

# Predicting Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) Volume at Age 15 with Early Traits

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## Summary

This paper presents data from a Douglas fir provenance progeny test located in southwestern France. This test was planted after intensive site preparation. It was thinned twice before trees were 15 years old (19 years from seed) so that tree crowns can be considered to have grown with little or no competition for light. After 15 years, individual tree volume was found to be twice as large as predicted in forest management tables.

The study concentrated on the two fastest growing provenances, namely Darrington and Enumclaw, each being represented by 15 open-pollinated progenies (611 trees all told). Height and girth measurements were taken periodically between ages 2 and 15.

All traits, especially girth at breast height, showed high levels of narrow-sense heritability as well as strong additive genetic correlations with stem volume at age 15 (V15). Different indirect selection schemes using early traits were explored with the aim of improving V15. At age 8 years after planting, an index combining total height and square girth procured on V15, 90% of the genetic gain which would be obtained on this trait through direct selection. On the contrary, the correlation between family means for total height at age 2 (nursery) and 19 (field) from seed was found weak.

Two main consequences are drawn from these results. First, when juvenile-mature correlations are looked at, height and girth growth rates need to be as high as possible in evaluation field trials; in particular, competition between crowns should be avoided. Second, it seems to be possible, under a few constraints, to shorten substantially the length of Douglas fir breeding cycles.

*Key words:* *Pseudotsuga menziesii* 1, Height, Girth, Volume, Growth, Competition, Heritability, Genetic correlation, Selection, Breeding cycle.

## Résumé

*Prediction du volume à 15 ans du Douglas (*Pseudotsuga menziesii*) grâce à des caractères juvéniles*

Cet article présente des résultats tirés d'un dispositif de comparaison de provenances et de descendances de Douglas situé dans le Sud-Ouest de la France. Ce dispositif, planté après labour et fertilisation, a été éclairci deux fois avant que les arbres aient quinze ans depuis la plantation (19 ans depuis la graine), si bien que l'on peut considérer que leurs cimes ont poussé complètement hors concurrence. A quinze ans de plantation, le volume individuel moyen était le double de la valeur indiquée dans les tables de production.

L'étude s'est intéressée aux deux provenances ayant la meilleure croissance, Darrington et Enumclaw, représentées chacune par 15 descendances maternelles (611 arbres en tout). Des mesures de hauteur totale et de circonférence ont été prises sur le terrain à différents âges, de deux à quinze ans.

Tous les caractères, et surtout la circonférence à 1.30 m, ont une hérabilité au sens strict élevée et de fortes corrélations génétiques additives avec le volume à quinze ans (V15). Différents scénarios de sélection indirecte uti-

lisant des prédicteurs juvéniles ont été simulés dans le but d'améliorer V15. A 8 ans de plantation, un index combinant le carré de la circonférence et la hauteur totale procure sur V15 90% de l'espérance de gain génétique attendue par sélection directe sur ce caractère. Au contraire, la corrélation entre les moyennes de familles pour la hauteur totale à 2 ans depuis la graine (pépinière) et à 19 ans (terrain) a été trouvée faible.

Deux conséquences principales sont tirées de ces résultats. D'abord, lorsque les corrélations juvénile-adulte sont étudiées, il est important que la croissance en hauteur et en circonférence des arbres en test soit aussi rapide que possible; en particulier, la concurrence entre cimes doit être évitée. Ensuite, il semble possible, sous certains contraintes, de raccourcir nettement la longueur des cycles d'amélioration du Douglas.

*Mots-clés:* *Pseudotsuga menziesii* 1, Hauteur, Circonférence, Volume, Croissance, Concurrence, Héritabilité, Corrélation génétique, Sélection, Cycle d'amélioration.

## Introduction

Forest trees are long-lived plants, grown for at least several decades and sometimes more than a century. As a result, tree breeders need to delay mating until genotypes under evaluation have aged to the point that their potential is fully expressed. Forest tree breeders, however, are increasingly being subject to pressures from economists to provide the maximum genetic gain per unit of time. Moreover, in many species, improvement in flower stimulation techniques now makes it possible to shorten the time span between generations (BIROT, 1982). Therefore, the need to make, as early as possible, reliable predictions of mature performance is increasing.

Several literature reviews have been published on the topic of "early testing": NANSON (1968); BARADAT (1976); FRANKLIN (1977); LAMBETH (1980); JIANG (1987). Some traits under strong genetic control, like bud-flushing date, can be efficiently selected very early. However it seems difficult, based on the literature, to generalize on the validity of "age-age" correlations for parameters measuring *growth rate*. For these traits, results vary widely according to the species, the time interval considered, the site, and various silvicultural effects.

In this paper, stem height and girth in a Douglas-fir progeny test are analysed over time (age 2 to 15 from planting), in order to investigate the evolution of genetic parameters for these two growth components. In addition, genetic correlations between these traits and stem Volume at age 15 are assessed, and expected genetic gains in Volume at age 15 are computed for different selection scenarios based on one or more juvenile traits.

## Materials and Methods

All data are from a progeny-test planted in fall 1971 in Dordogne. This test is located in an area where Douglas-fir is commonly used as an afforestation species: Lat. 45°02' N- Long. 0°50' E, Alt. 220 m, Ann. rainfall 850 mm. Seed was collected under IUFRO supervision (BARNER, 1971)

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in 26 natural provenances (10 to 15 open-pollinated families per provenance) ranging from northern to southern Washington State (U.S.A.) along the western foothills of the Cascades Mountains.

The field lay-out is an incomplete block design with single tree plots; a comprehensive description is given by CHRISTOPHE and BIROT (1979). Trees were 4 years old when planted on a well prepared site (ploughed and fertilized) at an initial spacing of  $2 \times 1.5$  m (3333 trees/ha). The experiment was thinned twice:

1) 8 years after planting, every other row was removed so that spacing was increased to  $2 \times 3$  m (1660 trees/ha). The maximum initial number of 48 trees per family dropped to 24. This systematic thinning left unchanged variances and covariances at within- and between-family level (MATTHESON and RAYMOND, 1984).

2) 13 years after planting, half of the provenances were removed. Average number of trees per hectare in the remaining 13 provenances was reduced to roughly 830, with average number of trees in the spared provenances being unaffected.

Both thinnings were performed early enough so that the crowns of the trees can be considered to have grown essentially free of light competition.

Because of time and cost required for accurate height measurements on trees more than 10 m-high, this study was limited to the 2 best growing provenances in this test of Dordogne: Darrington (Lat.  $48^{\circ}16'$  N, Long.  $121^{\circ}38'$  W, Alt. 150 m) and Enumclaw (Lat.  $47^{\circ}16'$  N, Long.  $121^{\circ}56'$  W, Alt. 240 m). Both provenances were represented by 15 families with an average number of trees per family at 15 years after planting being 20.4 (range: 20.9 to 19.9).

In fall 1986, 15 years after planting, precise stem measurements were made on 611 standing trees:

- Total Height (H15) and two anterior heights (H14 and H13) were measured with a tachymeter (unit: cm; precision: 2 cm).
- Girth at breast height (G15) (unit: mm; precision: 1 mm).
- Girth (g) at half of H15 was directly measured through climbing (unit: mm; precision: 1 mm).

Assuming stem shape to be a truncated cone, individual stem volume at age 15 (V15) was computed according to the formula:

$$V15 = (H15) (g^2)/(4\pi) \quad (1)$$

Height and girth data for the same trees were also available from earlier years (Table 1).

#### Data processing:

All analyses were performed with AMANCE statistical package (BACHACOU *et al.*, 1981).

After adjustment of individual phenotypic values to environmental effects, the homogeneity of matrices (within- and between-family) has been checked with a KULLBACK test (in LEGENDRE, 1979). Basically, this test compares

the global matrix determinant of I groups to the I determinants computed for each group:

$$X = \sum_{i=1}^I ((p_i-1)/2) \cdot \text{Log} ((\det(M))/(\det(M_i))) \quad (2)$$

where  $p_i$  is the unit number of group i,

M is the global matrix for all the groups,

$M_i$  is the matrix for group i.

X follows a  $\chi^2$  distribution with (I-1) NV (NV + 1)/2 degrees of freedom where NV is the number of variates used in the comparison of matrices.

The KULLBACK test, performed on the 2 populations for a set of 5 traits (H2, H8, H15, G8 and V15), gave non-significant values (1% probability) for both within- and between-family matrices (respectively  $X = 15.5$  and  $X = 9.3$  with 15 d.f.). Distribution into two different groups was thus not justified.

The general mixed model was then used:

$$Y_{ijk} = \mu + P_i + F_{j(i)} + W_{ijk} \quad (3)$$

where  $\mu$  = is the general adjusted mean of the experiment,

$P_i$  = is the mean fixed effect of provenance i.

$F_{j(i)}$  = is the mean random effect of family j in provenance i,

$W_{ijk}$  = is the residual effect for individual k of family j.

The genetic additive variance matrix of the composite population is obtained as follow:

$$\Sigma A = 4 \Sigma F/P \quad (3 \text{ bis})$$

where  $\Sigma F/P$  is the variance-covariance phenotypic matrix between family nested in provenance.

On the composite "Darrington + Enumclaw" population, the following genetic parameters were estimated.

heritability (narrow sense) of each trait x:

$$h^2_{(x)} = (V_{A(x)})/(V_{P(x)}) \quad (4)$$

where  $V_{A(x)}$  is the additive variance,  $V_{P(x)}$  is the phenotypic variance.

genetic correlation between traits x and y:

$$r_{(Ax,y)} = (\text{COV}_{A(x,y)})/(\sqrt{V_{A(x)} \cdot V_{A(y)}}) \quad (5)$$

where  $\text{COV}_{A(x,y)}$  is the additive covariance between traits x and y.

genetic prediction coefficient: this "Coefficient de Prédiction Génétique", written CPG, was introduced by BARADAT (1976):

$$\text{CPG}_{(x,y)} = (\text{COV}_{A(x,y)})/(\sigma_{P(x)} \cdot \sigma_{P(y)}) \quad (6)$$

where  $\sigma_{P(x)}$  is the phenotypic standard deviation of trait x (resp. y). This parameter, can also be expressed as

$$\text{CPG}_{(x,y)} = r_{A(x,y)} \cdot h_{(x)} \cdot h_{(y)} \quad (6 \text{ bis})$$

expected genetic gains: 2 situations were considered in the frame of a combined selection scheme:

- Single trait selection (from FALCONER, 1960)
- direct selection on trait y:

Table 1. — Symbolic names of growth traits assessed between ages 2 to 15.

Traits	Ages after planting									
	2	3	4	6	7	8	12	13	14	15
Total Height (cm)	H2	H3	H4	H6	H7	H8		H13	H14	H15
Girth (cm) at breast height						G8	G12			G15
Volume (dm <sup>3</sup> )										V15

$$G_{(y)} = i h^2_{(y)} \sqrt{1 + \frac{(n-1)(r-t)^2}{(1-t)(1+(n-1)t)}} \sigma_{P(y)} \quad (7)$$

where

$n$  is the average number of trees per family,  
 $r$  is the coefficient of relationship between trees of the same family; here  $r = 0.125$  for half sibs.  
 $t$  is the intraclass correlation coefficient (here  $t = h^2/4$ )

$i$  is the selection intensity.

indirect response on trait  $y$  when trait  $x$  is selected:

$$G_{(y/x)} = G_{(x)} \frac{CPG_{(x,y)} \sigma_{P(y)}}{h^2_{(x)} \sigma_{P(x)}} \quad (8)$$

— Mutitrait selection (from ROUVIER, 1969)

indirect response on trait(s) not included in the index of selected traits:

the vector of genetic gains  $G_{(y/x)}$  for correlated traits "y" not included in the index is assessed as follow:

$$G_{(y/x)} = C V^{-1} G_{(x)} \quad (9)$$

where:

$C$  is the additive *covariance matrix* between traits in the index and traits not included in the index,

$V$  is the additive *variance-covariance matrix* between traits in the index,

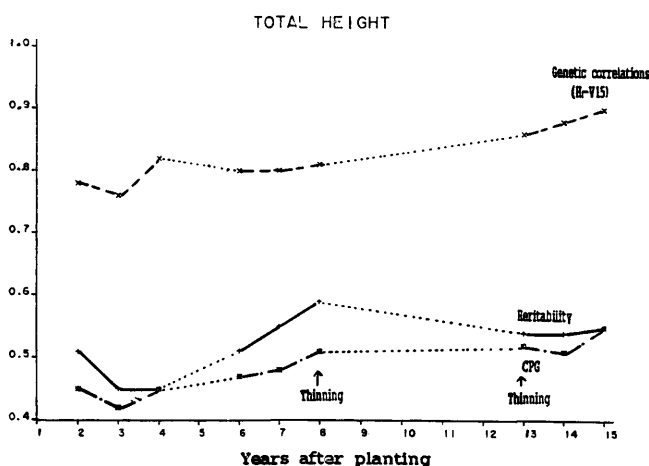


Figure 1a. — Evolution of Total Height heritabilities, genetic correlations and CPG (with V15).



Figure 1b. — Evolution of Square Girth heritabilities, genetic correlations and CPG (with V15).

$G_{(x)}$  is the vector of genetic gains of traits "x" in the index.

*Selection relative efficiency*

If one considers  $y$  as a target trait at mature stage and  $x$  a trait (or a set of traits) selected at juvenile stage, relative efficiency of an early selection is assessed as follow:

$$Q = (G_{(y,x)}) / (G_{(y)}) \quad (10)$$

Relative efficiency per unit time is given by

$$R = \frac{Q t(y)}{t(x)} \quad (11)$$

where  $t(x)$ , respectively  $t(y)$ , is the evaluation age of trait  $x$  (resp.  $y$ ).

## Results

### Growth measurements

Comparison with English Forest Management Tables (HAMILTON and CHRISTIE, 1971) shows that for Total Height, tree growth follows the same pattern as in the best yield class (Y.C. 24). This performance can be explained by the good site conditions, partially due to the investment in soil preparation, and also by the choice made *a priori* of the two fastest growing provenances.

For girth growth, trees in the provenances included in this study consistently bypassed yield class values at the same age:  $G_{15} = 50.9$  cm for the test trees against 40.2 cm in Y.C. 24 at the same age. The difference in mean tree volume at age 15 is even greater:  $V_{15} = 137$  dm<sup>3</sup> in test against 64 dm<sup>3</sup> in Y.C. 24. Very intensive silviculture applied on the test site, including early and heavy thinnings, explains the fast girth and volume growth observed on the field trees.

### Variation in genetic parameters over time

#### Total Height

Heritability of height and its genetic correlation and CPG with V15, were at their minimum three years after planting (Figure 1a). These low values probably are related to transplanting-shock effects, but the magnitudes of these "drop-downs" look relatively limited.

Both between- and within-family coefficients of variation decreased from age 2 to 8 and then stabilized from age 13 to 15. Height heritabilities were all estimated to be in the 0.4–0.6 range, which are relatively high values for these traits (BIROR, 1982). The maximum estimate of  $h^2$  was reached at age 8, with estimates very similar to the maximum value in years 13 to 15.

Genetic correlations between height and V15 grew steadily from age 4 to age 15, but in all cases were high, since the minimum estimate was 0.76. CPG between height and V15 grew slowly from age 3 to age 15, with values consistently close to 0.5.

#### Girth

Square Girth, which is proportional to basal area, will be considered for the rest of this study.

Both between- and within-family coefficients of variation increased from age 8 to 15 (by 40% and 20% respectively). Estimates of heritability were again quite high, the values being in the 0.6 to 0.8 range. This is likely due to the absence of competition between crowns. The general trend of both heritability and CPG ( $G_{15}^2$ -V15) was a constant increase from age 8 onwards (Figure 1b).

Genetic correlation with V 15, already very high at age 8, remained steady and close to 1.0 between ages 12 and

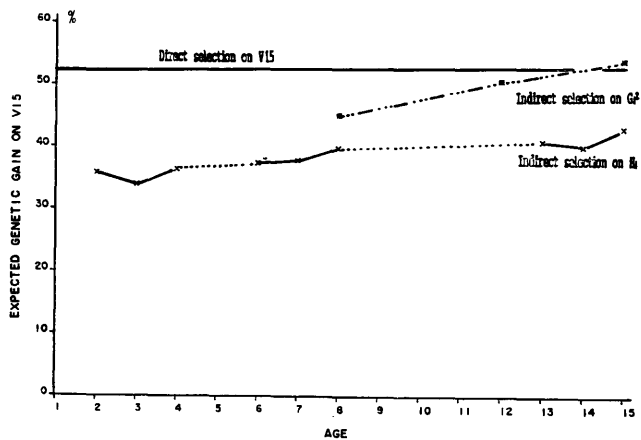


Figure 2. — Expected relative genetic gain on V15 in indirect combined selection on H or G<sup>2</sup> (selection intensity 5%).

15. This very high correlation is likely due to the use of girth (g) at mid H15 to compute total V15: g is strongly linked to G12 and G15. This result might have been different, had V15 been precisely measured on several stem units.

At age 15, CPG (G15<sup>2</sup>-V15) was greater in magnitude than the heritability of V 15 itself (0.71 vs 0.67), so that indirect selection on V15 through G15<sup>2</sup> will be more efficient than direct selection on V15.

*Expected genetic gains*

At age 15, combined selection directly on stem volume, with the top 5% of individual trees selected, would lead to a 51.8% expected relative genetic gain (formula (7)).

The expected results of indirect selection for total height or square girth at different ages, or for these two traits simultaneously at age 8, on the volume gain at age 15 are presented in Table 3 and Figure 2, when the same 5% rate of selection is applied.

As expected from the genetic parameter estimates, indirect selection for Volume at age 15, based only on Square Girth measurement, was slightly more efficient than direct selection on Volume itself. This result is explained by the strong genetic correlation between both

traits ( $r_A = 0.97$ ) and higher heritability for Square Girth than that found for volume (0.80 vs. 0.67). Since the cost of total height measurement increase dramatically with age, it is of interest to note that Girth by itself, a quickly measured trait, may be a powerful predictor of Volume.

Total Height and especially Girth at young ages appear to be *very good early predictors of Volume at age 15*. For example, at age 8, selection on height alone provides 77% of the genetic gain expected by direct selection on Volume at age 15. Indirect selection at the same age, based on girth squared, was 87% as efficient. When selection is done using an index combining both traits assessed at age 8, relative efficiency of indirect selection reaches nearly 90%.

Considering efficiency per unit time, it appears clearly that, for this test, selection based on total height carried out as early as possible is justified. However, this is of interest only if interbreeding of selected trees can occur very quickly after the selection has been carried out.

All the computations above were carried out using a single selection rate of 5% ( $i = 2.063$ ), whatever the age. Actually, before systematic thinning, which removed one tree out of two at age 8, the selection rate could have been halved (2.5% selected;  $i = 2.333$ ) for a given number of selected trees. Therefore since the systematic thinning did not modify the genetic parameters, genetic gain on V15, as well as relative efficiency of indirect selection, could be as much as 1.13 higher (2.333/2.063) than indicated (Table 2, Figure 2). Under this assumption, an index combined selection (rate 2.5%) on H8 and G8<sup>2</sup> would have been as efficient on V15 genetic gain as direct selection (rate 5%) performed on V15 itself 7 years later.

The results above were obtained under the assumption that progenies from both provenances could be pooled together, according to Kullback's test values. However, height, girth and volume genetic parameters estimates varied markedly from one provenance to the other. For example, heritability values are much higher in Enumclaw than in Darrington, whatever the trait. Therefore, in both provenances the values of expected genetic gain on V15 were checked in an indirect selection scheme using age 8 height and square girth as predictors. The results are given in Table 4.

Table 2. — Estimated means and genetic parameters for growth traits between 2 and 15 years after planting.

Traits	Mean	Coeff. of variation		h <sup>2</sup>	r <sub>A</sub> with V15	CPG with V15
		among families	within families			
<b>Total Height (cm)</b>						
H2	139	0.065	0.172	0.51	0.78	0.45
H3	192	0.054	0.152	0.45	0.76	0.42
H4	272	0.052	0.147	0.45	0.82	0.45
H6	466	0.044	0.114	0.51	0.80	0.47
H7	576	0.042	0.105	0.55	0.80	0.48
H8	685	0.042	0.100	0.59	0.81	0.51
H13	1127	0.036	0.091	0.54	0.86	0.52
H14	1214	0.037	0.094	0.54	0.88	0.51
H15	1290	0.039	0.096	0.55	0.90	0.55
<b>Sq. Girth (cm)</b>						
G8 <sup>2</sup>	836	0.105	0.247	0.62	0.90	0.58
G12 <sup>2</sup>	1877	0.119	0.262	0.69	0.97	0.66
G15 <sup>2</sup>	2588	0.148	0.295	0.80	0.97	0.71
<b>Volume (dm<sup>3</sup>)</b>						
V15	137.1	0.151	0.336	0.67		

Table 3. — Expected results of combined (individual plus family) selection for total height and stem girth at different ages on Volume at age 15.

Selected trait	Expected relative genetic gain (%) on :		Efficiency of indirect selection for V15(%)	
	selected trait	V15	Q (form. 10)	R (form. 11)
<b>SINGLE TRAIT</b>				
<u>Total Height</u>				
H2	5.2	35.8	69	517.5
H3	8.8	33.9	65	325.0
H4	6.4	36.4	70	262.5
H6	7.7	37.4	72	180.0
H7	8.6	37.9	73	156.4
H8	10.1	39.9	77	144.4
H13	12.5	41.1	79	91.2
H14	14.5	40.3	78	83.6
H15	16.4	43.3	84	84.0
<u>Square Girth</u>				
G8 <sup>2</sup>	35.2	45.2	87	163.1
G12 <sup>2</sup>	41.6	50.9	98	122.5
G15 <sup>2</sup>	54.7	54.3	105	105.0
<b>MULTITRAIT</b>				
<u>Sq. Girth and Total Height at age 8</u>				
	H8	G8 <sup>2</sup>		
	13.2	35.3	46.2	89
				166.9

Table 4. — Efficiency of indirect selection on V15 using height or girth at age 8 as predictors; provenances are considered separately or pooled. (Results expressed in percentage of genetic gain on V15 in a direct selection scheme).

Predictor	Enumclaw	Darrington	pooled
H8	73%	86%	77%
G8 <sup>2</sup>	82%	60%	87%

In Enumclaw, Girth has a higher predicting value of volume than height, whereas it is the reverse in Darrington. However, the values in Table 4 indicate that the main conclusion found with pooled progenies is still true when provenances are studied separately: at age 8, total height and girth are good predictors of volume at age 15.

#### Discussion

Results of this study would likely have been different with a slower-growing material or if intense competition was allowed to occur. NAMKOONG *et al.* (1972) published data from a 53 year-old Douglas-fir progeny test. Due to unfavorable environmental conditions (Total Height was only 3.7 m at age 15) and strong competition between trees (no thinning during the test life), positive and significant age-age correlations between total heights occurred only beyond age 18 at the family level. Another study of the test presented here is needed to explore the possibilities of using early traits to predict volume at age 15 or beyond in slower-growing provenances.

Table 2 and Figure 1 show that total height at age 2 in the field (i.e. 6 from seed) was strongly correlated genetically with volume at age 15 (i.e. 19 from seed). This is an indication that, in these progenies, the same group of genes controls the majority of growth processes during years 1 to 6 and 1 to 19. It should be mentioned that total height of trees at age 6 from seed was strongly in-

fluenced by their long stay (4 years) in nursery and by the limited magnitude of planting-shock. On the other hand, as pointed out by CHRISTOPHE and BIROT (1979), the nursery and field test are wide apart, so that risks of genotype  $\times$  site interaction are high. Unfortunately, total height of the trees at time of out-planting was not measured, but it was measured at age 2 in the nursery.

Based on all 26 provenances in the Dordogne test, CHRISTOPHE and BIROT (1979) found that the correlation of provenance means for total height at age 2 (nursery) with field height at age 8 from seed was 0.82 (\*\*, significant at 1% level). Within provenances, the correlation of family means averaged 0.66\*\*, significant for 21 provenances out of 26. Enumclaw was among the populations with a significant family correlation, Darrington was not. Similarly, correlations between family means for heights at age 2 and 19 from seed were lower in Darrington (0.13) than in Enumclaw (0.43), and in both cases the correlation were not significant at the 5% level. The nursery-field correlation, which looks weaker at the family-within-population level than at the provenance level, appears to differ between provenances and seems to decrease with age. In a recent paper, RUITERS (1987) looking at the growth of open-pollinated Douglas-fir families in seed-beds (less than 1 year old) and at age 15 in a field test, found results comparable to those we have for Enumclaw; at the family level, correlations between seedling and sapling heights averaged 0.5.

A last point about Douglas-fir is to determine if age 19 from seed belongs to the "mature" phase. According to FRANKLIN (1979), the "juvenile genotypic phase", during which height heritability decreases with age, extends, in Douglas-fir, from age 1 to 15 in the field. In the test presented here, this phase seems to have been much shorter (3 years only) and much less pronounced ( $h^2$  always greater than 0.4). We thus guess that "mature genotypic phase", during which height heritability increases with age until a plateau, actually began around age 6 in the field. FRANKLIN also suggests that "selection for gain in height . . . should be differed at least until half of rotation age". The rotation age commonly applied to Douglas fir in coming years in France should decline around 35 to 45 years. The present results are rather in accordance with FRANKLIN'S model since 15 years would then represent around half to one third of the rotation age.

Unfortunately, references concerning Douglas-fir are not numerous. Still, data recently published about different Pine species give results very much similar to ours:

— BOISSIERAS (1984) shows in *Pinus pinaster* that CPG between Total Height and Stem Volume at age 18 reaches its maximum by 8 to 10 years after planting. In this case however, values of CPG between juvenile growth traits and V18 are in the 0.2 to 0.3 range only.

— FOSTER (1986) assessed the relative efficiency in *Pinus taeda* of indirect selection for stem volume at age 15 based on survival and total height at the juvenile stage. Selecting the 3 best families among 11 at age 5 would lead to 85% of the genetic gain expected through direct selection on Volume at age 15. Similar possibilities for selecting *Pinus taeda* families for total height as early as 5 years old were previously reported by LAMBETH *et al.* (1983).

#### Consequences for progeny test management:

1 — It is of the greatest importance to minimize transplanting shock in field tests: proper soil preparation and fertilizer application, use of containerized seedlings, weed control, etc., can effectively contribute to reducing shock and accelerating growth of trees during early years in the field. However, with Douglas-fir, it looks difficult to reduce this period to less than 2 years if bare-root seedlings are utilized.

2 — Initial spacings should be chosen in such a way that no thinning is needed before age 8 after planting. A maximum number of measurements must be taken on trees before the first thinning in order to benefit from the high selection intensity possible in a large population.

3 — When trees are grown free of crown competition, girth may be a very good, and cheap, predictor of stem volume.

#### Possible consequences on selection handling:

In France, the main traits of economical interest in Douglas-fir are growth, lateness of bud flushing and stem and branch form. If only these traits are taken into account, and if it turns out that juvenile height can be a reliable predictor of mature volume, it seems possible to make early selections and to shorten breeding cycles in this species.

1. When the opportunity (financial, labor, . . .) for growing grafted copies of selected trees is available, a good breeding strategy might be to select very early (age 3—4 years after planting) a large number of individuals (say 2 to 4 times more than finally desired) on the basis of growth, phenology and total height, and then submit them

all to flower induction techniques. Confirmation of the early selections could then be achieved on growth and other traits (stem straightness, branching, . . .) around age 8. At that time, copies of the chosen ortets would be ready to be crossed in a mating scheme.

2. When these costly means are not at hand, a single stage of selection at age 8 based on phenology, growth and morphology traits might be most efficient. In this case, the time lost would be equal to the delay necessary to propagate trees and to induce flowering (at least 4 years). Time tables for both schemes are presented in Table 5, assuming that seedlings are raised in one year in the most intensive procedure (sch. I), three years in the slower one (sch. II).

Modified schemes would have to be used if great importance was given to traits on which selection can only be performed beyond age 8 in the field.

Table 5. — Time tables for two possible accelerated breeding cycles in Douglas-fir, using early selection or growth traits.

Operations	years from seed	
	sch. I	sch. II
* Nursery	1	3
* Selection and candidate propagation	5	11
* Selection confirmation	9	—
* Mating	10	15

#### Conclusion

The growing conditions of trees in this study are relevant to the new silvicultural policy in France for Douglas-fir, which emphasizes wide initial spacings so that the first thinning will already yield a high proportion of saw-logs.

Under these conditions of *no crown-competition* between trees, it appears that it is possible to get good correlations in the field between early height growth traits and volume at age 15. If results of the present study are confirmed with different provenances and in different sites, and if satisfactory genetic correlations are found between juvenile heights and volume at more advanced ages, short breeding cycles could be applied to Douglas-fir. Under this strategy, high genetic gains per unit of time would be obtained on growth, phenology, and morphology traits. However, this study does not provide evidence that family selection in the nursery is very effective in this species.

Finally, it must be stressed that this race against time has its limits. First, very early evaluation is not possible for all traits. For example, adult wood is not produced before age 15 or, in some instances, even later. Second, juvenile traits may have unfavorable correlations with mature traits of economic importance. Consequently, the Douglas fir breeder should keep in mind two objectives:

— to be able to create, if necessary, material improved for lately expressed traits;

— even if first selections can be performed early, maintain genetic material in tests long enough so that evaluations could eventually be possible on all traits which are important to the forester.

#### Literature Cited

BACHACOU, J., MASSON, P. and MILLIER, C.: Manuel de la programmation AMANCE 1981. INRA editeur. 516 p. (1981). — BARADAT, P.: Juvenile mature relationships in individual selection includ-

ing information from relatives. Advanced generation Breeding Proc. IUFRO Joint Meeting, Bordeaux, pp 121–138 (1976). — BIROT, Y.: Genetics of Douglas fir. Meeting on principles of species introduction. Lourizan — Spain, 34 p. (1982). — BIROT, Y. and CHRISTOPHE, C.: 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. *Silvae Genet.* 32 (5–6), 141–150 (1983). — BOISSIERAS, A.: Recherche de prédicteurs juvéniles de l'aptitude génétique à la croissance en volume chez le Pin maritime; détermination de l'âge optimum pour la sélection. Mémoire de stage BTS. 32 p. INRA, Laboratoire d'amélioration des arbres forestiers, Pierroton, Cestas (France), doc. int. (1984). — CHRISTOPHE, C. and BIROT, Y.: Genetic variation within and between populations of Douglas fir. *Silvae Genet.* 28 (5–6), 197–206 (1979). — COTTERILL, P.: Genetic gains expected from alternative breeding strategies including simple low cost options. *Silvae Genet.* 35, 212–223 (1986). — FALCONER, D. S.: Introduction to quantitative genetic. The Roland Press Co., N. Y. (1960). — FOSTER, G. S.: Trends in genetic parameters with stand development and their influence on early selection for volume growth in Loblolly Pine. *Forest Sci.* 32 (4), 944–959 (1986). — FRANKLIN, E. C.: Juvenile mature correlations. IUFRO Working

Groups in Quantitative Genetics, Bordeaux. 15 p. (1977). — FRANKLIN, E. C.: Model relating levels of genetic variance to stand development of four North American conifers *Silvae Genet.* 25 (5–6), 207–212 (1979). — HAMILTON, G. J. and CHRISTIE, J. M.: Forest management tables. Forestry Commission Booklet No 34. London. 201 p. (1971). — JIANG, ISRAEL BAU-JEN: Early testing in forest tree breeding: a review. *Forest Tree Improvement* 20, 45–78 (1987). — LAMBETH, C. C.: Juvenile mature correlations in Pinaceae and implications for early selection. *Forest Sci.* 26 (4), 571–580 (1980). — LAMBETH, C. C., VAN BUIJTENEN, J. P., DUKE, S. D. and McCULLOUGH, R. B.: Early selection is effective in 20 year old genetic tests of Loblolly Pine. *Silvae Genet.* 32 (5–6), 210–215 (1983). — LEGENDRE, L. P.: Ecologie numérique. Masson editeur, Paris (1979). — NAMKOONG, G., USANIS, R. A. and SILEN, R. R.: Age-related variation in genetic control of Height-growth in Douglas fir. *TAG* 42, 151–159 (1972). — NANSON, A.: La valeur des tests précoces dans la sélection des arbres forestiers. Dissert. Doct. Gembloux. Sta. Rech. Eaux. et For.; Groenendaal, H. S. No 38, 242 p. (1968). — RIJTERS, K. H. and PERRY, D. A.: Early genetic evaluation of open pollinated Douglas fir families. *Forest Sci.* 33 (2), 577–582 (1987). — ROUVIER, R.: Pondération des valeurs génotypiques dans la sélection par index sur plusieurs caractères. *Biometrics* 25, 295–308 (1969).

## Mating Systems in Open-Pollinated Families of Black Locust (*Robinia pseudoacacia*)

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### Abstract

The mating system of black locust (*Robinia pseudoacacia*) was investigated using six allozyme loci and the multi-locus model of RITLAND and JAN (1981). Estimated outcrossing rates averaged 0.83 across 23 seed sources, ranging from 0.46 to 1.12. Variation in outcrossing rates among sources may be due to the local patchiness of allele and genotype frequencies (Wahlund effect) and/or pollinator behavior. The estimates obtained are probably conservative because the sampling scheme employed could artificially induce Wahlund effects. The physical separation of stigmatal and antheral surfaces as well as the protogynous flowering habit encourages outcrossing in black locust. Among seed sources, germination rates were positively correlated with outcrossing rates. Low germination rates may be a manifestation of inbreeding depression in seed families with higher amounts of consanguineous mating.

*Key words:* Allozymes, Black locust, Outcrossing rates, Fixation indices.

### 1. Introduction

Non-obligate outcrossing behavior is characteristic and advantageous in colonizing, clonal entomophilous species because scattered individuals may be reproductively isolated (BAKER, 1965). Previous studies (PHILLIPS and BROWN, 1977; MORAN and BROWN, 1980; HOPPER and MORAN, 1981; YEH *et al.*, 1983; BROTSCHOL *et al.*, 1986) have shown that

outcrossing rates of entomophilous tree species are typically less than 0.90 and are sensitive to fluctuations in pollinator behavior and stand structure (BROWN *et al.*, 1989; AIDE, 1986). Black locust (*Robinia pseudoacacia*) combines several traits that might be expected to reduce effective rates of outcrossing. It is a colonizing species that spreads locally by vegetative growth and it has limited seed dispersal. It also flowers profusely and is primarily pollinated by hymenopterans. Even though black locust is economically important in Europe and ecologically important in the United States, little is known of its mating system.

From an applied standpoint, estimates of quantitative genetic parameters (i.e. additive genetic variance and heritability) important in tree breeding programs often rely on the assumption that open-pollinated progeny arrays are half-sibs. When considering entomophilous species such as black locust, it is unlikely that insect vectors randomly distribute pollen. Nearby individuals shedding pollen at the proper time probably sire a majority of the offspring of neighboring trees (WASER and PRICE, 1983). Such non-random pollen deposition creates correlated matings (SCHOEN and CLEGG, 1984; SYMTH and HAMRICK, 1984) and increases the genetic relatedness of open-pollinated progenies. Bias introduced by non-random mating behavior can lead to an overestimation of additive genetic variance, heritability, and subsequently, genetic gains (SQUILLACE, 1974).

In this study, six allozyme loci were used to estimate effective outcrossing rates for 23 geographic seed sources located throughout the natural range of black locust. Data were also used to determine whether pollen allele frequencies vary among individual trees within a geographic seed source.

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