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Heritabilities and genetic correlations for estimated growth curve parameters in maritime pine

Abstract Height growth curves and several other characters were measured in five maritime pine (*Pinus pinaster* Ait) progeny tests aged from 18 to 27 years (about half the rotation age), with sample sizes of 272–1555 trees. These curves were fitted with a reparametrized Lundqvist-Matèrn sigmoidal growth function with global estimation of two of the four parameters. Each curve was characterized by two parameters:
– the maximal growth rate (r), approximately proportional to the stem height at age 16 years, and essentially determined by the height increments around age 6 years.
– the asymptote (A), which is an extrapolation of growth after the measurement age. A is essentially determined by the latter growth period (around age 20 years), and is also related to the shape of the observed curve.
The modelling framework appeared to be well suited to the characteristics of the data studied, and the estimation standard errors of the parameters were reasonably low. The heritabilities yielded for the growth curve parameters were high, similar to the heritabilities of cumulative heights. The genetic correlation between r and A was low, pointing to a poor juvenile-mature correlation. Discrepancies from one trial to another in heritabilities and in the correlation pattern were observed, they probably originated from environmental stresses. Maritime pine is actually selected using height and butt angle of lean at age 10 years as criteria. Improvements in the breeding program are suggested.

Key words Height growth curves · Genetic parameters Nonlinear regression · *Pinus pinaster*

Introduction

In programs of tree improvement, selection is often made at young ages even though the ultimate selection criteria

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are usually stem volume and wood quality at rotation age. The assumption is made that early performance is indicative of later performance (Lambeth et al. 1983). Of the three stem volume components (height, diameter and taper), stem height is less sensitive to competition and has therefore often been used as a selection criterion for volume growth (Kremer 1992). Few studies on the genetic control of height growth curves have been made in forest trees, hence, the genetic determinism of the growth pattern along the growth-harvest cycle is generally not known. Only some forest tree progeny tests have reached rotation age, so the whole growth curve (i.e. through the final cut) can usually not be assessed. Consequently, modelling techniques providing extrapolations are very useful for studying growth patterns and for assessing juvenile-mature correlations in forest trees.

When longer growth series are available and when the shapes of all curves studied are close to the same mathematical function, nonlinear regression can be used for modelling. This technique provides several advantages: parameters have a prior defined signification, they have the same biological meaning in all datasets and some extrapolations can be made. However, these methods are faced with problems such as correlated estimates and ill-conditioning (Seber and Wild 1989). Early studies of the genetic variability of growth curves in forest trees (Namkoong et al. 1972; Magnussen 1993; Magnussen and Kremer 1994) yielded low genetic variance or very high correlations between estimated parameters. A reliable modelling framework was employed by Kachman et al. (1988) for mice weight growth curves. Fairly similar methods (Danjon and Hervé 1994), were used in the study presented here for maritime pine height growth curves and their reliability was controlled.

Maritime pine (*Pinus pinaster* Ait.) produces approximately 15% of the timber and pulp wood in France, with the production mainly located in the Southwest of France ("Landes de Gascogne" area) where one million hectares are intensively managed in even-aged stands. A breeding programme for Southwest France started in the early 1960s, using recurrent selection. Several progeny tests have now reached half the rotation age, providing valuable

material for genetic studies. Selection is conducted around 10 years of age with total height and butt angle of lean (assessment of stem straightness) as selection criteria. At the present time, two selection cycles have been completed. Maritime pine is well suited to growth curve analysis because it has a simple monopodial architecture. Precise height/age chronologies can be measured on felled trees using branch whorls as morphological markers of annual shoots (Kremer 1981a).

In the study presented here, height growth curves were measured in five progeny tests aged from 18 to 27 years. As in Lambeth et al. (1983), the sample included several trials with nearly the same structure but various genetic compositions. In one test of the present study, the sample size (100 families and 1555 trees) was sufficient to allow accurate estimations of genetic parameters (data used in Magnussen and Kremer 1994). Less precise estimations were made in the four other tests since the samples were smaller (from 272 to 669 trees). However, heritabilities were not used for gain estimations in selection but rather to compare the magnitude of heritabilities of various traits, as in Velling and Tigerstedt (1984). This work was not developed to be a guideline directed toward selection using growth curve parameters (as in Namkoong and Matzinger 1975 or Kachman et al. 1988), because growth curves are difficult to measure in routine assessment. It is more an investigation of the inheritance of growth pattern and its relation with other characters, thereby providing keys for a greater efficiency of selection. Heritabilities of growth curve parameters were computed and compared to those obtained for directly measured traits. Genetic correlations between the estimated parameters and all of the studied characters were then determined.

Materials and methods

Materials

Data were collected between 1979 and 1992 in five maritime pine progeny tests from the local provenance established in the "Landes de Gascogne" area (Table 1). All test plots were located in Cestas (Gironde) near Bordeaux, except trial C, which was established in a drier site (Soustons - Landes) close to the Atlantic coast (Illy 1966). The soil was a semihumid podsolic sand of low fertility. These tests had almost all the same features: sowing in the spring in nursery beds and planting 6 months later at spacing of 1.10×4 m. Experimental designs consist either of blocks nested in complete randomized replications or of randomized incomplete blocks (Table 2). Fertilization and weeding were done at age 2–5 years. Systematic thinnings, in which each second tree was removed, were conducted between age 11 and 15 years in all the tests. A second systematic thinning was done at age 15, 16 and 17 years in tests E, F and B. These practices approximate actual intensive stand management techniques.

Measurements

Measurements were carried out during systematic thinning operations to save the progeny tests for future measurements. Maritime pine produces either one or two branch whorls each year (polycyclism). The height of each primary and secondary whorl was measured with a tape from the tip to the whorls of age 2 (Table 2), providing a precise height-age chronology and an assessment of polycyclism. Older contemporary height measurements were used for control purposes. All the measurements were expected to have approximately the same precision, which is not the case for con-

Table 1 Characteristics of the progeny tests

Test	Number	Layout	Design	Plot type - size	Spacing	Age thinned[a]	Families[b]	Genetic level[c]
B	2–44–03.1	1965	9 reps×5 bl.	5×2 tree-row	1.5×3 m	12 (1/2) 17 (1/5)	100 HS (in situ)	0 and PT/2
C	2–44–03.2	1965	6 reps×5 bl.	5×2 tree-row	1.5×3 m	15 (1/2)	100 HS (in situ)	0 and PT/2
D	2–44–01	1962	82 blocks[d]	5×2 tree-row	1.5×3 m	13 (1/2)	40 HS (in situ)	PT/2
E	2–44–13	1970	9 reps	1 to 3×2 t.-r.	1.1×4 m	11 (1/2) 15 (1/4)	64 HS (polycross)	PT/2
F	2–44–09	1968	12 reps	4×1 to 3 t.-r.	1.1×4 m	11 (1/2) 16 (1/5)	144 FS (hierarcal)	PT

[a] Proportion of trees removed in brackets
[b] HS, half-sib; FS, full-sib; pollinization mode in brackets
[c] 0, No selection; PT/2, plus tree mother; PT, plus tree parents
[d] 5 plots per block

Table 2 Samples for growth curve analysis and traits measured (*dbh* stem diameter at breast height, *bss* butt sweep of stem, *bal* butt angle of lean, *form* 20-point visual scoring, *taper* stem diameter every 2m)

Test	Age (yr)	Number of trees	Sample	Repetitions used	Families used	Heights (yrs)	Diameter	Form
B	22	1555	each second row	all	100	2 to 22	dbh	age 10 bss
C	27	500	one tree per plot	5 reps	100	2 to 27	dbh + taper	age 27 form
D	18	669	1.7 trees per plot	all[a]	40	4 to 18	dbh + taper	age 9 bss
E	22	318	1 tree per rep	5 reps[a]	63	2 to 22	dbh + taper	age 22 bal + form
F	22	272	4 trees per plot	2 reps[a]	34[b]	2 to 22	dbh + taper	age 22 bal + form

[a] Ten blocks were defined in these tests for further analyses
[b] Eight fathers with each 2–5 mothers

Table 3 Summary statistics for estimates of the growth curves parameters (*mean SE* mean estimation (within curve) standard error, *SD* standard deviation of the population)

Trial	Deleted curves	Mean residual[a]	m (global)	h_0 (cm) (global)	A (m)			r (cm/year)			(A,r) correlations		H50 mean
					Mean	Mean SE	SD	Mean	Mean SE	SD	e-corr[b]	pheno-typic[c]	
B	2	0.20	0.078	0.05	51.5	1.10	5.65	101.0	0.52	7.35	−0.35	0.06	25.9
C	2	0.21	0.235	3.93	27.5	0.47	3.27	82.4	0.40	6.76	0.50	0.32	22.6
D	1	0.20	0.140	2.73	34.9	0.94	4.77	104.1	0.61	8.56	0.13	0.14	24.7
E	2	0.27	0.164	8.59	39.1	1.05	5.41	101.0	0.63	8.98	0.30	0.09	27.8
F	0	0.19	0.155	2.49	37.8	0.74	4.10	97.7	0.44	7.45	0.36	0.24	26.3

[a] Mean of absolute values
[b] Estimation correlation (mean"within curve" correlation)
[c] "Between curve" phenotypic correlation

temporary measures where the precision usually diminishes as trees age.

Some other traits were also measured (Table 2):

- stem diameter at breast height (dbh) and stem diameter every 2 m (referred to as "taper")
- stem volume was computed from the taper when available, or from the cone volume formula
- stem straightness, assessed either with the measure of butt angle of lean (bal) on the first meter, with a measure of butt sweep of the stem (bss) on the first 3 m or with a 20-point visual scoring (a large scale lowers threshold effects) referred to as "form".

Samplings were done to gain fairly orthogonal designs (equal number of trees for each family in each replication).

Modelling

Almost all of the sampled trees had a regular sigmoidal shaped height growth curve. Danjon and Hervé (1994) have shown that older maritime pines (up to 80 years old) have a sigmoidal growth pattern. Only variable shape models were tested to keep a maximal flexibility ensuring a close fitting. While the Lundqvist-Matèrn (Matèrn 1959) model provided a slightly better fit than the Chapman-Richards (Richards 1959) model (Danjon and Hervé 1994), the same conclusions concerning the genetic determinism of height growth were still reached with both models (Danjon 1992).

According to Ross (1970) the classical Lundqvist-Matèrn function was reparametrized to gain stable parameters. Such parameters have a direct biological meaning and an influence on a limited part of the curve:

$$h(t) = A \exp$$

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

with h: height, t: age, A: asymptote, r: maximal growth rate, m: shape parameter, i.e., relative height of the inflexion point, and h_0: height at age 0.

Ordinary least squares estimations were computed via the Gauss-Marquardt algorithm following the implementation recommended by Moré (1977), using a software designed by Hervé.

It is useless to estimate all four parameters for each individual curve (Day 1966), especially for short curves. For m and h_0, a single value was estimated for the whole trial (global parameters). For A and r, one value was estimated for each individual curve (local parameters). This could be done only after reparametrization because the global parameters must have similar values for all curves. In the present case, trees were evenly aged, hence h_0 was similar for all trees, and it had been shown that m had a low genetic variability even

at the provenance level (Danjon 1994). The initial slope of the Lundqvist-Matèrn model was a little too low, consequently, very low positive values were obtained for h_0 (Table 3).

The whole available growth sequence including the zero point was used for all trials. For trial D, the global estimation for h_0 converged to 0, yielding very high A estimates (62 m mean) and a low estimate for m (0.06). This phenomenon may be due to the data structure (heights from 4 to 18 years were only available). Hence, upon examination of the results on other datasets, m was fixed to 0.14 and h_0 was estimated globally, yielding a mean of 35 m for A.

The predicted heights at age 30, 40 and 50 (H30, H40 and H50)[1] were analyzed because H50 (or H40) can be considered to be the target trait for wood volume selection: 50 years is generally the actual lower bound for clear-cutting, though it is likely to decrease due to sylvicultural and genetic improvements.

Estimation of genetic parameters

The growth curve parameters were treated as normal measured variables, with their intrinsic estimation standard error ignored. All datasets were analyzed with complete replications and incomplete nested blocks [model (1) - trial B and C] or with incomplete blocks or complete replications[(model (2) - trial D, E and F]:

$$Y_{ijkl} = \mu + R_i + B_{j(i)} + F_k + RF_{ik} + E_{ijkl} \tag{1}$$

$$Y_{jkl} = \mu + B_j + F_k + BF_{jk} + E_{jkl} \tag{2}$$

Where Y is the observed value, μ the population mean, R_i the effect of replication i, $B_{j(i)}$ the effect of block j within replication i, F_k the effect of family k, RF_{ik} and BF_{jk} the corresponding interactions and E_{ijkl} the random error term.

For trial C, no interaction was computed since only 1 tree per repetition was sampled, and for trial F (full sibs), a father effect and a mother×father interaction were used instead of the family effect.

All effects were assumed to be random. Restricted maximum likelihood (REML) estimations of heritabilities (with their standard errors) and genetic correlations were computed with the Select-INRA software (INRA 1991; Mangin and Vincourt 1992). Narrow sense individual heritabilities were estimated as:

$$h_{ns}^2 = \frac{4\sigma_F^2}{\sigma_F^2 + \sigma_R^2 + \sigma_B^2 + \sigma_{RF}^2 + \sigma_E^2}$$

For trial F the father variance was used instead of the family variance and the mother×father interaction was pooled to the denominator. Variance due to repetitions and block effects were included in the denominator of estimates of heritability. Therefore, gain calculations from selection on data corrected for repetition and block effects will be underestimated (Cotterill 1987).

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[1] h will then refer to observed heights and H to predicted heights

Results

Fitting

The reliability of fitting was determined on plots of the observed and predicted heights and of the residuals (Figs. 1 and 3), on bivariate distributions of parameters with approximate confidence ellipses (Fig. 2), and with summary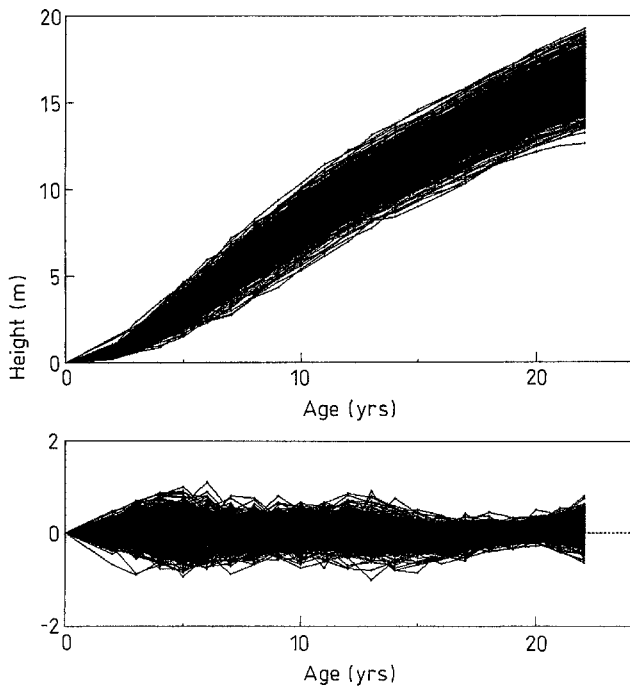 statistics (Table 3). The graphs provided a synthetic representation of the fitting (Danjon and Hervé 1994). Non convergence of the solutions was never observed. Of the curves, 0.2% were deleted because their estimates of A were very far from the mean (for example, 100 m for a tree in trial B) or because their confidence ellipses appeared too large. These trees all had a very slow start and very rapid later growth, consequently, their curves had non sigmoidal shapes and their parameter estimates were meaningless. A and r were normally distributed.
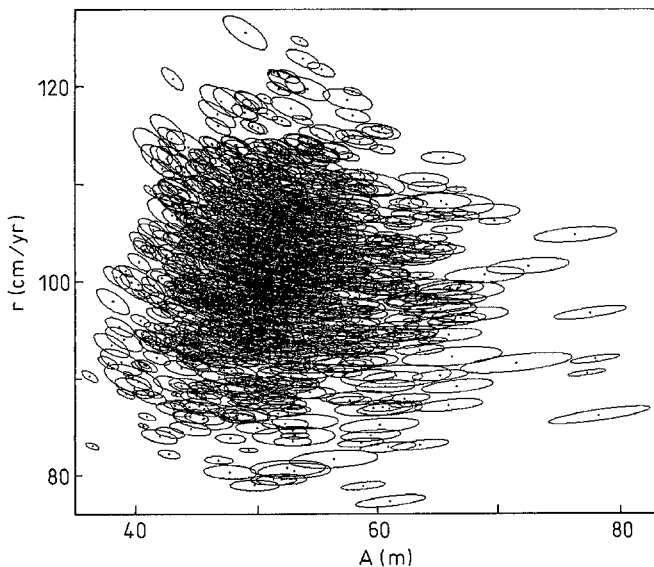
In major cases the fitting curves were very close to the observed points (Fig. 3). The mean absolute value of residuals at each point was around 20 cm. No striking trend was detected on graphs of residuals, showing that the fitted function was well-suited to the shape of the curves (Fig. 1).

The effect of reparametrization can be seen in the low estimation correlations (-0.4–0.5), which ensured a good identifiability of parameters (Table 3). Except for a low positive correlation, the (A,r) bivariate distributions did not show any particular structure, and confidence ellipses were reasonably small compared to the spread of points in the (A, r) plane (Fig. 2).

The global estimates of the shape parameter (m) ranged from 0.08 (very straight curves) to 0.23. High m estimates were associated with low A estimates owing to the structural correlation between these parameters (Danjon and Hervé 1994). The standard deviation of A was proportional to the mean. Estimation standard errors for A and r were estimated for each curve. The ratio of standard deviation divided by the mean standard error was 5 for A and more than 10 for r: estimations of r were more precise than estimations of A. The five trials had similar mean r values, except for the C trial, which was located in a drier zone (Fig. 4).

Fig. 1 Trial B: Observed height growth curves (*top*) and corresponding residuals (*bottom*)

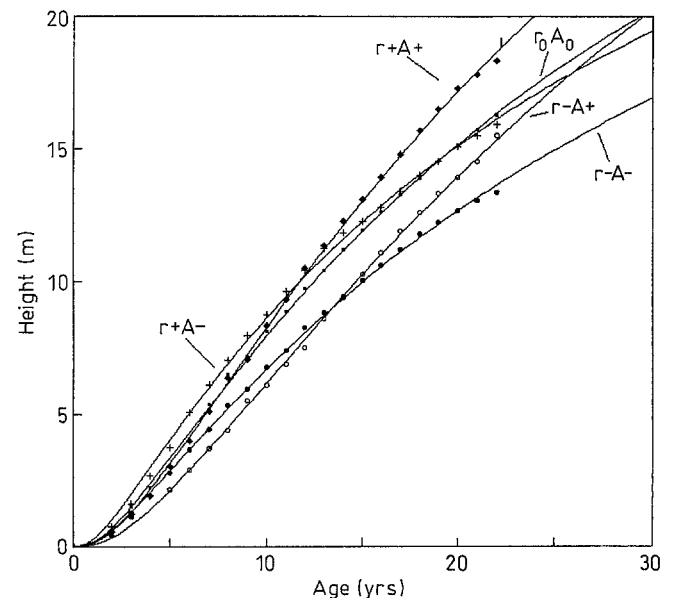**Fig. 2** Trial B: Bivariate distribution of A and r with approximate 50% confidence ellipses

Fig. 3 Trial B: Five fitted growth curves with contrasted growth patterns (for maximal growth rate: $r- \approx 86$, $r_0 \approx 101$, $r+ \approx 110$ cm/yr, for asymptote: $A- \approx 41$, $A_0 \approx 50$, $A+ \approx 66$ m)
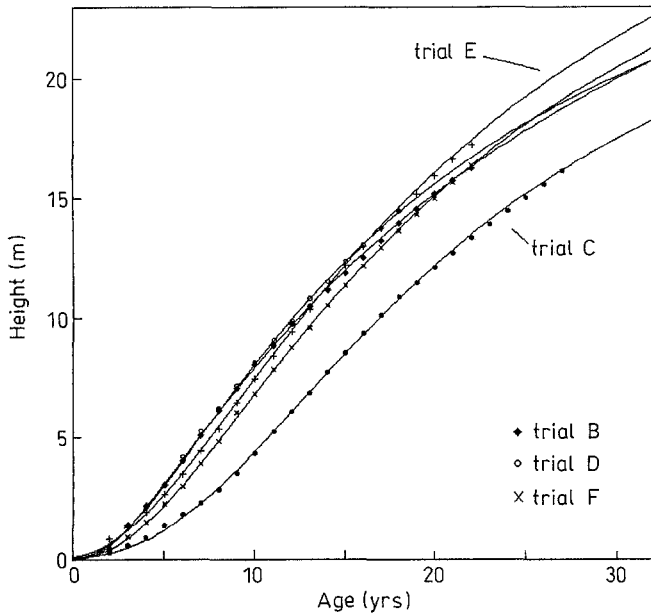
Fig. 4 Mean observed and mean predicted curves for the five trials

after age 13 years; the same pattern was observed for correlations of A with annual height increments, which were positive after about age 8 years. Correlations of heights with H50 were greater than correlations of heights with A; they reached 0.75 between H50 and the later 5-year height increment.

These correlation patterns point to the significance of the estimated parameters:

– r was essentially determined by height around age 16 years, and is approximately proportional to the slope of the observed curve over the first 16 years. It should be noted that r was especially determined by the juvenile height increments.

– A is an extrapolation of growth after the measurement age, based on the observed curve. It is essentially determined by the last measured height increments (rate of decline), but is also determined by the shape of the observed curve, as indicated by the negative correlations between A and height at age 5 years. Five contrasted growth patterns were plotted on Fig. 3: for example, a tree with a very low early growth but a rapid later growth (r-A+ in Fig. 3) is expected to reach a high asymptote.

Information carried by r was not very different from information furnished by height at age 16 years, but A provided original information that was not displayed by any examined single trait nor by the ratio of juvenile growth (h5) divided by the latter growth (h20 - h15). The correlation between A and h5/(h20 - h15) ranged from 0.64 to 0.71, but no higher. For prediction purposes, the estimated height at age 50 years was used rather than A because the former represents the target selection trait. H50 is principally correlated to A, but also to r. The phenotypic correlation between A and H50 is 0.88 for trial B and around

Phenotypic correlations

The phenotypic correlations between growth curve parameters and successive heights and height increments were approximately the same in all of the tests studied (Table 4). r was highly correlated to heights after age 10 years, the correlation peaking at $\rho=0.96$ around age 16 years (age 23 for trial C). r was especially correlated to height increments around age 6 years.

Correlations of A with heights were generally slightly negative at young ages and became increasingly positive

Table 4 Phenotypic correlations between estimated parameters (r, H50 and A) and measured traits

Estimated parameters	Trial	Cumulative heights				5-year height increments			Other measured traits			
		h5	h10	h15	h20	Δh5-10	Δ10-15	Δ15-20	dbh	Vol	FPOLY	Form[a]
r	B	0.61	0.91	0.95	0.89	0.68	0.28	0.21	0.57	0.61	0.17	0
	C	0.51	0.70	0.87	0.97	0.67	0.50	0.48	0.80	0.82	0.19	0.26
	D	0.65	0.93	0.97	0.95[b]	0.65	0.44	0.40[b]	0.81	0.84	0.15	0.06
	E	0.63	0.87	0.96	0.97	0.65	0.40	0.43	0.74	0.81	0.31	0.15
	F	0.58	0.85	0.97	0.98	0.79	0.44	0.37	0.78	0.84	0.27	0.08
H50	B	–0.01	0.30	0.63	0.80	0.37	0.75	0.73	0.54	0.57	–0.06	–0.05
	C	–0.16	–0.11	0.15	0.46	–0.06	0.53	0.83	0.50	0.54	–0.04	0.24
	D	–0.24	0.16	0.51	0.63[b]	0.45	0.85	0.74[b]	0.40	0.44	0	0.01
	E	–0.30	–0.01	0.35	0.56	0.30	0.73	0.73	0.42	0.47	0.07	0.08
	F	–0.17	0.07	0.48	0.68	0.22	0.78	0.72	0.36	0.45	0.04	0.26
A	B	–0.34	–0.16	0.20	0.43	0.06	0.72	0.72	0.30	0.33	–0.16	–0.06
	C	–0.37	–0.40	–0.16	0.16	–0.34	0.42	0.79	0.27	0.31	–0.13	0.18
	D	–0.47	–0.16	0.21	0.35[b]	0.25	0.76	0.67[b]	0.16	0.20	–0.06	0
	E	–0.56	–0.35	0	0.23	0.07	0.63	0.62	0.15	0.19	–0.06	0.03
	F	–0.43	–0.26	0.16	0.39	–0.07	0.72	0.69	0.10	0.19	–0.06	0.25

[a] Straightness scoring when available, else bss (a high bss means a bad form)
[b] h18 and Δh13–18 for trial C

Table 5 Phenotypic correlations between r, H30, H40, H50 and A

Trial	(r,H30)	(r,H40)	(r,H50)	(r,A)	(A,H30)	(A,H40)	(A,H50)	(H30,H50)	(H40,H50)	(H30,H40)
B	0.74	0.60	0.51	0.06	0.70	0.82	0.88	0.96	0.99	0.98
C	0.91	0.72	0.60	0.32	0.66	0.88	0.95	0.86	0.98	0.94
D	0.67	0.52	0.43	0.14	0.81	0.91	0.95	0.96	0.99	0.98
E	0.74	0.54	0.42	0.09	0.71	0.87	0.93	0.92	0.99	0.96
F	0.80	0.65	0.55	0.24	0.76	0.89	0.94	0.94	0.99	0.97

Table 6 Narrow sense heritabilities and standard errors for the growth curve parameters

Trial	Parameter estimates				
	r	H30	H40	H50	A
B	0.63 ± 0.12	0.68 ± 0.13	0.66 ± 0.12	0.63 ± 0.12	0.53 ± 0.10
C	0.08 ± 0.11	0.10 ± 0.12	0.16 ± 0.12	0.22 ± 0.13	0.31 ± 0.14
D	0.18 ± 0.09	0.33 ± 0.13	0.34 ± 0.13	0.34 ± 0.13	0.31 ± 0.12
E	0.29 ± 0.17	0.18 ± 0.16	0.15 ± 0.16	0.17 ± 0.17	0.17 ± 0.17
F	0.87 ± 0.58	0.99 ± 0.63	0.91 ± 0.59	0.83 ± 0.54	0.57 ± 0.40

Table 7 Narrow-sense heritabilities and standard errors of measured traits

Trial	Cumulative heights				5-years height increments			Other traits			
	h5	h10	h15	h20	Δh5-10	Δh10-15	Δh15-20	dbh	Vol	FPOLY	Form[a]
B	0.30±0.08	0.52±0.11	0.67±0.12	0.65±0.12	0.32±0.08	0.41±0.09	0.45±0.10	0.29±0.07	0.34±0.08	0.58±0.11	0.08±0.05
C	0.09±0.11	0.13±0.11	0.20±0.12	0.16±0.12	0.16±0.12	0.35±0.14	0.35±0.14	0	0	0.60±0.18	0.45±0.17
D	0.08±0.07	0.19±0.09	0.21±0.10	0.15±0.08[b]	0.20±0.10	0.32±0.12	0.12±0.08[b]	0.02±0.06	0.04±0.06	0.70±0.20	0.29±0.11
E	0.23±0.17	0.36±0.19	0.27±0.17	0.28±0.18	0.13±0.16	0	0.24±0.18	0.06±0.16	0.20±0.17	0.52±0.22	0.15±0.17
F	0.25±0.20	0.59±0.43	0.74±0.53	0.92±0.60	0.63±0.45	0.45±0.33	0.23±0.22	0.45±0.33	0.36±0.82	0.43±1.32	0.26±0.27

[a] Straightness scoring when available, else bss
[b] h18 and Δh13–18

0.93 for the other tests; correlations between H40 and H50 were all higher than 0.98 (Table 5).

The phenotypic correlations between both estimated parameters were small and positive (0.06–0.32, Table 5), indicating that there was no striking relation between early and later height growth. The correlations depend on the data and on the duration of observed curves: generally the phenotypic correlation increased when the curves were shortened (Danjon 1992), which was not apparent in the present study.

Correlations between r and dbh or volume at the measurement age were fairly high (Table 4), reflecting the general vigor at this time. Polycyclism tended to be positively correlated to r and negatively correlated to A. Both estimated parameters tended to be slightly positively correlated to the stem form evaluated at later ages.

Heritabilities for growth curve parameters

In trial B, the narrow-sense heritabilities of both growth curve parameters were high (0.53 and 0.63, Table 6) and very close to the heritabilities yielded for cumulative heights after age 10 years (Table 7); the standard errors were also similar. For the three other half-sib tests, heritabilities were smaller (0.2–0.3, except for r in trial C), and standard errors were large, most certainly because of the small sample sizes. The low heritability of r in trial C may be due to limiting factors at young ages: trial C was located in a drier area; in addition, a severe drought occurred in 1970 (Lemoine 1979). Heritabilities of height at age 10 years and of the 5- to 10-year height increment were also unexpectedly low in this trial. In trial F, the heritability estimates obtained from full-sib analysis were high (0.57–0.99), they might have been biased upwards by maternal and dominance variance.

Several contemporary measurements were made on larger samples in the trials. Estimated heritabilities are reported in Table 8. Height was measured on standing trees with a pole before age 15 years, with a dendrometer after; heights from Kremer (1981a-c) were measured with a tape.

For heights, heritabilities for the four samples of trial B (9000, 2700, 1560 and 1500 trees) were similar. Thus, heritabilities from our trial B sample may be reliable. For trials C and D, the heritabilities were generally greater in the large samples, especially for traits with low heritability. These results agree with those of McCutchan et al. (1989): heritabilities computed from more than 800 observations should be reliable, whereas samples of fewer than 500 trees provide imprecise estimations, especially when the heritability is low and when the number of families is high (optimal number of offspring per family is $4/h^2$, Cotterill and James 1984).

Table 8 Narrow-sense heritabilities and standard errors of contemporary measurements on large samples

Trial	B								C				D	
Trees	9000			2700[a]			1500[b]		2400[a]			3060	4100	
Trait	h5	h8	bss10	h8	h10	bal10	h29	dbh29	h8	h10	bal10	dbh27	h10	bss10
h^2ns	0.24	0.37	0.16	0.32	0.51	0.24	0.48	0.26	0.42	0.42	0.25	0.15	0.45	0.23
SE	0.04	0.06	0.03	0.06	0.09	0.06	0.10	0.07	0.08	0.08	0.06	0.04	0.11	0.06

[a] Data from Kremer 1981a–c
[b] From Bergoin 1993

Table 9 Genetic correlations between A, r, H40 and H50

Trial	(r,H40)	(r,H50)	(A,r)	(A,H40)	(A,H50)	(H40,H50)
B	0.70	0.77	0.22	0.85	1.20	0.99
C	0.45	0.33	0.16	0.96	0.99	0.99
D	0.55	0.86	0.31	0.96	1.60	0.99
E	0.17	-0.02	-0.65	0.80	0.90	0.98
F	0.89	0.85	0.72	0.95	0.95	1.00

Heritabilities for measured characters

The heritability of cumulative heights generally increased after age 5 years and remained fairly constant after age 10 years (Table 7). For the 5-year height increments, heritability tended to increase steadily with increasing age. However, in four trials, heritability decreased during a given period (around age 25, 16, 12 and 17 years for trials C–F; in trial C, heritabilities of height at age 27 years and height increments between age 20 and 27 years were null). The rapid increase of heritability after age 8–10 years was shown by Kremer (1981c, 1992).

Heritabilities of diameter and volume at the measurement age reached 0.35 in trial B but were very low in the other trials, perhaps because of high inter-tree competition at the later ages. Heritability of polycyclism frequency was high in all tests, averaging 0.60. The stem form has an average heritability (around 0.3) except, unexpectedly, in trial B (0.1). In test F, a significant amount of dominance variance was yielded for the polycyclism frequency and for the stem form only (not shown).

In first and second breeding-generation progeny trials, heritabilities around 0.1 for dbh, around 0.2 for bss and bal, and around 0.3 for pole-measured heights were obtained during routine measurements at age 10 years (Durel 1990).

Genetic correlations

The genetic correlations between A and r were negative, positive or null (-0.65 to 0.72, Table 9), they were never really high. The correlation between the target traits (H40 and H50) and r ranged from 0 to 0.9. The target selection traits were highly correlated to A, and H40 and H50 were highly correlated (more than 0.98).

The genetic correlations with measured traits followed fairly closely the same patterns as the phenotypic correla-

Table 10 Genetic correlations between estimated parameters (r, H50 and A) and measured traits, in italics when the heritability of at least one trait is less than 0.1

Param-eter	Trial	h5	h10	h15	h20[a]	Δh5-10	Δh10-15	Δh15-20[a]	dbh	vol	FPOLY	Form
	B	0.88	0.97	0.99	1.21	1.24	0.65	0.27	0.99	0.70	0.27	*-0.14*[b]
	C	*0.43*	*-0.16*	*0.76*	*0.45*	*-0.36*	*1.48*	*0.43*	–	–	*-0.65*	*0.88*
r	D	0.22	*0.94*	0.99	0.90	1.09	0.46	-0.33	*0.75*	*0.86*	0.03	0.28[b]
	E	0.87	0.95	1.06	0.93	1.16	–	0.22	*1.06*	1.06	0.68	0.58
	F	0.54	0.99	1.00	0.99	0.98	0.77	0.88	0.83	0.99	0.06	-0.06
	B	0.25	0.44	0.71	0.87	0.48	0.97	0.86	0.61	0.66	-0.20	*-0.54*[b]
	C	*-0.81*	-1.20	-0.50	0.46	-1.30	0.73	1.05	–	–	-0.59	0.51
H50	D	*-0.89*	0.07	0.63	0.83	0.60	1.04	1.05	*0.59*	*0.76*	-0.41	*-0.57*[b]
	E	-0.75	-0.34	*0.06*	0.34	0.66	–	0.82	*-0.85*	0.21	0.26	0.07
	F	-0.14	0.61	0.92	0.90	0.83	1.02	1.01	0.66	0.75	-0.30	0.48
	B	-0.16	-0.02	0.32	0.69	0.09	0.89	1.24	0.53	0.42	-0.40	*-0.56*[b]
	C	*-0.59*	-1.20	-0.52	0.03	-1.20	0.58	0.98	–	–	-0.53	0.60
A	D	*-0.91*	-0.13	0.45	0.75	0.46	1.00	1.00	*0.46*	*0.56*	-0.45	*-0.72*[b]
	E	-1.10	-0.78	-0.49	-0.19	-0.06	–	0.49	*-1.33*	-0.49	0.04	-0.39
	F	-0.05	0.40	0.82	0.71	0.43	1.05	0.96	0.54	0.57	-0.43	0.62

[a] h18 and Δh13-18 for trial C
[b] Butt stem sweep (a high bss means a bad form)

tions (Table 10): r was essentially correlated to cumulative heights after age 10 years (especially to h15) and to the height increment between 5 and 10 years, it was poorly correlated to height increment between ages 15 to 20 years. For A and H50, the correlations with heights generally followed the same pattern from one trial to another, but they had not the same magnitude: in nearly all trials, A and H50 were increasingly correlated to the later heights and later 5-year height increments, but with a shift ranging from trials B and F (higher correlation) to trial E and C (lower correlation).

In trial C, both estimated parameters were negatively correlated to growth around age 7 years; this discrepancy in the correlation pattern may have the same origin as those reported for heritabilities. However, these genetic correlations were imprecise and not relevant since the genetic effects showed a low level of significance for r, h5 and h10 in this trial.

A and H50 were moderately correlated to diameter and volume at the measurement age (around 0.5 for A and 0.6 for H50). Diameter and volume were highly correlated to r (more than 0.7). Thus, height appears, in fact, to be closely related to volume production.

The frequency of polycyclism was negatively correlated to A (around -0.5), except in trial E, and slightly positively correlated to r. H50 was in all cases associated with a better stem form ($\rho^g \cong 0.5$, except for trial E), but not r. Excluding trial C, h10 was moderately correlated to H50 (from -0.4 to 0.6), and correlations between H50 and the height increment between age 5 and age 10 years were all positive (0.5–0.8). Hence, families with a greater final height tend to have a better stem form and to produce fewer polycyclic shoots in the first 20 years.

Discussion

Growth curve analysis

The modelling procedure appeared to be well-adapted to the description of the maritime pine height growth curves, and ill-conditioning in parameter estimation did not appear in the analyses. An example of ill-conditioning was given by Namkoong et al. (1972) in fitting the original Chapman-Richards curve to *Pseudotsuga menziesii* [Mirb.] Franco height growth curves. These authors reported that sometimes the parameters obtained varied widely even if the growth patterns were similar: the number of local parameters used was too high, and the parameters themselves were not "stable".

Magnussen and Kremer (1994) fitted the dataset from trial B with a three-parameter exponential model; even though heritabilities for measured heights were high, low heritabilities (0.09, 0.1 and 0.13) with highly correlated (up to -0.98) non-meaningful parameters were obtained. A similar modelling framework was used by Magnussen (1993) on 36-year-old *Picea glauca* [Moench] Voss height

and volume growth curves, but with fairly meaningful parameters. Heritabilities were higher (0.14, 0.25 and 0.44), though estimated parameters remained highly correlated (up to -0.99), indicating an overparametrization.

Estimations of heights at age 30, 40 and 50 years must be examined with the appropriate scepticism since they were only extrapolations based on the hypothesis of general regularity of curve and no strong interaction between genotypes and the modelling structure. However, it is a good way to gain a qualitative insight in the future evolution of the growth pattern and to study juvenile-mature correlations.

Heritabilities and genetic correlations

As r was strongly related to height at age 16 years, its heritability was expected to be fairly similar to those obtained for observed heights: compared to heritabilities of later cumulative heights, the heritability of r was increased by the smoothing of annual fluctuations (as can be noticed in Balocchi et al. 1993), but it was also lowered because of the estimated standard error that accounted for the residual variance. The magnitude of the dominance effects could not be assessed precisely in this study. The fairly high heritabilities for A indicated that there was a large genetic variability in the latter part and in the shape of the observed growth curves.

Age trends in heritabilities of height growth were fairly similar in the five trials: heritability increased after age 5 years, which is a common pattern in forest species (see Franklin 1979; Lambeth et al. 1983; Balocchi et al. 1993). However, a period with depressed heritability was observed in four trials (before the last thinning in trials C, D and F). This decrease in heritability may be due to higher inter-tree competition, limiting factors, and climatic stresses, and may also be a consequence of small sample sizes.

The genetic determinism of height growth appeared to be affected by environment: in maritime pine, heritabilities often diminish before thinnings, when inter-tree competition is high (Danjon 1992). Cannel (1982) and Cotterill and Dean (1988) also observed that heritability was lowered by competition. Conversely, Franklin (1979) observed a rapid increase in heritability at the time of crown closure, though the relation between competition and the level of heritability was not explicitly shown in this paper. Kremer (1981a, b, c) reported differences in the genetic control of height growth between trial B and the drier trial C. Discrepancies from one trial to another for heritabilities and correlations between estimated growth curve parameters and for juvenile-mature correlations may also originate from environmental stresses.

For trials B, C and D the genetic correlation between A and r were low and positive, as was their phenotypic counterparts. The higher positive and negative correlations in trial F and E, respectively, could not be easily explained: both trials had approximately the same growth pattern (Fig. 4), the same mean parameters (Table 3), but they differed

in the period of depressed heritability (this phenomenon occurred earlier in trial E). The juvenile-mature phenotypic and genetic correlations appeared particularly low in trial E. It should be noted that because of the low sample sizes in four trials, estimates of genetic correlations were imprecise and essentially gave only indications about the sign of the correlations and their magnitude (high or low).

Phenotypic and genetic age-age correlations were generally higher in trial B, where no diminution of heritability was observed. As suggested by McKeand (1988), a better understanding of the effects of environmental stresses on genetic parameters may be useful for avoiding the emergence of such periods in a progeny trial by appropiate sylvicultural management. Moreover, commercial maritime pine production stands are now often planted at wide initial spacing and a low level of competition is then maintained by thinnings.

The growth curve study provided a global description of the growth history of each tree. A complementary study should be done on a finer scale (height increments) for a better understanding of discrepancies in the heritability and correlations pattern; diameter growth curves should also be addressed.

Juvenile-mature correlations

The genetic correlations between early heights and height at rotation age were expected to be small. This can also be seen in the correlations between height at age 5 years and the height increment at ages 15 to 20 years: the phenotypic correlations were definitely null (from −0.11 to 0.06), and the genetic correlations were null or negative (−0.17, −0.73, −0.99, −0.2 and 0.09 for trials B–F, respectively).

Only a few studies have been made on age-age correlations with trees older than half the rotation age. From a broad synthesis between former studies on pines and douglas-fir, Lambeth (1980) showed that age-age correlations for tree height were predictable. He expected a 0.5 age-age correlation between height at age 10 and age 50 years, and a maximal gain per cycle for selection at age 8 years. Kremer (1992) used the dataset from trial B and the growth model from Lemoine (1991) to compute the age-age correlations between the height of the parent trees and the mean value of their progeny; he found that the correlation between age 10- and age 50 year heights may range between 0.44 and 0.76 in fertilized sites, depending on the evolution of genetic variance and on the age-age correlation structure after age 22 years. In the present study, the genetic correlation between h10 and H50 found in trial B (ρ^g=0.44) is in the lower bound of the predictions of Kremer (1992). Nevertheless, the genetic correlation between h10 and H50 varied widely in the four other tests, ranging from −1 to 0.6. Therefore, this correlation may generally be lower than the one yielded in trial B (the phenotypic correlations were also higher in trial B).

The correlation between height at age 10 and height at age 50 years is a part-whole correlation (h10 is part of h50,

Kang 1991); this correlation is generally higher when h10/h50 is greater. While reaching 30% in the good locations (respectively 30%, 19%, 33%, 27% and 26% for trials B–F, respectively), h10/H50 was especially low in trial C, which partly explains the poor phenotypic and genetic correlations between h10 and H50 in this trial. In the same way, Kremer (1992) obtained higher juvenile-mature correlations in fertilized sites because in the model, fertilization only increased growth before age 22 years.

Age-age correlations may be progressive or distributed discontinuously in age groups where correlations are high within groups and low between groups (Franklin 1979; Riemenschneider 1988). In maritime pine, correlations of successive heights with predicted height at age 50 years seem to be fairly continuous. A juvenile group may exist, including approximately the first 5 years. A mature age group for correlation (i.e., between 30 and 50 years of age) may have been hardly detected by the procedure used, since the extrapolations were only based on measurements before age 30 years. In the same way, the three phases in genetic control proposed by Franklin (1979) could not really be detected in the present study. It should be noted that self-thinning generally does not occur in maritime pine stands because of frequent artificial thinning, thus the "co-dominance-suppression phase" from Franklin (1979) may never be reached in commercial plantations with actual intensive sylvicultural practices.

Juvenile-mature correlations appeared to be fairly small in maritime pine; in the same way, Kremer (1992) showed that annual increments separated by more than 13 years were no longer genetically correlated. In forest species, the juvenile-mature correlation has been found to be generally high when examined on a shorter time period (e.g. Rehfeldt et al. 1991 in *Pinus monticola* Dougl. and Ying and Morgenstern 1979 in *Picea Glauca*). When examined on half the rotation age, the age-age correlations appeared to be high in *Pseudotsuga menziesii* (Bastien and Roman-Amat 1990), *Pinus radiata* D. Don (Lambeth et al. 1983; Cotterill and Dean 1988) and *Picea sitchensis* (Bong.) Carr (Gill 1987) and in several other species (Lambeth 1980), but they appeared to be moderate or low in *Pinus elliottii* Engelm (Hodge and White 1992) and *Picea glauca* (Magnussen 1993). Namkoong et al. (1972) and Namkoong and Conkle (1976) also observed negative juvenile-mature correlations in *Pseudotsuga menziesii* and *Pinus ponderosa* Laws., but these results do not appear to be reliable since the family differences were not significant (Lambeth 1980).

Namkoong and Conkle (1976) hypothesized that the poor juvenile-mature correlations originate from differences in resource allocations to root development. This may also be the case for maritime pine, with possibly the following strategies: during the first years, some families develop especially their aerial parts (the "sprinters", Illy 1966), and other families develop larger root systems at the expense of height growth (the "stayers"). Then, after the onset of high inter-tree competition, stayers outrun the sprinters, since water and nutriments are the main limiting factors in the Landes de Gascogne area. This hypothesis is

supported by the positive genetic correlations between form traits and H50 (a better form is expected to be and indicator of better rooting) and the negative correlations between H50 and polycyclism (high juvenile polycyclism means a rapid early development of aerial parts). In addition, negative genetic correlations were noted in all trials between polycyclism and straightness, except in trial E (0.14, −0.22, 0.89, 0.48 and −0.66 for trials B–F, respectively), phenotypic correlations were null. Guignard (1983) also showed that in 1-year-old maritime pines, progenies from monocyclic families had a better rooting system than progenies from polycyclic families.

Practical implications

The genetic correlations observed in the present study suggest the use of a selection criteria that is more correlated to H50, such as height at age 20 or the height increment between ages 15 and 20 years. However, gain per unit of time will be lowered, and the selection can hardly be delayed after the first thinning, at age 12 years. In addition, 5-year increments often have a lower heritability than cumulative heights, and it is more difficult to measure older trees.

The coefficient of genetic prediction (CPG(X,Y) $=cov_g(X,Y)/\sigma^X\sigma^Y$, Baradat 1976) is a measure of expected change in the breeding value at the mature age (trait X) when selection is done at juvenile ages (trait Y, Balocchi et al. 1993). CPGs between H50 and h10, Δh5-10 and Δh10-15 are reported in Table 11: for the later juvenile characters, they reached approximately a quarter of the heritability of height at age 50, i. e. four cycles of recurrent mass selection may have the same effect on the target trait (h50) than one cycle of mature selection with the same selection intensity. It should be noted that the heritability of height at age 10 years was never far from the maximum level over the period studied, which is a valued quality for early selection.

Butt angle of lean and total height at age 10 years are the actual selection criteria. A better improvement of height at rotation age may be achieved using, for instance, the height increment between age 5 and 12 years as selection criterion for vigor. Form parameters always had favorable genetic correlations with H50, and form defects are very important in maritime pine, weight of bal in the selection index should therefore be increased.

Although the growth curve parameters cannot be used

in routine selection, a selection in the families tested in the present study may be employed in controlled pollination seed-orchards (Shelbourne et al. 1989). The selection should be made with predicted height at age 40 or 50 years and stem straightness as criteria, regardless of the values of both original growth curve parameters. This selection is simpler to carry on than the "selection for an optimum growth curve" employed in Namkoong and Matzinger (1975), Magnussen (1993) and Magnussen and Kremer (1994): in Namkoong and Matzinger (1975) practical use of the latter selection index gave unexpected results.

Conclusion

Nonlinear regression proved to be an efficient tool by which to study height growth curves of maritime pine after reparametrization and global estimation of some parameters. The better reliability of nonlinear regression over exponential models was clearly shown. This framework can be used for other forest trees or several species, but longer growth series must be available and all individual curves should have a sigmoidal shape.

The main features of the genetic determinism of height growth appeared to be predictable, but the origin of the variations in the general pattern were not clearly determined.

Since fairly low juvenile-mature correlations were observed, the actual selection criteria may provide a low genetic gain in rotation age height. A more practical study should be conducted to determine optimum selection criteria. It can be concluded from this study that a juvenile selection will essentially increase the juvenile growth, whereas selection at rotation age is expected to improve principally mature heights.

Table 11 Coefficients of genetic prediction between H50 and h10, Δh5-h10 and Δh10-h15 and heritabilities for h10 and H50

Trial	h10	Δh5-h10	Δh10-h15	h^2 for h10	h^2 for H50
B	0.06	0.06	0.13	0.52	0.63
C	−0.02	−0.06	0.05	0.13	0.22
D	0.00	0.00	0.09	0.19	0.34
E	−0.02	0.01	–	0.36	0.17
F	0.11	0.17	0.16	0.59	0.83

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