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Genetic Structures and Expected Genetic Gains from Multitrait Selection in Wild Populations of Douglas fir an Sitka spruce II. Practical application of index selection on several populations

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(Received 17th December 1982)

Summary

The paper reports the use of a series of multiple trait selection indexes to maximise expected gains following selection in some Douglas fir and Sitka spruce populations. The vector of genotypic values of an individual is derived from performances of its open pollinated half sibs, from its provenance, and from the phenotypic and additive genetic covariance matrices between some economically important characteristics. The problem was to derive a linear combination of these genotypic values which would maximise gain in desirable characteristics (growth, flushing) and minimise the increase in undesirable ones (sinuosity, budset branching).

Many weighting coefficients were tested and the one providing the most desirable outcome was chosen. The resulting distribution of selected individuals among provenances and progenies is given.

Multitrait index selection appears to be useful in practical selection, and the genetic gains are substantial even when starting from wild populations. The problems of clonal seed orchard constituted of clones selected in different populations are discussed with respect to variations of genetic structure between populations.

Key words: Multitrait selection, *Picea sitchensis, Pseudotsuga menziesii*, Index selection, Genetic gains.

Zusammenfassung

In der Arbeit wird über die Verwendung einer Serie multipler Merkmals-Selektionsindices berichtet, um den nach Selektion zu erwartenden genetischen Gewinn in einigen Douglasien- und Sitkafichtenpopulationen zu maximieren. Der Vektor genotypischer Werte eines Individuums wird von der Erscheinung seiner frei abgeblühten Halbgeschwister, von seiner Provenienz und von den phänotypischen und additiven genetischen Kovarianzmatrizen zwischen ökonomisch wichtigen Merkmalen abgeleitet. Das Problem bestand darin, eine lineare Kombination dieser genotypischen Werte zu erzielen, bei der ein genetischer Gewinn erwünschter Merkmale (Wachstum, Austrieb) maximiert und gleichzeitig der Anstieg unerwünschter (Krummwüchsigkeit, Blütenansatz, Astigkeit) auf ein Minimum herabgesetzt wird.

Zahlreiche gewogene Koeffizienten wurden getestet und derjenige, der für die Auswertung am effektivsten war, ausgewählt.

Die daraus resultierende Verteilung selektierter Individuen in Provenienzen und Nachkommenschaften ist gegeben.

Die Index-Selektion auf multiple Merkmale erschien in der praktischen Selektion brauchbar, und die genetischen Gewinne waren beträchtlich, selbst wenn man von Wild-populationen ausgeht. Die Probleme mit Klon-Samenplantagen, die mit selektierten Klonen aus verschiedenen Populationen erstellt worden waren, werden hinsichtlich der Variation der genetischen Struktur zwischen Populationen diskutiert.

1. — Introduction

The procedure of index selection is commonly used in animal and plant breeding. Generally the aim of the breeders is to improve the average genetic worth (H) of a population, with H being a linear function of additive genetic values, i.e., $H = \Sigma a_i G_i$, with the coefficient a_i being exactly defined from economical consideration. Since genetic values cannot be observed directly, selection will concern an observable variable I, jointly distributed with H. For many authors, the major problem in applying the theoretical model is to evaluate the economic coefficients a_i. Thus some methods avoiding assumptions concerning economic weights were developed especially by Rouvier (1969).

The method of "desired genetic gains" was furthermore studied (Pesek and Baker 1969, Mallard 1976, Baker 1974): this method seems to be more attractive for the breeder because it implies a good knowledge of the material in selection, and of the relative importance the breeder attaches to each of the traits. In forest tree breeding, the problem of economic weights was pointed out by Arbez and Millier (1972), Arbez *et al.* (1974), Mauge *et al.* (1974), Namkoong (1976).

Forest tree breeders are mainly interested in selection of individuals with good additive genetic performances so that subsequent clonal seed orchards constituted with this material will produce commercial seeds of high quality. In order to make selection as efficient as possible, the basic populations should exhibit, good mean performances, a wide genetic variability as well as favourable genetic correlations between traits to improve.

The present experiment takes place after recent studies on genetic variability of two economically important forest tree species: Douglas-Fir (Christophe and Birot 1979) and Sitka Spruce (Gillet 1981). The knowledge of all genetic parameters enabled the application of multitrait index selection, which combines all informations about phenotypic performances and genetic structures. In order to avoid too many related individuals among the selected ones, it seemed to be interesting to start the selection from mixed populations. Theoretical considerations about calculation of index selection when dealing with several populations are given in Christophe (1979), and the results on its application for two forest tree species are presented and discussed here.

The "desired genetic gains" are determined here by the optimum attainable for each of additive genetic values, i.e., the best realized performance for each trait at progeny level: the coefficients a_i are chosen so that expected genetic gains estimated from index selection are as close as possible to these desired genetic gains.

2. — Material and Methods

2.1 *Experimental design*

Populations and within population sampling as well as experimental design and statistical model are described in Birot and Christophe (1982). Information about location of 26 and 21 provenances of Douglas Fir and Sitka Spruce respectively are given in *Table 1*. Fifteen open-pollinated progenies were sampled from each population (assumed to be half sib progenies). For Douglas-Fir the results presented here concern 371 progenies being represented on average by 20 individuals in the whole experiment. For Sitka Spruce, each of the 262 progenies was represented by 50 trees. All traits, which seem to be economically important, were measured on all trees in the plantations: they concerned growth characteristics (total height and girth) as well as adaptive characteristics (flushing time and bud set time) and form characteristics (forking, sinuosity and branch angle). As we will see later some of these traits were desirable and others undesirable for forest tree breeding.

The linear random model used in the study cited above permitted estimates all components of total variability: between provenances (Σ_p), between progenies within provenance (Σ_f) and within progeny, i.e. residual (Σ_w).

In the present study, the provenances are considered as randomly sampled: thus applying a pooled nested model on the phenotypic values, the estimates of genetic and statistic parameters may be obtained on average over all provenances. The calculation of index depends on these estimates and considerations on gains to expect from selection.

2.2 *Theoretical model of selection indexes*

The theory of genetic selection indexes which combine multivariate informations on each individual and its relatives is now well known: see Williams (1962), Henderson (1963), among others. The individual index value is a linear combination of the estimates of the additive genetic values for all (c) traits to be selected:

$$I_{ijk} = \Sigma_c a_c \hat{G}^c{}_{ijk} = {}^t a \, \hat{G}_{ijk}$$

with *a* being the vector of weighing coefficients and $\hat{G}$ the vector of estimated additive genetic values (the sign ^ over a symbol means an estimate and ${}^t a$ means the transposed af a).

As in Rouvier (1969), the vector G_{ijk} is estimated by multiple linear regression from the assessed phenotypical values Y_{ijk} on the k^{th} individual of j^{th} progeny of i^{th} provenance.

In the reported experiments, there were three levels of variation: provenance, half sib progeny within provenance and individual within half sib progeny. Therefore the regression equation can be written as below:

$$\hat{G}_{ijk} = B_1 \left[y_{ijk} - y_{ij.} \right] + B_2 \left[y_{ij.} - y_{i..} \right] + B_3 \left[y_{i..} - y_{...} \right]$$

or with matrix notation, $\hat{G} = VP^{-1} Y$.

.Y is the vector (3c) of phenotypical values comprising three vectors (c):

individual $y_{ijk} - y_{ij.}$
Progeny $y_{ij.} - y_{i..}$
Provenances $y_{i..} - y_{...}$

.P is the matrix (3c, 3c) of variances-covariances between all phenotypical components.

.V is the matrix (c, 3c) of variances-covariances between additive genetic values to predict and phenotypical values used as predictors.

The nested model of variance analysis was used to estimate the components of total variation: $\Sigma_t = \Sigma_p + \Sigma_f + \Sigma_w$ obtained by pooling all populations.

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'	90	11
	Perry Creek	1059	W	48°03'	121°28'	610	15
	Gold Bar	1063	W	47°51'	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'	121°34'	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	1085	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°08'	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
	Humptulips	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
	Necanicum	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
	Biq Qualicum	3062	BC-VI	49°23'	124°37'	0	20
	Haney	3063	BC-ML	49°14'	122°36'	90-300	11
	Vedder	3064	BC-ML	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 prefixe "10".

(2): Because of their relatively poor performances at nursery stage the provenances 3064, 3067 and 3073 were dropped for the field stage.

The calculation of elements of the matrices P and V derive from statistical and genetic considerations: all these elements are combinations of Σ_p, Σ_f and Σ_w (details about the statistical and genetic models are given in Christophe 1979). Thus, it is theoretically possible to estimate the vector $\tilde{G}$ from the phenotypical values measured on the trees.

Then the practical problem is first to choose the traits to be selected and in a second step to evaluate the weighting coefficients for each trait.

3. — Calculation of Selection Indexes

3.1 *Traits to be selected*

All tree breeders are interested in improving the volume production thus the growth traits. For the Douglas-Fir experiment, the traits: total height age 12 (TH 12), total height increment from age 6 to 12 (HI) and girth age 12 (G 12) were chosen, whereas for Sitka Spruce there were total height age 8 (TH 8) and annual increment of 8th year (HI 8). Besides, the improvement of lateness in flushing of Douglas-Fir seems to be of major interest due to high spring frost hazards in France and is possible because of wide variation between and within provenances; therefore, flushing time (FLU 9) was included among the selection criteria for Douglas Fir. By contrast, precocity of bud set time (BS) should be improved for Sitka Spruce because of autumn frost occurence in some areas.

In addition to growth and phenological traits, it was of interest to improve form (stem and branching) characteristics for Douglas Fir. The studied traits were forking, sinuosity and branch angle:

— forking presented a small variation between progenies (within provenance), but there was some variation between provenances. However the provenances with a relatively high number of forks (1050, 1063, 1069, 1080, 1084) were also early flushing and would have been rejected when selecting for late flushing. The only embarrassing case was the provenance 1075 (ENUMCLAW) at once vigorous, late flushing and with a rather high forking defect. Fortunately in this population, the additive genetic correlations between forking and total height (TH 12), forking and lateness in flushing (FLU 9), were both negative (respectively —.52). Therefore, because selecting for TH 12 and FLU 9 would have indirectly decreased the forking defect, forking was not included in the calculation of selection index.

Table 2. — Parameters of linear multiple regression.
below the diagonal : additive genetic correlations
over the diagonal : correlations at provenance level
last row : heritabilities

	TH 12	HI	G 12	FLU 9	SIN 12
TH 12		.98	.96	.40	.89
HI	.98		.96	.40	.88
G 12	.82	.75		.27	.78
FLU 9	.32	.31	.25		.13
SIN 12	.1	.09	.08	-.15	
h^2	.33	.3	.32	.95	.4

A Douglas Fir

	TH 8	HI 8	BS
TH 8		.99	.83
HI 8	.88		.90
BS	.6	.6	
h^2	.42	.31	.35

B Sitka Spruce

— branch angle (BRA 12) showed little variation between provenances, but had a good level of heritability (.49). This trait (evaluated by scoring 1 to 5) was selected by independant culling level method: all index selected trees with score greater or equal than 3 were finally excluded.

— Stem sinuosity (SIN 12) is an important defect in Douglas-Fir and the variation between provenances was important as well as between progenies within provenance. Two different ways were used, first including sinuosity (SIN 12) in the multitrait index, second selecting against sinuosity by independent culling level method as for branching.

In summary, the following indexes were computed:

1⁰) Douglas-Fir

$$I = a_1 \hat{G}_{TH\ 12} + a_2 \hat{G}_{HI} + a_3 \hat{G}_{G12} + a_4 \hat{G}_{FLU\ 9}$$

$$I = a_1 \hat{G}_{TH\ 12} + a_2 \hat{G}_{HI} + a_3 \hat{G}_{G12} + a_4 \hat{G}_{FLU\ 9} + a_5 \hat{G}_{SIN\ 12}$$

2⁰) Sitka-spruce

$$I = a_1 \hat{G}_{TH\ 8} + a_2 \hat{G}_{HI\ 8} + a_3 \hat{G}_{BS}$$

The genetic parameters estimated for all traits in both species are given in *Table 2*.

Given the traits to be improved and the estimates of the regression parameters, the next step was to determine the weighting coefficients and then to compute the index.

3.2. *Determination of weighting coefficients*

Due to the long term of rotation and to the difficulty to evaluate economic progresses of such or such traits, the use of economic weights seems to be a non sense for the forest tree breeder. It is the reason why it is more realistic to try to define the target in biological terms: what should be the desired ideotype and what should be the genetic gains to reach it, according to the relative importance given to each trait (Baker 1974, Mallard 1976, Tallis 1962). Obviously, the more distant from the ideotype the mean value for a given trait, the more important is the genetic gain.

The desired genetic gain arising from individual selection should be towards this "ideotype" which combines all desired performances (here the best progeny means for each trait). Selection index can be written as $I = t_a VP^{-1}y$ (matrix writing) and the vector of expected genetic gains is estimated as follows:

$$\hat{\Delta G} = \frac{VP^{-1}\, {}^{t}Va}{\sigma^2_I} \quad \Delta I = \frac{i}{\sigma_I}\, VP^{-1}\, {}^{t}Va$$

with i = selection differential ($\triangle I/\sigma I$)

σI = standard deviation of I ($\sigma^2_I = t_a VP^{-1}\, {}^{t}Va$)

$\triangle I$ = truncation on distribution of individual values I.

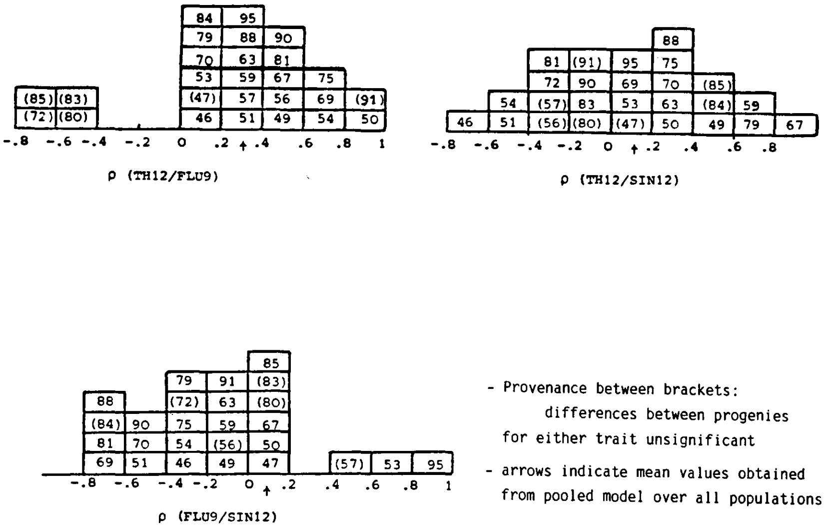
With P, V and i given, the estimated value of $\triangle G$ depends in a large part on the values of vector a. By using different sets of components for the vector a, computation of corresponding genetic gain $\triangle G$ is possible. Subsequently the aim is to find the most efficient set, i.e., that one which gives for each trait the expected genetic gain as close as possible to the desired gain towards to the ideotype. In the case of really unfavourable genetic correlation between traits, one solution is to select for the trait considered as the most important, maintaining the other one at a fixed level: a second one is to create two different varieties.

The above described methodology was applied to the Douglas-Fir and Sitka Spruce progeny tests. The computational procedures to test many sets of *a* and to calculate the vector $\triangle G$ as well as the I values, are given in Christophe (1978).

4. — Application to Forest Tree Breeding

4.1. *Selection of weighting coefficients*

For Douglas-Fir improving volume production (TH 12 and G 12) and at the same time lateness of flushing (FLU 9) was the first objective: the genetic correlation between both traits being slightly positive (.3), simultaneous selection was possible. In addition, stem sinuosity (SIN 12) should at least not be augmented in the population of selected trees. On average over all populations the genetic correlations TH 12/SIN 12 were both nonsignificant (.10 and —.15). But for FLU 9/SIN 12, 22 provenances among the 26 under test exhibited favourable (i.e. negative) genetic correlations whereas for TH 12/SIN 12, 15 provenances only followed the same pattern (see *Fig. 1)*. Into the best growing provenances (1054, 1051, 1075, 1067) which were simultaneously the worst for sinuosity (due to high correlation at provenance level), FLU 9 was always favourably correlated with both TH 12 (positive) and SIN 12 (negative). It was therefore decided to put an important weight on flushing trait, which would lead to indirect selection for growth traits without increasing general sinuosity. As mentioned above, two series of indexes were computed without (sets 1—7) and with (sets 8—11) including the sinuosity. *Table 3* shows the expected gains calculated according to (1) for i = 1.75 (i.e. 10 % of selected individuals) according to the different sets of coefficients. Sets 1 to 7 gave a constant weight to growth traits and a decreasing weight on flushing, so that the relative expected genetic gain slightly increased from 11 to 14 % for total height (TH 12) and decreased from 74 to 51 % for flushing time. The coefficient of correlation between index values computed with the extreme sets 1 and 7 was of .88. This result emphasizes clearly that most of trees would have been selected whatever the set. Sets 8 to 11 were tested for a fixed weight in growth and flushing traits and a decreasing weight against sinuosity. This procedure



- Provenance between brackets: differences between progenies for either trait unsignificant
- arrows indicate mean values obtained from pooled model over all populations

Figure 1. — Douglas fir: Estimates of within population additive genetic correlations.

Table 3. — Douglas Fir: Expected genetic gains for several sets of weighting coefficients when 10 % trees are selected.

	a_{TH12}	a_{IH}	a_{G12}	a_{FLU9}	a_{SIN}	$E(\Delta G)_{TH12}$ (in %)	$E(\Delta G)_{IH12}$ (in %)	$E(\Delta G)_{G12}$ (in %)	$E(\Delta G)_{FLU9}$ (in %)	$(E\Delta G)_{SIN}$
Set_1	1	1	20	60		10.6	9.9	11.4	73.6	
Set_2	1.5	1	20	60		11	10.3	11.9	72.3	
Set_3	2	1.5	20	60		11.6	10.9	12.5	69.9	
Set_4	1	1	10	30		11.8	11.1	12.8	69	
Set_5	1	1	20	30		12.3	11.5	13.6	66.4	
Set_6	1	1	20	20		13.1	12.2	14.6	60.6	
Set_7	1	1	20	10		13.8	12.8	15.7	51	
Set_8	1	1	0	50	-30	9.76	9.23	10.1	75.7	-1.08
Set_9	1	1	0	40	-40	10.2	9.65	10.6	74.6	- .94
Set_{10}	1	1	0	40	-20	10.4	9.79	10.8	74.3	- .1
Set_{11}	1	1	0	40	-10	10.4	9.86	10.8	74.2	.3

gives an expected genetic gain around 10 % for growth traits, 74 % for flushing and a slight decreasing of genetic gain on sinuosity from —.1 to .3. An heavier weight against sinuosity would have led to unacceptable losses on growth traits. *Table 4* gives the phenotypical mean values of selected individuals for the sets 1, 7, 8 and 10 and three selection intensities (20,5 and 1 %). Set 1 and set 10 are very similar for the intensity 1 %. The mean performance of selected individuals reached the level of the best progeny for growth and exceeded the best progeny for flushing, whereas the values of sinuosity did not change on average.

For Sitka Spruce the problem was at the same time to reduce the bud set time and to improve the growth traits, even though the genetic correlation between both traits was positive thus unfavourable (see *Table 2*). For total height, the weighting coefficient was fixed to 1, whereas for bud set time it decreased from 0 to —2.0. Under —2.0, the expected gain calculated as noticed above in (1) for growth was considered as too low. Expected genetic gains on total height and bud set time corresponding to each set are given in *Table 5* for i = 1.75 (10 % of selected individuals). With the set 1, the maximum gains for

Table 4. — Douglas Fir: Phenotypical mean values of selected individuals for several sets of weighting coefficients and three intensities of selection (1—5 and 20 %).

Traits	Initial Grand mean	Set_1			Set_7			Set_8			Set_{10}		
		20 % selected	05 % selected	01 % selected	20 % selected	05 % selected	01 % selected	20 % selected	05 % selected	01 % selected	20 % selected	05 % selected	01 % selected
TH_{12} (cm)	637	698	712	727	723	757	792	693	704	719	696	711	723
IH_{12-6} (cm)	512	557	565	575	574	595	621	555	561	570	557	566	572
G_{12} (cm)	26	29	29	29	30	31	31.9	28.4	28.4	28.8	28.6	28.7	29
FLU9 (days)	9.9	16	19.8	22	14.4	18	20.7	16.3	19.9	22.2	16.2	19.8	22.1
SIN (score 0-5)	2.23							2.22	2.19	2.2	2.24	2.2	2.22

Table 5. — Sitka spruce: Expected genetic gains with 10 % selected individuals.

	$a_{TH\ 8}$	a_{BS}	$\widehat{\Delta G}_{TH\ 8}$ (in %)	$\widehat{\Delta G}_{IH9}$ (in %)	$\widehat{\Delta G}_{BS}$ (in %
Set$_1$	1	0	18	23	4.34
Set$_2$	1	-0,5	17,8	22,7	3,93
Set$_3$	1	-0,7	17,7	22,5	3,7
Set$_4$	1	-1,0	17,2	21,8	3,28
Set$_5$	1	-1,25	16,6	21,0	2,83
Set$_6$	1	-1,50	15,7	19,7	2,28
Set$_7$	1	-1,75	14,4	18	1,62
Set$_8$	1	-2,0	12,7	15,7	0,875

Table 6. — Sitka spruce: Phenotypical mean values of selected individuals with Set$_1$.

		TH8 (cm)	IH8 (cm)	BS (in days)
Grand mean		203,9	54,3	244,8 (September 1st)
Set$_1$	20%	247	64,6	257
	10%	258	68,7	258
	5%	269	72,3	259
	2%	285	79,2	260
	1%	293	79,7	261 (September 16 th)

TH 8 (18 %) and IH 8 (23 %) were obtained, but due to the positive correlation between total height and bud set time, lateness of bud set increased (4 %). By contrast with set 8 the bud set time was slightly increased (.9 %) while the expected gains on total height and height increment were only 13 % and 16%. The phenotypical mean values of selected individuals with the set 1 and with different levels of selection intensity (20, 10, 5, 2, 1 %) are given in *Table 6*. With the intensity of 1 %, the selected individuals exhibited phenotypic gain of 50 % (mean of 293 cm versus a grand mean of 204) for total height but were fifteen days later for bud set time; these values are exactly the same as the performances of the most vigourous progeny and of the latest bud setting progeny. In the ecological conditions of future use of this material the risk of increasing the bud set time from 1st to 15 September is acceptable because of the lateness of autumn frost. Therefore the set 1 could be chosen for practical selection, the major objective for this species being the improvement of total vigour.

4.2. *Distribution of selected individuals*

The selected individuals are chosen on the basis of their additive genetic values. At the next step, it is intended to propagate them by a vegetative way and to set up the copies into a clonal seed orchard, where the seed will be collected for practical forestry. Achieving good genetic gains, implies that all individuals mate each other, but crosses between relatives (here half sibs) should be avoided. Selecting from several populations with a multi-population seed orchard increases the occurence of non-related individuals: thus the genetic diversity will be high, probably higher than in a natural population. Therefore it is necessary to control the results of the index selection and to check where do the selected individuals come from in terms of provenance and progeny.

For Douglas-Fir the set n⁰ 10 was used with the following weights:

$$I = \hat{G}_{TH\ 12} + \hat{G}_{IH} + 40G_{FLU\ 9} - 20\ \hat{G}_{SIN\ 12}$$

With a selection intensity of 2 % a total number of 157 individuals were selected, belonging to 21 provenances and 90 different progenies (see *Table 7*). Within the selected populations the selection intensity ranged from .3 % to 10 % (provenance 1057); for four provenances (1053, 1054, 1057, 1075) the selection intensity was over 8 % and it was 5 % for the provenance 1067. In these five provenances 107 individuals were selected among the 157 i.e. 68 %. The number of selected individuals within the same progeny

Table 7. — Douglas Fir: Distribution of selected individuals per progeny into provenance (selection intensity: 2 %).

Provenance number	Total by provenance	in % of the initial total	Progeny number														
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1047	7	(2,4 %)	1		1	1	2			1			1				
1051	5	(1,7 %)		1		1				1				2			
1053	27	(8,7 %)	1	1	1		3	2	3	1	5	1		1	3	2	3
1054	20	(8 %)	6	2	4	2	1					3	1			1	---
1057	19	(9,9 %)	2	1	1	1	2	1	2	1	5	2	1	---	---	---	---
1067	15	(5.2 %)	7	1		1	1	2					1		1		1
1075	26	(8.6 %)		3			2	12	1	1		1		1	2	1	2
1070	8	(2 %)		1	1				2			2			2		
1063	4	(1.4 %)							1		3						---
1088	6	(2.4 %)		2						1	2		1				
1080	2	(.8 %)													1	1	---
1050	1	(.3 %)		1													
1056	2	(.7 %)						1				1					---
1069	1	(.5 %)						1									---
1072	3	(1.1 %)						1			1				1		
1081	1	(.4 %)											1				---
1085	1	(.4 %)												1		---	---
1090	1	(.4 %)										1					---
1091	4	(1.4 %)	1		1					1	1						---
1049	3	(1.2 %)				1		2									
1095	1	(.3 %)					1										
Total	157	2%															

--- = Progeny not available or not included in the test.

Table 8. — Sitka Spruce: Distribution of selected individuals in progeny and provenance according to the selection intensity A (5 %) B (1%).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Total
3001											2						▨	▨	▨	▨	2
3002				1									3					▨	▨	▨	4
3003	2					1									1			▨	▨	▨	4
3004	1									1		1	8		▨	▨	▨	▨	▨	▨	11
3005				6															▨	▨	6
3006		1					1									▨	▨	▨	▨	▨	2
3007						1				3	1		2	2			▨	▨	▨	▨	9
3008	1		4	1	4	3	1		2					2	17	▨	▨	▨	▨	▨	35
3009	3	9			1	1		2	19	3	1	2	22	1		▨	▨	▨	▨	▨	64
3010				3	4			1	21								▨	▨	▨	▨	29
3011	11	17	13		1		11	25	17	12	13		9	23		▨	▨	▨	▨	▨	152
3012	1	1		11		5	28			1		▨	▨	▨	▨	▨	▨	▨	▨	▨	47
3013	1	6	18	12	3		1	3		21	15	1	11	8	5	2	▨	▨	▨	▨	107
3014	8	12	▨	▨	25	▨	22	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	67
3062				1																	1
3063		▨			▨						▨	▨				▨	▨	▨	▨	▨	0
3065								3								▨	▨	▨	▨	▨	3
3066	6	32		5	2	11	6		11		3	19	18		4	▨	▨	▨	▨	▨	117
90 unrelated																				Total	661

A (5%)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Total
3001																	▨	▨	▨	▨	
3002																		▨	▨	▨	
3003	1																	▨	▨	▨	1
3004													2		▨	▨	▨	▨	▨	▨	2
3005																			▨	▨	
3006																▨	▨	▨	▨	▨	
3007																	▨	▨	▨	▨	
3008														1	3	▨	▨	▨	▨	▨	4
3009		1								1				6	1	▨	▨	▨	▨	▨	9
3010										4							▨	▨	▨	▨	4
3011	1	6	4						8	2	1			4		▨	▨	▨	▨	▨	26
3012				2		1	6					▨	▨	▨	▨	▨	▨	▨	▨	▨	9
3013			3	3						4	5			1			▨	▨	▨	▨	16
3014	2	12	▨	▨	7	▨	6	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	27
3062																					
3063		▨			▨						▨	▨				▨	▨	▨	▨	▨	
3065												1				▨	▨	▨	▨	▨	1
3066		9		1	1	1			2			1	4		2	▨	▨	▨	▨	▨	21
37 unrelated																				Total	120

B (1%)

▨ Progeny not available or not included in the test.

ranged from 1 to 5 (1053-9, 1057-9) 6 (1054-1), 7 (1067-1) and even 12 in the outstanding progeny 1075-6.

Within each one of the five best populations cited above, the selection index procedure was applied independently with the same selection intensity of 5 %: the calculations of index values were performed for each population with its own genetic parameters and its own weighting coefficients determined by equation (1). The results showed that all selected individuals with the intra-population selection index at 5 % were already selected with the over all populations selection index at 2 % on average using pooled estimates. Consequently the pooling of all populations seemed to be efficient since no loss of good genetic material was observed.

Several provenances with poor performances on one trait (1088 early flushing, 1070 slow growing) present some selected individuals because of their favourable genetic parameters: heritability of total height was high for the provenance 1088 whereas the genetic correlation between flushing time and stem sinuosity was strongly negative (—.7). The provenance 1070 was late flushing, and heritability of total height was high; moreover genetic correlations between total height and flushing, total height and sinuosity were not different from zero whereas the correlation between flushing and sinuosity was favourable (—5). By contrast, the provenance 1047 showed rather good performances but with unfavourable genetic parameters (heritability and genetic correlation nearly null). Provenance 1072 too seemed to be interesting, due to its lateness in flushing and its good stem characteristic. Nevertheless heritability of flushing was null, thus with its bad performance in vigour and the unsignificance of genetic correlations, very few individuals were retained.

For Sitka Spruce, the set n^{0} 1 was used with the following weights:

$$I = \hat{G}_{TH\ 8} + 0.\ \hat{G}_{IH} + 0.\ \hat{G}_{BS}$$

With a strong selection intensity of 1 %, 120 individuals were selected from 11 provenances (among the 18) and from only 37 different progenies (see *Table 8)*. The number of selected individuals per provenance ranged from 1 to 27 and per progeny from 1 to 12.

Four provenances contribute the most to the selection (75 %): 3014 which includes only 4 progenies (but highly represented after selection) 3013, 3011 and 3066 from southern Vancouver Island because of their superior growth. With a selection intensity of 5 % *(Table 8)*, all provenances but one contribute to the selection with 661 individuals from 90 different progenies. The four provenances cited above contribute to 67 % of the number of selected individuals. In terms of seed orchard or breeding population, the best approach would be to use the selection intensity of 5 % which allows the selection of 90 unrelated individuals versus only 37 with 1 %. Of course the genetic gain on growth is less than with 1 %, but at the same time the population of selected individuals is earlier in bud setting.

5. — Discussion and Conclusion

5.1. Strategy of selection

Both examples reported above showed the real interest of index selection, when many traits have to be improved simultaneously and when the population of individuals to be selected is nested in different levels (here provenance-progeny-individual). The efficiency of this method may be already proved by the realized phenotypic gains: for Douglas-Fir the sample of selected individuals reaches or surpasses the fixed objective, i.e., the means of best progeny for total height, girth and flushing and the initial mean of population for sinuosity. Given the medium values of heritability for growth traits (.3) and the very important one for flushing (.9), it is reasonable to hope that expected genetic gains will be achieved in clonal seed orchard, so that subsequently produced seeds will be of high quality.

The example of Sitka Spruce revealed the difficulty of simultaneous selection when two traits are highly correlated in a sense unfavourable for selection: in this case, the breeder must come to a decision, knowing the risks he will run. In the present study, where the main objective was to improve the growth traits, the breeder accepted to increase the lateness in but setting in the selected material, in order that a maximum progress could be observed for total height. Thus it is not always possible to reach the desired "ideotype", and the strategy should be consequently changed: according to ecological conditions for future planting, selection may lead to divergent varieties.

5.2. Progresses in the future

The purpose of improving the mean additive genetic worth of the population implies an important part of additivity of selected traits as well as random matings between selected individuals, so that the next generation will exhibit a real phenotypic superiority. These assumptions are not verified here, due to the nature of material: in order to widen the genetic diversity and to avoid too many relatives in selected trees, the basic populations in both species were in fact constituted by pooling many natural provenances. No informations exist up to now about results of crosses between provenances having good performances but with genetic structures rather different: for example, provenances 1075 and 1054 presented egal genetic correlations between flushing and total height (.7) as well as between flushing and sinuosity (—.3), while between total height and sinuosity genetic correlation was .3 for 1075 and —.5 for 1054. Even with wide confidence interval of the estimates of genetic correlations, what will give crosses between individuals of both populations?

Is the additive part of intraprovenance variability transmitted to the next generation after interprovenance matings?

Some authors (Nanson 1972) let expect better performances from inter population crosses. Therefore, in order to verify these assumption and to test the validity of index selection on several populations, the next step of the study will be to achieve a great number of intra- and interprovenances crosses.

5.3. Selection in wild populations

The current strategy on forest tree breeding is first to select tree in natural stands, to put out all selected trees or their progenies in experimental designs and afterwards to make a second selection on this materal. The first step is rather expensive, because of the time spent and the difficulty to collect material on the selected trees.

The results presented here showed the avantage of another approach as already noted by Samuel and Johnstone (1979): the systematic collection of random trees in performing natural sources, i.e., without loss of time for choosing the trees to be harvested, may lead to basic material of good quality for subsequent selection (Silen 1966). This is particular to forest tree breeding, because of the broad variability in wild populations.

With an intensity of selection rather strong (2 % for Douglas-Fir and 5 % for Sitka-Spruce), it is already possible to create commercial clonal seed orchards. It is necessary now to test the quality of commercial seeds to be produced there.

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A basis for selecting Hevea clones stable to unpredictable agro-climatic variability

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(Received 27th December 1982)

Summary

Joint regression analysis for the two characters first height measurement and survival rate showed, that the genotype × environmental interaction among ten *Hevea* clones was mainly non-linear. Thus the regression coefficient alone cannot be used to explain the stability of *Hevea* clones to environmental variation. Therefore the variance of each clone over all environments has been used as the index of stability. A method is described to select *Hevea* clones stable to unpredictable types of agro-climatic variability, with desired levels of mean performance.

Key words: *Hevea*, Genotype-environment interaction, variance, stability, mean performance, selection.

Zusammenfassung

Die durchgeführte Regressionsanalyse für die beiden untersuchten Merkmale hat nachgewiesen, daß die Genotyp-Umwelt-Interaktion bei den 10 *Hevea*-Klonen in erster Linie nicht linear ist. Daher kann der Regressionskoeffizient allein nicht verwendet werden, um die Stabilität der *Hevea*-Klone gegenüber variierenden Umwelteinflüssen zu erklären. Deshalb wurde die Variabilität der einzelnen Klone gegenüber allen Umwelteinflüssen als Stabilitätsindex benutzt. Es wird ein Verfahren zur Selektion von *Hevea*-Klonen beschrieben, die gegenüber unvorhersehbarer Stabilität gegenüber agroklimatischer Variabilität das gewünschte Niveau als durchschnittliche Leistung aufweisen.

Introduction

In the presence of genotype × environment interaction the relative performance of clones varies with the environment.

Results of clone evaluation trials can be used to select and recommend a clone adapted to a particular agro-climatic condition if the agro-climatic differences can be defined and differentiated by factors such as rainfall, light, temperature, humidity and soil. Unfortunately agro-climatic conditions are complex and the factors which go to form them are unpredictable and cannot be controlled. Therefore the only possibility open is to use clones stable to a wide range of agro-climatic variability.

Finlay and Wilkinson (1963) have used regression coefficients of each clone (obtained by regressing the mean performance of each clone in each environment on the mean of all the clones in that environment) as a parameter of stability. This is useful only if the response of clones to environmental variation is linear.

In the presence of significant non-linear genotype × environment interaction, a stability parameter which takes into account both the linear and non-linear portions of the interaction component has to be used.

In this paper a basis is suggested for selecting *Hevea* clones that are stable to unpredictable types of environ-

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