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Observed Selection Effects on Height Growth, Diameter and Stem Form in Maritime Pine

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Summary

Effects of plus tree selection in local mature stands, and of early combined index selection performed in progeny trials, were assessed in a maritime pine (*Pinus pinaster* AIT.) test established in 1965 in 2 sites. Nonlinear regression was used for the characterization of selection effects on height growth curves. Diameter growth, stem straightness and the proportion of polycyclic annual shoots were also examined.

The plus tree selection was shown to be effective on the asymptote, i. e. on mature growth, whereas the early combined index selection was effective mainly on the maximal growth rate, i.e., on juvenile growth; both selections improved the stem form. No consistent genotype x environment interaction was observed. For height growth, provenance effects were found in the area studied.

It was hypothesized that, due to a low juvenile-mature correlation for vigour, selection at a given time altered the shape of the growth curves. Thus, several cycles of early selection could improve the stem volume at rotation age, though they could have a much greater effect on early height. Undesirable effects on wood structure and architecture were then expected.

Key words: height growth curves, nonlinear regression, polyclism, genetic gain, plus tree selection, combined selection, *Pinus pinaster.*

FDC: 165.4; 165.62, 174.7 *Pinus pinaster.*

Introduction

The main objectives of forest tree breeding programs are usually the increase in wood production and in wood quality yielded at clearcut. Because of the rotation length, selection is made at young age and few genetic studies have been published for ages greater than 20 years (REHFELDT *et al.*, 1991). In the same way, very little long-term data is available for improved stands (BIROT, 1986; TALBERT and HYINK, 1987). Genetic gains estimated at a young age are often assumed to be highly correlated with gains at rotation age (KNOVE and FOSTER, 1989).

Early maritime pine (*Pinus pinaster* AIT.) progeny tests are older now than half the rotation age. Taking advantage of the original structure of a progeny test established in 1965 (ILLY, 1966), effects of "plus tree" selection (*in-situ* phenotypic selection) and of early combined index selection in progeny test were assessed, and genetic gains on height at clearcut (age 40 to 60 years) were predicted, using a modelling technique. This work provides information on the performance of improved material, now widely used in the "Landes de Gascogne" forest, and some keys for the management of improved stands were inferred. As a result, genetic effects may then be incorporated into stand simulation models.

The selection program for maritime pine in Southwest-France (the "Landes de Gascogne" area) started in 1960 with selection of plus trees in the local provenance, in stands older than 30 years (ILLY, 1966). Then, a recurrent selection program was developed with height and stem straightness at approximately age 10 years as main selection criteria (BARADAT and PASTUSZKA, 1992). No extended evaluation of genetic gains at later ages have been made so far.

In some stands, seeds from trees of average performance (control trees) were collected in addition to plus tree seeds. One hundred plus tree and control tree progenies were established on 2 sites (trial B and trial C).

Table 1. – Geographic data for the 5 source districts of parent trees and for both trials.

no	District	Locality*	Latitude	Longitude	Elevation (m)	km from sea	Stand strength
71	La Tremblade	Les Mathes	45° 43' N	1° 10' O	10	3	6
13	Castelnau	Le Temple	44° 53' N	1° 00' O	40	17	11
0	Parentis	Parentis	44° 21' N	1° 05' O	30	14	17
43	Mimizan	Mezos	44° 05' N	1° 09' O	40	13	12
38	Castets	Lit et Mixe	48° 90' N	1° 15' O	40	7	10
B	Audenge	Cestas	44° 44' N	0° 45' O	61	38	/
C	Soustons	Vieux Boucau	43° 45' N	1° 24' O	8	2	/

*) where most of the stands were sampled or where the test is located.

Height is a major component of stem volume, and is less influenced by competition than diameter and so has therefore been used as a selection criterion for vigour in maritime pine. Height growth curves can be easily measured on felled trees, using branch whorls as morphological markers of the different annual shoots (KREMER, 1981a). Height growth curves were measured in 1987 in trial B and studied by KREMER (1992a). He compared plus tree progenies to control tree progenies for successive heights and height increments to age 22 years. KREMER (1992b) also studied the correlations between the height of the parent trees and the mean value of their progeny. He showed that phenotypic selection for height in adult stands was not effective for height growth until age 12 years; after this age, the genetic gains increased constantly with time.

Using data from trial B and the model of MAUGE (1975), DUREL (1990) has established that the plus tree progenies significantly exceed control trees by 3.1% for the predicted height at age 53 years, the asymptote being not significantly different. However the biological meaning of the first parameter of the model is unclear and the prediction has been made using only 3 heights (heights at age 9, 15 and 22 years).

MAGNUSSEN and KREMER (1994a and b) used the trial B dataset to estimate the heritability of parameters of an exponential model, and to study the genetic variability of polycyclism: maritime pine develops either 1 or 2 (even more than 2 in the first years) annual growth flushes on the leader shoot (LANNER, 1976). The development of more than 1 flush is referred to as polycyclism (occurrence of a second shoot).

The present study also employs the dataset of trial B, with additional measurements made at age 27 years in trial C. In DANJON (1992, 1994a and b), a growth model has been used to study the genetic variability of height growth: high heritabilities for growth curve characteristics have been obtained with nonlinear regression. This technique procures a summary of the growth history and some insight into the future, the latter of value since no progeny test has yet attained maturity. The modelling procedure used provides reliable estimates for parameters which have direct biological meaning (DANJON, 1992, 1994a and b; DANJON and HERVE, 1994).

The objective of the present study was to assess changes in height growth patterns resulting from plus tree selection and from early combined selection in progeny tests. Other characters including polycyclism, diameter and stem form were studied together with the height growth curves, providing a comprehensive analysis of the effects of selection.

Material and Methods

Material

The plus tree selection for the local breeding program was made in the "Landes de Gascogne" area (1 million hectares),

since the local geographical race of this area appeared to be the best adapted in provenance tests (ILLY, 1966). 360 plus trees were selected in mature stands using volume and stem form as criteria, comparisons being made with the 30 nearest neighbours ("comparison tree method" – LEDIG, 1974). 200 additional plus trees were collected in Southwest-France with wood density and diseases and insects resistance as major criteria (DUREL, 1992). Scions and cones were sampled on plus trees and sometimes on one control tree which was considered representative of the 30 nearest neighbours. Open-pollinated seeds from 44 plus tree – control tree pairs were used in the test. This sample was supplemented with the progenies from 12 other plus trees.

The Landes forest was divided into 17 districts of approximately 15 km radius for a systematic prospecting for plus trees. The families originated from 5 main districts (Tab. 1 and
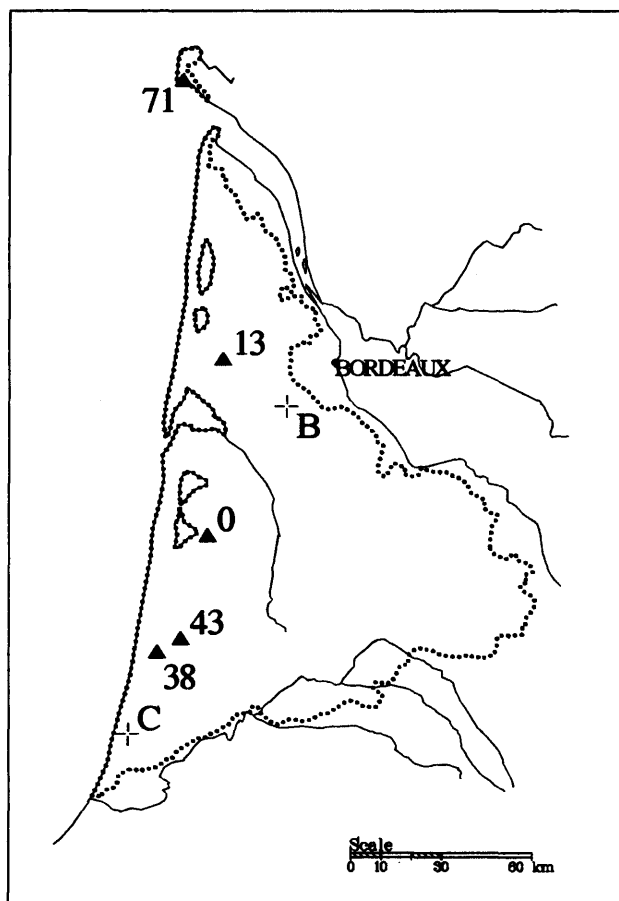

Figure 1. – Location of the plus tree sample areas and of the progeny trials (dotted line: boundaries of the Maritime pine "Landes" and "La Coubre – La Tremblade" forests).

Fig. 1), 3 stands from other areas were pooled to the nearest districts for district effect analysis. All districts are located along the Atlantic Coast, the interior part of the Landes forest not being represented in this study. It should be noticed that 80% of all the 360 plus trees were sampled at a distance less than 25 km from the ocean. The Landes de Gascogne area is almost flat (except the coastal dune area), reaching 160 m elevation at the east border. All used progenies originate from low elevation sites.

Since the majority of pollen fertilizing a given tree comes from nearby trees (BARADAT *et al.,* 1984), most of the male parents should be from the surrounding stand. Thus the stand effect originates from both mother trees (plus tree and control tree of the stand) and from almost all the male parents.

The progeny test

The test was established in the fall 1965 in 2 locations on a sandy podzol. The B trial was located in a semi-humid moorland, characterized by a 0.3 m (winter) to 1.6 m (summer) deep water table (LOUSTAU, pers. comm.). The C trial is located 2 km from the ocean, in the "Marensin" region, in an ancient area of dune; in contrast to test B, the ground-water level is fairly deep, and trees may suffer from drought in the summer, despite the important annual rainfall (1200 mm).

The experimental design was a triple lattice 10 • 10 repeated 3 times in trial B and twice in trial C. Seeds were sown in spring 1965 in nursery beds. Each of the 100 families were planted in 5 x 2-tree row plots in 9 repetitions in trial B and 6 repetitions in trial C, in 1.50 m x 3 m spacing. Trees were fertilized 1 year after plantation.

In trial B, a systematic thinning was carried out in spring 1977, leaving every second tree in each row, and a second systematic thinning removed 1/5 of the trees in spring 1982. The third thinning was executed in spring 1987 where each second row was removed entirely, all felled trees being measured. In trial C, the first systematic 50% thinning was done in spring 1980, the second systematic thinning took place in spring 1992, a sample of 500 trees being measured. At that time, the stocking density was very high (41 m²/ha basal area versus 35 m²/ha for trial B in 1987), resulting in a high intertree competition.

A combined index selection (which integrates both individual and family information) was made in trial B with the 3 year height increment between age 5 and 8 years (i.e. 5 and 8 growing seasons after sowing), the age 10 years stem straightness, and the age 10 years torsiometer measurement as criteria. It resulted in a respectively 7.2%, –10% and 2.7% expected genetic gain for these traits with a 10% selection rate. The stem straightness was evaluated as the butt sweep of the stem (sag of the stem on the 3 first meters, described as the "crook of the stem" in PERRY, 1960). The torsiometer was used to measure in situ the torque strain required to drive an increment borer in the tree at a given depth (see POLGE and KELLER, 1970). The selected trees served as maternal trees in the mating design source of the second generation progeny test – seed orchard (DUREL, 1992).

In trial C, using a systematic sample of 2400 trees, KREMER (1981b) computed 2 parameters for the genotype x year interaction: the general response to annual conditions (b) and the stability around the response (d) (see EBERHART and RUSSEL, 1966). The 4 year height increment between age 8 and age 12, butt angle of lean at age 12, lb – 1l and d served as criteria for the combined index selection in the sample. Genetic gains of 9.2%, –17.2%, 11.1% and –7.8% were expected respectively with a 10% selection rate.

These selections performed in progeny tests will be subsequently referred to as early combined selections ("EC selection" or "ECS"). Early combined selection favoured the plus tree offsprings, especially in trial C: 64% (71% in trial C) of the trees selected by early combined selection are plus tree offsprings, compared to only 56% in the whole population *(Tab. 2)*. Besides, in the sample of EC selected trees studied in trial C, the proportion of plus tree offsprings is higher than in the whole trial (88% vs. 71%), because of the very low sample size.

Table 2. – Number and origin of trees selected by early combined selection (ECS).

	ECS selected trees in whole trial		ECS selected trees in sample studied	
	total number	number of plus tree offsprings	total number	number of plus tree offsprings
trial B	161	103 (64%)	57	37 (65%)
trial C	59	42 (71%)	8	7 (88%)

Measurements

The heights of all branch whorls were measured on felled trees, providing precise height-age curves and an assessment of polycyclism. In trial B, the sample included 1565 trees (2 to 3 trees per plot – KREMER, 1992b), 5 trees being eliminated from analyses due to measurement errors. In trial C, 1 tree was chosen at random in each plot, in the 5 repetitions showing the highest growth. To avoid bias, only trees with very severe injuries were eliminated.

In trial C, the diameter of all standing trees was measured in 1991, and under bark diameter growth curves were recorded on the felled trees on slices taken at 0.5 m height.

Intersections between tree rings and 8 radii were digitalized on a graphic tablet. The inside bark diameter curve was computed using the quadratic mean of the radii (PARDE and BOUCHON, 1988).

Polycyclism on the stem was studied as the frequency of polycyclic shoots (FPOLY) and relative length of second shoot (LPOLY – see DANJON, 1994a). The stem form was assessed as the butt sweep of the stem (in cm) at age 10 in trial B and as a subjective straightness scoring for the whole stem at age 27 in trial C (scale from 0 to 20, 0 = awful, 20 = very straight). The form assessment in trial C was expected to highly correlate with the form at rotation age, an important target trait.

Fitting methods

Following ROSS (1970), the LUNDQVIST-MATERN model (MATERN, 1959) was reparametrized to gain stable parameters, which have a direct biological meaning (DANJON and HERVE, 1994):

$$h(t) = A \exp\left[-\left[(\log\frac{A}{h_0})^{(1+\log m)} - \frac{rt(1 + \log m)}{A \exp[(\log m)(\log(-\log m))-1]}\right]^{\frac{1}{1+\log m}}\right]$$

The 4 parameters are A (asymptote), r (maximal growth rate), m (shape parameter, i.e., height of the inflexion point expressed as a proportion of A) and h_0 (height at age 0). h: height, t: age.

As proposed by DAY (1966), a global estimation of 2 of the 4 parameters was computed for each trial, only the asymptote (A) and the maximal growth rate parameter (r) were estimated for each individual curve (DANJON and HERVE, 1994). The r parameter is principally related to heights around age 16 years and to early height increments. A is an extrapolation of growth after the measurement age, and is essentially determined by the later observed height increments (i.e., after age 15 years),

but also, to a certain extent, by the shape of the observed curve (DANJON, 1994b). Predicted heights at age 30, 40 and 50 (H30, H40 and H50) were computed using the growth model.

Data analysis

The test was interpreted as a design comprising 9 (trial B) and 5 (trial C) repetitions and 5 incomplete blocks per repetition. Separate analyses were made; the first to assess the district, stand and plus tree selection effects and the second to assess the early combined selection effect, using 2 models for individual tree observations *(Tab. 3)*:

$$Y_{ijklmn} = \mu + R_i + B_{j(i)} + D_k + S_{l(k)} + P_m + RP_{im} + DP_{km} + RD_{ik} + E_{ijklmn} \quad (1)$$
$$Y_{ijkl} = \mu + R_i + B_{j(i)} + G_k + RG_{ik} + E_{ijkl} \quad (2)$$

Table 3. – Analyses of variance table: degrees of freedom.

Model	Factor	trial B	trial C
	Replications	8	4
	Bloc	44	20
	District	4	4
	Stand	51	51
(1)	Plus tree selection	1	1
	RP interaction	8	4
	DP interaction	4	4
	RD interaction	32	16
	Error	1402	395
	Replications	8	4
(2)	Early Combined selection	1	1
	RE interaction	8	/
	Error	1537	494

For the first model: Y_{ijklmn} is the observed value, μ the general mean, R_i the effect of replication i, $B_{j(i)}$ the effect of block j within replication i, D_k the effect of district k, $S_{l(k)}$ the effect of stand l within district k, P_m the plus tree selection effect, RP_{im}, DP_{km} and RD_{ik} the corresponding interactions and E_{ijklmn} the random error term.

For the second model: Y_{ijkl} is the observed value, μ the general mean, R_i the effect of replication i, $B_{j(i)}$ the effect of block j within replication i, G_k the early combined selection effect k, RG_{ik}, the interaction between replication i and early combined selection effect k, and E_{ijkl} the random error term.

For the C trial, no interaction could be computed in model (2), because of the very small number of selected trees in the sample. All effects were considered to be fixed. The SAS "proc GLM" variance analysis was used with type III sum of squares (SAS Institute, 1989). Least-square means ("lsmeans") were computed for each effect, giving population marginal means. The SCHEFFÉ multiple comparison test was employed for classification of districts.

For the plus tree progenies, only the maternal tree is a plus tree. Thus, expected genetic gains when both parents are plus trees (as for seeds from unrouged grafted plus tree seed-orchards) are twice the phenotypic gains observed in the test. Plus tree selection genetic gains were computed from the plus tree progenies phenotypic mean (μ_{pt}) and from the control tree progenies phenotypic mean (μ_{ct}), for trees with 2 plus tree parents:

$$\Delta G_{+T} (\%) = 2 \bullet 100 \bullet (\mu_{pt} - \mu_{ct}) / \mu_{ct}$$

Expected gains for progenies of trees retained by the early combined selection were estimated as gains resulting from the average phenotypic superiority of these trees (as for a phenotypic selection). They were computed from the phenotypic

mean of selected trees (μ_s) and from the narrow sense heritability (h^2_{ns}) estimated with an REML procedure (DANJON, 1994b):

$$\Delta G_{ECS} (\%) = 100 \bullet h^2_{ns} \bullet (\mu_s - \mu) / \mu \qquad (\text{GALLAIS, 1989})$$

Results

Fitting of growth curves

Fitting was generally close and estimates were poorly correlated: the "estimation correlation" (correlation between the parameter estimates for each curve) averaged –0.35 in trial B and +0.5 in trial C. This indicated that the modelling procedure chosen was well adapted to both sets of data. The maximum growth rate (r) was on average 20% higher in trial B than in trial C (respectively 101 cm/yr and 82.4 cm/yr), which was certainly due to the better fertility and water supply of this location. The curves of trial B were more linear *(Fig. 2)*, and as a consequence, the global estimation of the shape parameter (m) yielded a low value for trial B and a high value for trial C (respectively 0.078 and 0.235). This explains the very high expected asymptote in trial B (51.5 m versus 27.5 m in trial C), because of a strong structural correlation between m and A (see DANJON and HERVE, 1994), which had no practical importance for further analysis since m was estimated globally in each trial.

Growth curve parameters and predicted heights

Plus tree progenies had a significantly greater asymptote (A) in both the B and the C trials, resulting in almost a 10% genetic gain *(Tab. 4a)*. However the maximal growth rate (r) was higher only in trial C (with a 4.7% gain). The plus tree effect on predicted heights at age 30, 40 and 50 years was high in both trials (with a 6% gain). The heights at age 40 or 50 years (H40 and H50) could be considered as the target selection trait for vigour.

In trial B, the early combined selection effect was highly significant for r (with a 4.7% gain), though not for A, and the effect on predicted heights decreased from age 30 to 50 years.
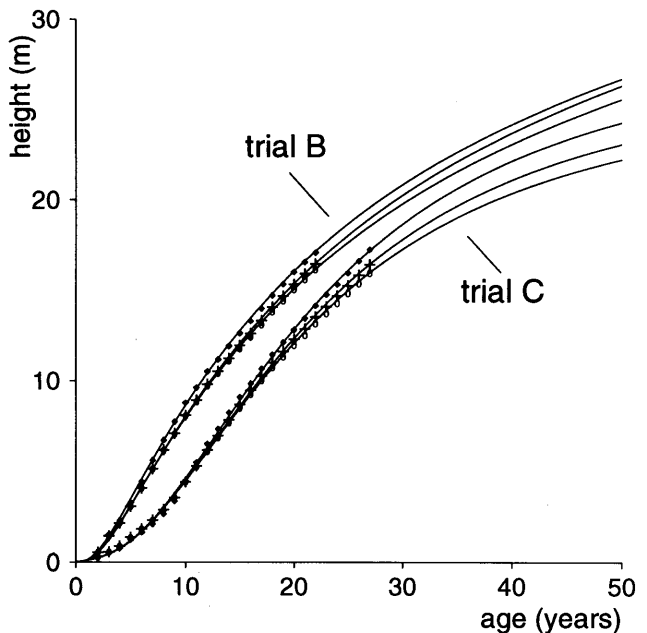

Figure 2. – Observed and predicted mean height growth curves for control tree progenies (0), plus trees progenies (+) and for the trees selected by early combined selection (◆).

Table 4a. – Analyses of variance results for the estimated parameters and for diameter, volume, polycyclism and stem form: overall mean, significance levels for the tested factors (model (1): 5 factors, model (2): 2 factors), and estimated genetic gains (ΔG_{+T} for plus tree selection and ΔG_{ECS} for early combined selection). The selection differential (S (%) = 100 · $(\mu_s - \mu)/\mu$) and the narrow sense heritability (h^2_{ns}) were also reported for the EC selection.

Trial		Model	Estimated parameters					Other traits				
			r	H30	H40	H50	A	dbh	vol	FPOLY	LPOLY	form
	overall mean		1.01	19.9	23.3	25.9	51.5	0.24	0.30	0.39	0.17	6.1
	replication	(1)	****	****	****	****	****	***	**	****		**
	block	(1)	***	****	****	****	****	****	****	****	**	*
	district	(1)	****	****	****	****	****	**	***	****	*	
	stand	(1)	****	****	****	****	****	****	****	****	***	**
B	+ tree selection	(1)		****	****	****	****	***	****			**
	ΔG_{+T} (%)		1.6	4.7	5.5	6.1	9.9	8.1	19.9	-0.8	-2.5	-18.1
	replication	(2)					*			*		
	EC selection	(2)	****	****	**	*		*	**	*		***
	S (%) for ECS		7.4	3.8	3.0	2.4	-1.1	5.8	14.4	16.1	8.1	-26.8
	h^2_{ns}		0.63	0.68	0.66	0.63	0.53	0.38	0.34	0.58	0.13	0.10
	ΔG_{ECS} (%)		4.7	2.6	2.0	1.5	-0.6	2.2	4.9	9.4	1.0	-2.7
	overall mean		0.82	17.4	20.6	22.6	27.5	0.20	0.25	0.43	0.18	13.9
	replication	(1)	****	****	****	****	****		*			
	block	(1)			*	**	**					
	district	(1)			**	***	****			*		
	stand	(1)								**	*	*
C	+ tree selection	(1)	**	***	****	****	***			-12.9		****
	ΔG_{+T} (%)		4.7	5.7	6.6	7.2	8.6	5.6	19.0	-12.9	-4.0	23.8
	replication	(2)	****	****	****	****	****	*	***			
	EC selection	(2)	*	**	**	*	*					
	S (%) for ECS		5.6	6.8	7.4	7.7	8.3	6.6	20.6	-5.5	3.3	7.5
	h^2_{ns}		0.08	0.10	0.16	0.22	0.31	0.15	0.00	0.60	0.24	0.45
	ΔG_{ECS} (%)		0.5	0.7	1.2	1.7	2.6	1.0	0.0	-3.3	0.8	3.4

Statistical significance is indicated as follows: *, P < 0.05; **, P < 0.01; ***, P < 0.001.
h refers to observed heights and H to predicted heights (h5 = height at age 5 years). "form" refers to butt stem sweep (in cm) in trial B and to a subjective straightness scoring (scale from 0 to 20) in trial C.
All height and diameter measurements and growth curve parameters are in meters except r (m/yr), the volume is in m^3.
The following significant interactions found in trial B were not reported in *table 4*:
repetition * district for r (**), and plustree * repetition for A (*).

Table 4b. – Analyses of variance results for heights (h) and height increments (Δh)
(see heading of *Table 4a*).

Trial		Model	cumulative heights					5 years height increments		
			h5	h10	h15	h20	h22/27[a]	Δh5-10	Δh10-15	Δh15-20
	overall mean		2.9	7.9	11.7	15.1	16.2	5.0	3.8	3.3
	replication	(1)	***	****	****	****	**	***	***	****
	block	(1)	***	**	****	****	****	**	*	****
	district	(1)	**	****	****	****	****	****	****	****
	stand	(1)	****	****	****	****	****	****	****	****
B	+ tree selection	(1)			**	****	****		****	****
	ΔG_{+T} (%)		-1.2	-0.2	2.0	3.6	3.8	0.4	6.8	9.1
	replication	(2)							*	**
	EC selection	(2)	***	****	****	****	****	****		
	S (%) for ECS		8.5	9.4	6.6	5.2	4.8	10.0	0.8	0.3
	h^2_{ns}		0.30	0.52	0.67	0.65	0.66	0.32	0.41	0.45
	ΔG_{ECS} (%)		2.5	4.9	4.4	3.4	3.1	3.2	0.3	0.1
	overall mean		133	438	856	1213	1620	305	418	357
	replication	(1)	****	****	****	****	***	****		****
	block	(1)		**	***	**		****		**
	district	(1)	*	***	**			***		****
	stand	(1)								
C	+ tree selection	(1)				**	**		***	**
	ΔG_{+T} (%)		5.7	-0.3	3.6	4.5	5.3	-2.9	7.8	6.7
	replication	(2)	****	****	****	****	****	****		****
	EC selection	(2)				*	*		**	
	S (%) for ECS		-7.7	1.2	5.6	5.6	6.5	5.1	10.2	5.5
	h^2_{ns}		0.09	0.13	0.20	0.16	0.00	0.16	0.35	0.35
	ΔG_{ECS} (%)		-0.7	0.2	1.1	1.0	0.0	0.8	3.8	1.9

[a]) h22 for trial B and h27 for trial C

In trial C, effects on A and r are weakly significant, resulting in a 0.5% and 2.6% genetic gain.

The district and the stand effects were highly significant for the parameter estimates in trial B, whereas in trial C, the stand effect was never significant and the district effect was only significant for H40 and H50 and for the asymptote.

The northern district (La Tremblade – 71) had the lowest value for both growth curve parameters and for H50 in both trials *(Tab. 5)*. The district of Mimizan (43) had a lower early growth (a low r) but a rapid later growth (a high A), the opposite to that observed for the district of Calstelnau (13). The districts of Parentis (0) and Castets (38) had intermediate features. The southern provenances seemed to have a slightly higher asymptote than the northern ones (5% between extremes). No striking district x location interaction appeared for height growth.

To check if the model summarized the same information for selected and non-selected trees, a type of "annual residual" was computed as the difference between each observed annual height increment and the corresponding height increment predicted by the growth curve modelling (suggested in FITZHUGH, 1976). Thus, interactions between the model and the studied factors, and specific reactions to climatic stresses could be detected.

Severe droughts were reported at age 6, 12, 17, 22, 25 and 26 years (corresponding to 1970, 1976, 1981, 1986, 1989 and 1990 respectively; GUEHL *et al.,* 1994), a severe frost occurred at age 20 years (January 1985), and thinnings took place at age 12 and 17 (trial B) and age 15 years (trial C). Similar patterns for annual residuals were observed in both trials after age 12 years *(Fig. 3)*, though before age 12, the trends were less consistent, which could be due to higher juvenile variability and no close fitting in the first years.

Annual residuals seemed to be similar for selected and unselected trees: significant differences for plus tree selection were only seen for age 17 year residuals in trial B, and for age 6 and 14 year residuals in trial C. For early combined selection, the differences were statistically significant for age 3, 6, 9 and 13 years in trial B and age 10 and 24 years in trial C. For the different selection levels, no specific response to climatic stresses was detected.

In summary, plus tree selection was effective on the later growth period, and had a small effect on juvenile growth. On the other hand, early combined selection was effective essentially in the early growth period. The location of selected plus trees seemed to have an influence on progeny value, particularly the district location: the expected final height was greater for southern provenances. No real district x environment or selection x environment effects for height growth were shown.

Cumulative heights and annual height increments

The plus tree selection effect on cumulative heights began to be increasingly significant after age 14 years in trial B (KREMER, 1992a) and after age 16 years in trial C. For annual height increments, it was increasingly significant after age 10 in trial B and between age 14 and 19 years in trial C *(Fig. 4)*. On 5 year height increments, this effect could be detected between age 10 to 15 and age 15 to 20 years in both trials *(Tab. 4b)*.

There was a small early combined selection effect for cumulative heights after age 19 years in trial C, whereas it was highly significant in trial B after age 3 years. This effect was significant for annual height increments from age 3 to 9 years and for age 13 years in trial B, and only for age 10 to 12 and 26 years in trial C *(Fig. 4)*: significance was almost only observed for the annual increments included in the selection criteria.

In trial B, the district and stand effects were high except in the very early years. For height increments, the significance level was generally greater after age 12 years, though the pattern was not clear. In trial C, the stand effect on cumulative heights was not significant, whereas the district effect was significant only between age 5 and 17 years (age 5 to 9 and 17 to 21 years for height increments – not shown).

These results were consistent with previous conclusions concerning the parameter estimates. They provide, at a finer scale, a complementary approach to growth curve parameters analysis which is more global.

Diameter and volume

In trial B, the district, stand and plus tree effects were highly positive on diameter at breast height (dbh) and volume at age 22 years, resulting in respectively 8% and 20% genetic gains for plus tree selection *(Tab. 4a)*. The early combined selection effect was less significant (with 2.2% and 4.9% gain). At age 27 years in trial C, no effect was significant; on all standing trees (3060 trees), the plus tree (with a 5.5% gain), district and stand effects on dbh were significant, though the early combined selection effect was not significant.

Table 5. – Growth curve parameters and polycyclism: SCHEFFÉ multiple stage test for district means. Districts with the same vertical bar are not significantly different at a 5 % level.

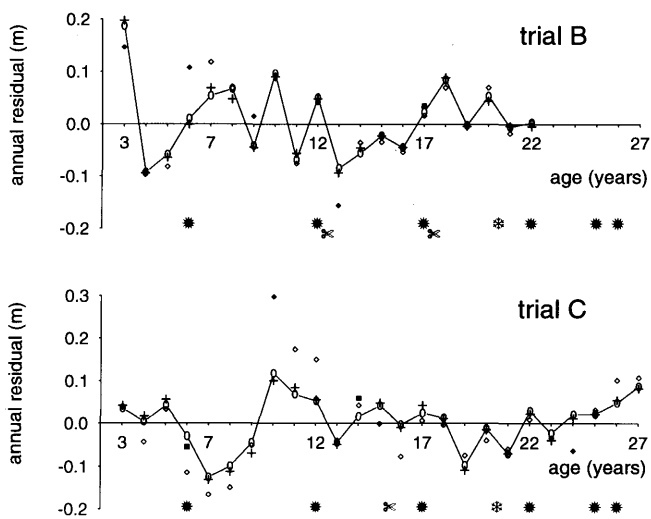| Trial	r		H50		A		FPOLY	
	lsmean	district	lsmean	district	lsmean	district	lsmean	district
	102.3	38	26.1	43	52.6	43	0.45	13
	102.2	13	26.0	0	51.7	0	0.40	71
B	101.3	0	25.9	38	51.1	38	0.40	0
	100.0	43	25.7	13	50.4	13	0.37	38
	99.4	71	25.1	71	49.3	71	0.33	43
	83.3	38	23.2	43	28.7	43	0.47	13
	82.9	13	22.7	38	27.6	0	0.46	71
C	82.1	43	22.6	0	27.5	38	0.43	43
	82.0	0	22.1	13	26.6	71	0.42	38
	80.7	71	22.0	71	26.4	13	0.39	0

Figure 3. – Least square means for annual differences between predicted and observed height increments (control tree progenies (0), plus trees progenies (+ and ■) and trees selected by early combined selection (◇ and ◆) – black when the effect is significant at a 5 % level). Time of thinnings (✕), heavy frosts (❀) and heavy droughts (✳) were reported

Figure 4. – Least square means for annual height increments (see key in Fig. 3).

For under-bark successive diameters from age 3 to 27 years (trial C), no significant effects were apparent for the 4 factors studied with the exception of the district effect on age 6 and age 18 years increments (at age 6 years, the growth of provenance 43 was depressed, at age 18 years, the northern provenances suffered).

Polycyclism

The plus tree selection effect was never significant for the frequency of polycyclic shoots (FPOLY) and for the mean relative length of second shoots (LPOLY – *Tab. 4a)*. The early combined selection effect on FPOLY was significant at the 5% level in trial B with nearly 10% gain: more polycyclic shoots were produced especially in the first 13 years.

The stand and district factors also had an effect on polycyclism: the southern districts appeared to have a lower polycyclism (25% between extremes in trial B – *Tab. 5)*. It should be noted that trees from the most vigorous districts tended to have lower FPOLY. No provenance x location interaction was observed.

Form traits

The plus tree selection effect on form was very high in both trials, with gains reaching 24% on straightness at age 27 years in trial C, and 18% for the butt sweep of the stem at age 10 years in trial B. The early combined selection effect was null in trial C but high in trial B resulting in almost 3% gain. For both trials, the district effect was absent and the stand effect was low.

Discussion

Old genetic tests of forest species are often not well suited to contemporary objectives (REHFELDT *et al.,* 1991). The test studied appears valuable for several reasons: the number of repetitions is rather high, it was established on 2 sites and only systematic thinnings were made. Selective thinnings would have created a dependence between genotypic and environmental effects (KING and BURDON, 1991). Moreover, the retrospective technique used to measure the annual height 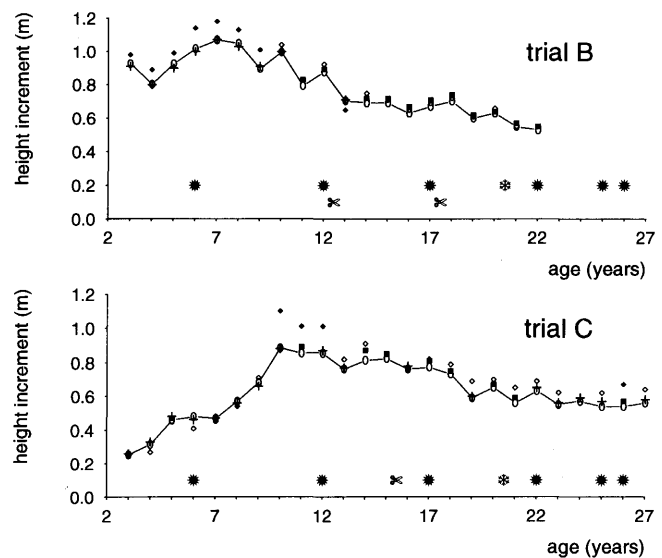increments is more precise than successive contemporary measurements (as in BALOCCHI *et al.,* 1993) or stem analysis (as in MAGNUSSEN, 1993). Finally, the modelling method used in this paper is expected to give more reliable results than former studies, since the estimates of the parameters were poorly correlated, the fit was close, and the parameters had precise biological meaning. Nevertheless, estimations of heights at age 40 and 50 years (H40 and H50) are only height predictions, they must therefore be judged with appropriate scepticism.

Genetic gains on stem form (in trial C), diameter, and polycyclism were assessed at half the rotation age, giving only rough indications about final gains. Hence, the presented gains on volume at clearcut are imprecise.

Plus tree mature selection

Assessment of the plus tree selection effect is efficient since the sample size used is large. The corresponding genetic gain estimations appear sufficiently reliable to be used in a stand simulation model. The stand effect is also estimated with an appropriate sample size. Conversely, for the district effect, the sample studied covers not the whole Landes forest, giving only some indications on genetic differentiation in this area.

The expected gain for seeds from grafted plus-tree seed orchards will be around 6% for final height. Since no extrapolation has been made for diameter growth, the 8% gain for diameter at age 22 years in trial B is used to predict final gains on volume: almost a 25% gain is expected in favourable locations. A 20% improvement in stem straightness is also expected.

Considering the narrow sense heritabilities and the additive genetic coefficients of variation usually found in forest species, CORNELIUS (1994) computed the expected genetic gains from plus tree selection: it resulted in a 6% to 16% gain for diameter and height, about 8% to 20% gain for stem straightness, and up to 30% gain on volume. The high variability of stem straightness in maritime pine may explain the particularly high expected genetic gain for this character.

Earlier reports about plus tree selection efficiency in other species present contradictory results. These discrepancies may originate from differences in juvenile-mature correlations from one species to another, since the assessments of genetic gains had often been made before age 10 years (KREMER, 1992a).

In the present study most of the stands used for selection originate from artificial afforestation, therefore, nearby trees are unrelated. This may explain why the "comparison tree method" provided high genetic gains (DUREL, 1990). Moreover, the prospecting was conducted in even-aged stands of the local provenance, in a flat sandy area, which are favourable conditions for phenotypic selection.

BUTCHER and HOPKINS (1993) have reported results for plus tree selection in 30-year-old maritime pine stands. A low gain on diameter (+2% at age 18 years, compared to the local Australian source) but high gains for stem quality were found, with no genotype x environment interaction. Phenotypic selection in a young *Pinus banksiana* stand resulted in an improved growth at age 3 years but no significant effect on height and form characters at age 6 years (MAGNUSSEN and YEATMAN, 1987); conversely, a genetic gain on stem form at age 23 years was obtained for offspring of trees selected in older stands (MAGNUSSEN, 1990). During the first growing season, the average performances of *Picea abies* plus tree progenies appear similar to those of the control trees progenies concerning height, timing of budset and autumn frost hardiness (JOHNSEN and ØSTRENG, 1994).

Geographic structuration

In DANJON (1994a), great differentiation in vigour is observed throughout the natural geographic range for maritime pine, though no significant differences are apparent between the Southwest-France provenances (Tremblade, Mimizan and Mimizan-Coastline). In the present study, a significant district effect is found for height growth, district differences for the target traits (H40 or H50) reaching 5%, the southern districts being more vigorous. It should be noted that 42% of the 360 selected plus trees originate from the Southern districts and 25% originate from the district number 0. Nevertheless, to keep a maximal genetic variability, plus trees from the whole area should be used in the local selection program. Differences were also found for polycyclism, though not for stem form. In DANJON (1994a), differences between provenances of the whole natural range appear for polycyclism but not for stem straightness: the frequency of polycyclism was generally lower for the Atlantic Coast provenances, which were also the most vigorous. Genetic differentiation from stand to stand is also high in trial B, but not significant in trial C.

Early combined selection in progeny tests

Assessment of the early combined selection effect is not very precise, because the sample of selected trees is small, particularly in trial C, and because gains are estimated from the phenotypic means. Heritabilities estimated in trial C are low, which is certainly due to the small sample studied (see DANJON, 1994b).

In trial B, the genetic gain for direct early combined selection is rather high, reaching 5% on age 10 year height. Conversely, only 1.5% gain was yielded for indirect selection of height at rotation age. With a 2.2% gain on dbh at age 22 years, a 6% gain on clear cut volume can be expected. The early combined selection in trial C may procure 4% genetic gain on final volume, despite the very low heritabilities. Gains on straightness may be around 3% for both trials.

Gains for polycyclic shoots frequency also reached 10% in trial B. As discussed by CARSON and INGLIS (1988) there is a balance between knot size and number of whorls, and economic incidence of polycyclism depends on the requirements of the final uses.

The selection criteria used in trial C seemed to be more effective for the selection of clear cut characteristics, probably because the selection took place at an older age: later increments may be more heritable (KREMER, 1981c) and better correlated to mature growth (KREMER, 1992b; DANJON, 1994b). These results may also originate from use of stability parameters as selection criteria. Such type of criteria was only used in this test; thus, the selection carried in test B is much more representative of early combined selection practices in the French maritime pine breeding program. More experiments are needed to identify traits that are better correlated with high final performances.

Since approximately 1980, the routine selection criteria have changed to total height and butt angle of lean at age 8 to 11 years (BARADAT and PASTUSZKA, 1992). Butt angle of lean has generally a better heritability than the butt sweep of the stem measured in trial B. On the other hand, the height increment between age 5 and 10 years has the same genetic correlation with height at age 50 years than total height at age 10 years (DANJON, 1994b). Thus, gains for early combined selections conducted after 1980 might be similar to those yielded in trial B for final heights, and to those yielded in trial C for the stem form.

Practical consequences

CANNEL (1982) suggested that the progeny tests generally favour the selection of genotypes which grow rapidly as widely-spaced individuals or compete highly against their neighbours, to the detriment of "crop ideotypes". In the studied test, 80% of the 10 nearest neighbours of a plus tree offspring originated also from a plus tree. Hence, gains estimated on an individual basis are expected to be similar for pure stands of plus tree progenies (i. e. without control tree progenies). Gains for pure stands of ECS selected trees cannot be predicted.

Although less significant, the plus tree selection gains in trial C were slightly higher for height, and lower for diameter, compared to gains in trial B. Thus, selection gains from plus tree selection were significant even with high inter-tree competition.

Schematically 3 breeding levels exist now for maritime pine in Southwest-France (see BARADAT and PASTUSZKA, 1992; and DUREL, 1992: here G0, G1 and G2 refer to the populations which produce the improved material):
- the base breeding population (G0 = generation 0, i. e. the clones of plus trees);
- trees selected in the plus tree progeny tests (G1 = first breeding generation);
- trees selected in the tests of the G1 progenies (G2 = second breeding generation).

Gains for G0, G1 and G2 compared to the base Landes forest population were computed as in DUREL (1992). For example, for G2 (considering that trees from the G0 originate only from the population of 360 plus trees and that the genetic variance remains constant):

$$\Delta G\ (G2) = (1 + \Delta G_{+T})(1 + \Delta G_{ECS})(1 + \Delta G_{ECS})$$

The gain estimates for height growth, volume and stem straightness are shown in *figure 5* and *table 6*: juvenile growth (up to age 15 years) is not affected by plus tree selection, the sylvicultural treatments in stands originating from grafted plus tree seed orchards (G0) should remain unchanged during this period. After age 20 years, growth of these stands might be faster, requiring more frequent thinnings.

For early combined selection, the high increase in juvenile growth implies less weeding though more frequent or heavier thinnings in the 25 first years, when wood is less valuable.

Table 6. – Estimates of the genetic gain for the base breeding generation (G0), and for the first (G1) and second (G2) breeding generation compared to the Landes maritime pine provenance (considering that all trees originate only from plus trees). Separate estimations were made from the results in each trial.

trial	ΔG (G0)	ΔG (G1)	ΔG (G2)
height at age 10 years (h10)			
B	-0.2%	3.6%	8.7%
C	-0.3%	-0.2%	0%
predicted height at age 50 years (H50)			
B	6.1%	7.7%	9.3%
C	7.2%	9.0%	10.9%
stem volume at age 22 (trial B) and 27 (trial C) years			
B	19.9%	25.7%	31.9%
C	19.1%	19.1%	19.1%
stem straightness			
B	18.1%	26.0%	34.5%
C	24.0%	27.8%	31.9%

Such a growth pattern may also result in a higher proportion of juvenile wood, which is inferior for stiffness (CASTERA and MORLIER, 1993).

In practice, offsprings from the first (G1) and the second (G2) breeding generation will have a rapid growth during the whole rotation: offsprings from the second breeding generation (G2), will be approximately 10% higher than the control both at age 10 and 50 years. As a result, all sylvicultural operations should be more frequent, and the rotation length may then be shortened. For the second breeding generation (G2), gains on final volume may reach 40%, and gains on straightness may reach more than 30%, with a 50 years rotation.

BARADAT and PASTUSZKA (1992) mentioned 7% gain on volume for grafted plus trees seed orchards, 15% for the first generation seed-orchards and 35% for the second generation seed orchards (respectively 10%, 20% and 30% for butt angle of lean), compared to the local provenance. Especially the 10 years routine measures were used for these gain predictions, which may explain the discrepancies in the gain estimations.

It should be noted that the selection practices were not the same for all French maritime pine seed-orchards, hence genetic gains will vary, but may be predicted approximately from our results. To incorporate genetic effects into stand simulation models, a site index lift alone (as in REHFELDT *et al.,* 1991) will be inefficient.

Conclusion

This study and results from DANJON (1994b) suggest that in maritime pine, effects of direct selection for height are high, though indirect selection suffers from a lack of juvenile-mature correlations.

Consequently, the selection at a given age alters the shape of the growth curves: early combined selection in progeny tests increases principally early vigour, and mature plus tree selection increases mature vigour. LAMBETH (1980) showed that for several pine species, the genetic gain per unit of time is maximized with a selection at age 7 years for a 50 year rotation age. In maritime pine, gains at clear cut expected from 4 cycles of early combined selection may also be greater than gains provided by plus tree selection, though the gains are not evenly allocated on the whole growth trajectory: several cycles of early selection may modify greatly the shape of the height-age curves.

Altering the growth curve shape was often considered useful by animal breeders, and single trait selection at a given age was found to be ineffective for this purpose (FITZHUGH, 1976).
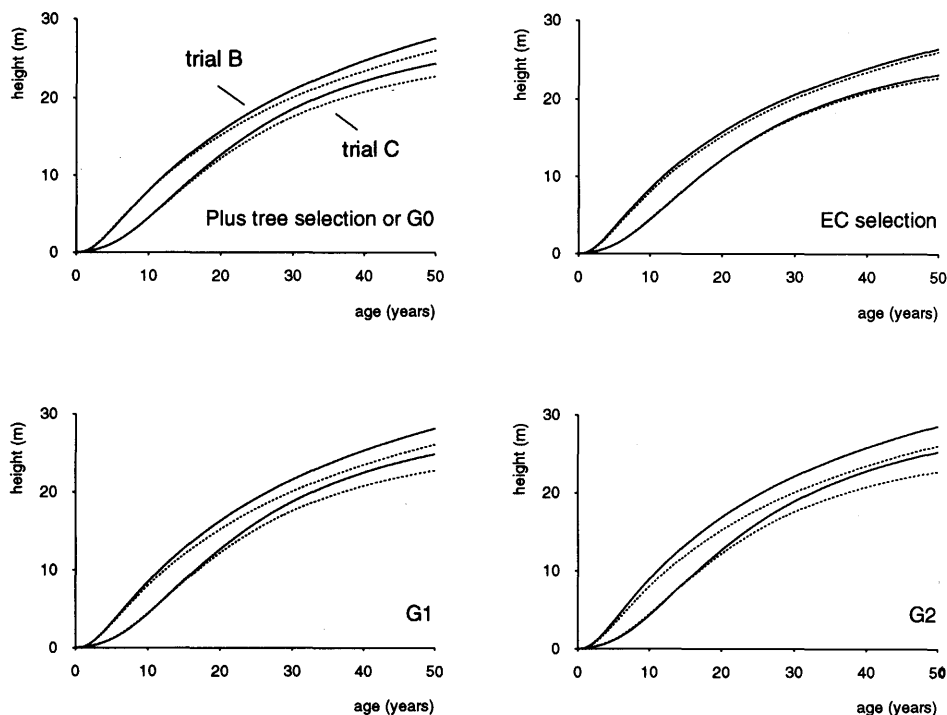
Figure 5. – Expected mean height growth curves for plus tree offsprings (G0, with 2 plus tree parents), for trees selected trough early combined selection, for the first breeding generation (G1) and for the second breeding generation (G2) (solid lines). These curves are compared to the control Landes population (dotted line). The genetic gains were computed from results in trial B and trial C (shown in Tab. 4a).

For maritime pine, the shape alteration resulting from early combined selection is expected to modify the wood structure and architecture, and to require new management practices. Nevertheless, if this alteration is deemed undesirable, selection cannot be delayed until age 25: during the first thinning (at age 10 to 12 years for maritime pine), half of the trees tested in progeny trials must be cut and after age 12 years, height measurements are less precise. FRANKLIN (1979) suggested hastening the onset of the mature phase by manipulating environmental factors. It may also be possible to find selection criteria which are better correlated to later growth.

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