}$$

Arising from the study of model (4) the assumption of equality in $\sigma_{f(i)}$ was accepted (cf 331). Therefore there were two possible ways for estimating a general value of σ^2_g : either the arithmetic mean of $\sigma^2_{g(i)}$ computed in each provenance

$$\left[\sigma^2_g = \frac{4 \sum_{i=1}^{26} \sigma^2_{f(i)}}{26} \right]$$

with the model (4), or 4 times the value $\sigma^2_{D/P}$ obtained from the general model (3). Consequently, σ^2_P estimates σ^2_G .

3.3.3. — Heritability of provenance means h^2_P

Let h^2_P be the coefficient of regression of the genetic value G_i of one provenance on its phenotypic value (NANSON, 1970).

$$E(G_i/Y_{i..}) = h^2_P (Y_{i..} - \mu) = \frac{\sigma^2_P}{\sigma^2_P + \frac{\sigma^2_{D/P}}{f} + \frac{\sigma^2_w}{nf}} (Y_{i..} - \mu)$$

As expected, h^2_P reaches very high levels ($h^2_P \geq .93$) for all traits, confirming the importance of seed sources selection

According to the formula of genotypic gain $E(\Delta G) = i h^2_P \cdot \sigma_{Y_{i..}}$ the selection of 5% of the best provenance (in this experiment the best one) would lead to a relative gain

Table 7. — Values of heritability

	Nursery			After planting			
	Total height 1 year	Total height 2 years	Flushing 2nd year	Total height 3 years	Total height 4 years	Height increment 4th year	Flushing 5th year
h^2 minimum				.10	0	0	.11
h^2 maximum				.64	.66	.36	1.70
mean of h^2_i	.60	.46	.84	.30	.26	.20	.90
general value from nested analysis				.33	.26	.20	.95

of 8% for total height (4 years after planting), 7% for flushing, 18% for height increment (4th year).

3.3.4. — Individual heritability within provenance

h^2_i was computed for each provenance as the coefficient of regression of genetic additive value on its phenotypic value:

$$E(g_{ijk}) = h^2_i (Y_{ijk} - \mu) = \frac{\sigma^2_{gi}}{\sigma^2_{f(i)} + \sigma^2_{w(i)}} (Y_{ijk} - \mu) = \frac{4 \sigma^2_{f(i)}}{\sigma^2_{f(i)} + \sigma^2_{w(i)}} (Y_{ijk} - \mu)$$

Mean and extreme values are given in table 7.

As expected from the variance analysis (cf table 6), a general decrease of heritability for height growth with age is clear. However, this trend is not systematic in all provenances; in some populations this reduction of heritability levels is strong whereas it is slight in other populations. One must keep in mind that the estimation of heritability depends very much on experimental conditions.

In addition there was no correlation between h^2 of provenances for total height (4 years) and height increment (4th year) ($r = .23$). Provenances 1088, 1075, 1085, 1070 had a high heritability for total height whereas they were not outstanding for height increment.

There were also imprecisions on the estimate of heritability (mainly overestimation) because of removing the block effect in the total variance, of probability of full-sib in the progenies, and of the limited number (11 to 15) of progenies within each provenance. This is the reason why some values of heritability for flushing reached a level as high as 1.7. Obviously this value has no proper interest, but is only to be compared relatively to other values.

It is interesting to compare also the values of $\sigma^2_{f(i)}$ (and $h^2_{(i)}$) with the mean value of provenance (i) (cf fig. 5, 6, 7). As mentioned previously, the behaviour of provenance 1059 seems to be particular. There is a large variation between populations for heritability. In the group of fast growing provenances, for example, it would be more efficient for

the tree breeder to select within a population having a good heritability. In addition, some populations with a lower performance than 1063, but having a large genetic variability would be at least as interesting for breeding purpose, as provenances better performing (1053, 1047) but less varying.

YANG *et al.* (1977) suggested on the basis of isozyme studies a reduction of rate of heterozygosity (for loci EST B and GOT B) in Douglas Fir populations with increasing elevation of seed sources. Such a pattern could lead to a reduction of the "between progenies" variance in the population from higher elevation, for traits like height growth. This trend has not been found in our study, perhaps because differences in elevation of provenances were not so high.

3.3.5. — Genetic correlations between height growth and flushing

Within each provenance, the genetic correlation r between additive values of two traits X and Y can be written:

$$r_g = \frac{\text{cov}(g_X, g_Y)}{\sigma_{gX} \cdot \sigma_{gY}} = \frac{\text{cov} f(X, Y)}{\sigma_{fX} \cdot \sigma_{fY}}$$

σ_f and cov_f were obtained from the one way variance analysis (model 4)

$$\sigma^2_f = \frac{\text{MS}_{\text{between}} - \text{MS}_{\text{within}}}{n_0}, \text{ with } n_0 = 35.$$

On all provenances, estimation of r_g may be obtained from the nested analysis of variance (model 3) performed through the computer programme HIERA. Corresponding values of r_g are given in table 8 for the different pairs of traits, with the extreme values computed separately by provenance.

In general, the genetic correlations between flushing (lateness) and height growth were positive; this result fa-

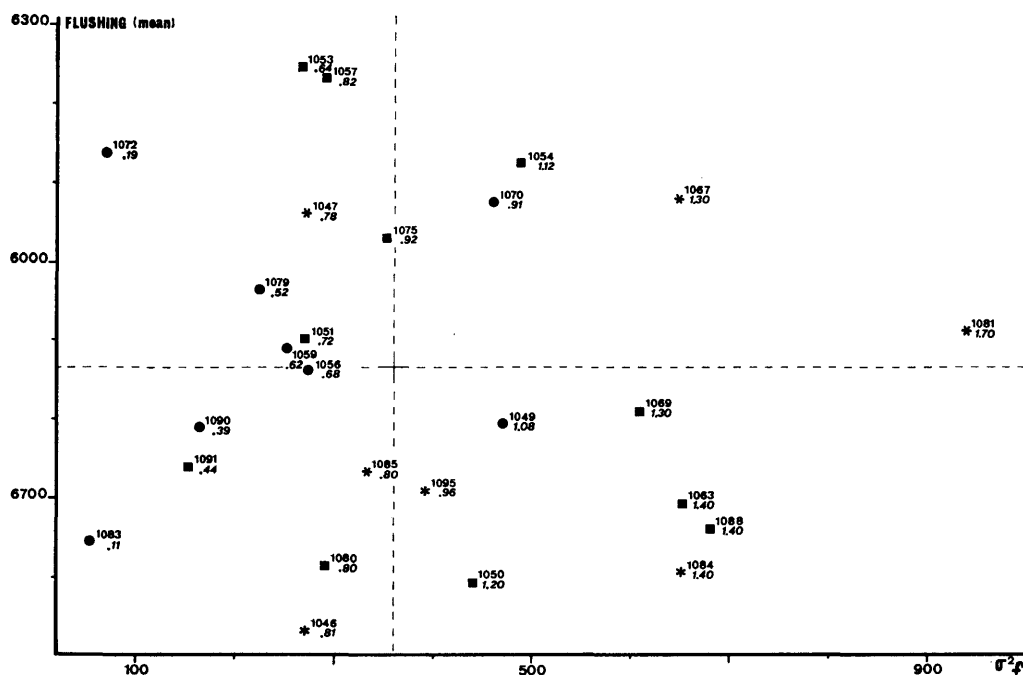


Figure 5. — Relation between provenance means and σ^2_f for flushing. (values in italic are values of h^2).

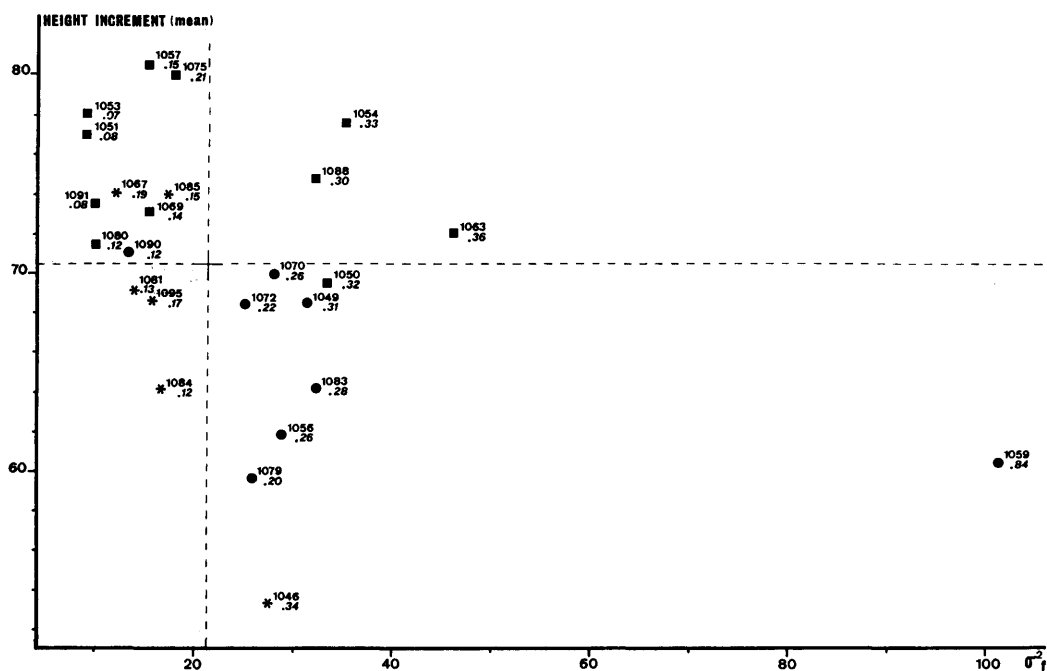


Figure 6. — Relation between provenance means and σ_f^2 for total height. (values in italic are h^2).

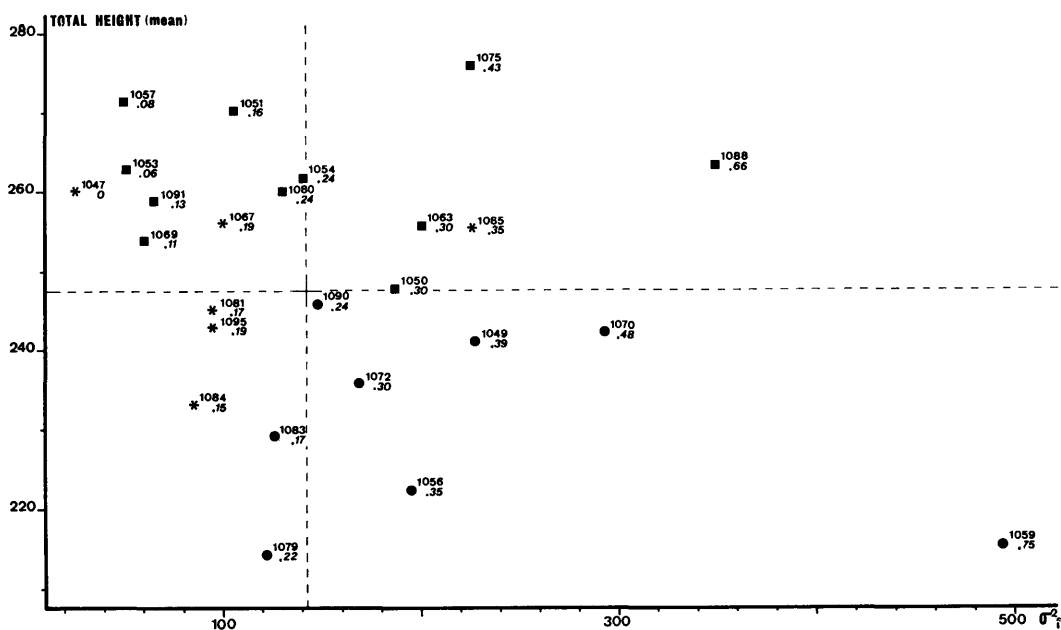


Figure 7. — Relation between provenance means and σ_f^2 for height increment. (values in italic are h^2).

vours the selection for both traits. As mentioned previously for the “between” correlations, there was a group of fast growing provenances (1054, 1075, 1091) with strongly positive genetic correlation, and another group with slighter correlation.

Once more, correlation between flushing and height increment was higher than between flushing and total height: in a multiple trait selection, a major weight should be put on flushing and height increment, provided the latter trait is a good predictor of further total height.

4. Discussion and Conclusions

1) The results about the variation between provenance means confirm the possibility to select outstanding popu-

lations for flushing (lateness) and height growth (1075, 1054, 1053, 1057) as seed sources, in order to maximize the economic gain of artificial plantations. Moreover, some of these populations can be used as basic material for breeding programmes. However the tree breeder needs to know more than just the variation between provenance means. There are indeed provenances with good mean characteristics but only slightly variable (within provenance variation) and with genetic correlations around zero. In contrast, there are provenances with medium performances but with a high level of genetic variation and with a favourable genetic correlation; therefore these parameters lead us to expect higher gains by individual selection.

Because of the small number of progenies per provenance (maximum 15), it was unfortunately not possible to statisti-

Table 8. — Additive genetic correlations

	Total height 2 years	Total height 4 years	Height increment 4th year
Total height 4 years	1.10 (.93) .64		
Height increment 4th year	1.00 (.70) .32	1.10 .88 .64	
Flushing 5th year	.63 (1054) (.17) -.48 (1085)	.55 (1075) (.22) -.50 (1085)	.92 (1069) .42 -.29 (1085)

first value: maximum between brackets: mean
last value: minimum

cally discriminate groups of provenances, for example according to the value of the genetic correlation between flushing and height growth. Only trends have been stated. It is suggested to collect seeds on a larger number of trees especially in provenances located below 500 meters in order to confirm the trends appearing from this study. It would be important to know whether other countries or institutions are interested in the same project, so that a common organization of seed collection can be set up perhaps with the help of IUFRO.

2) Within each provenance, the good levels of heritability of lateness of flushing, the moderate level of heritability of height growth (except for some provenances) and the trend towards a positive genetic correlation between both traits support the use of multiple trait combined selection (index of selection). A problem arises concerning the continuous decrease with age of progeny effects in the total variation for height growth trait. Further assessments are needed in order to check whether this trend is confirmed in the future.

3) Theoretically, a combined (provenance, progeny, individual) selection could be used by computing a new heritability; this parameter would be estimated by plotting the individual genetic value against the phenotypic value:

$$E(G_i + g_{ijk}) = \frac{\sigma_G^2 + \sigma_g^2}{\sigma_P^2 + \sigma_{D/P}^2 + \sigma_w^2} \cdot (Y_{ijk} - \mu) = \frac{\sigma_P^2 + 4\sigma_{D/P}^2}{\sigma_P^2 + \sigma_{D/P}^2 + \sigma_w^2} \cdot (Y_{ijk} - \mu)$$

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In the within provenance selection, it is of major interest to estimate g_{ijk} , because of its additive inheritance. But in the case where trees, belonging to different populations, mate each other, the estimation of the genetic value within a given population of an individual is about useless.

In this case, prediction of the part transmitted to offsprings is impossible. Interactions between effects ($G_i + g_{ijk}$) and ($G_i + g_{ij,k}$) may presumably be expected. For example, how well would perform offsprings from the mating between parents belonging to provenances 1075 and 1053? The former is fast growing, rather variable for growth traits ($h^2 = .43$), late flushing and also variable for this trait ($h^2 = .92$) and has a good genetic correlation between total height and flushing ($r = .55$) or between height increment and flushing ($r = .79$); the latter is fast growing but not varying ($h^2 = 0$) for this trait, late flushing and varying for this trait ($h^2 = .64$) and the genetic correlation between height growth and flushing is $r \approx 0$. To expect gains from heterosis effects is unrealistic until fact is proved.

However, the establishment of multiple provenance seed orchards would be extremely interesting for enlarging the genetic diversity and for minimizing inbreeding due to matings between relatives (NANSON, 1972). Since genetic parameters vary from a population to the other, it is suggested to estimate also new parameters, on the basis of progeny tests from controlled crossings between provenances. These parameters could be used to predict expected gains from a combined selection (provenance, progeny, individual) and as guidelines for optimal management of multiple provenance seed orchards.

Acknowledgements

The authors wish to thank D. AUBERT, M. FAUCHER and R. LANARES for their technical assistance in data processing, establishment and assessment of the experiment.