

GENETIC PARAMETER ESTIMATES FOR MARITIME PINE IN THE ATLANTIC COAST OF NORTH-WEST SPAIN

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Received December 15, 2003; accepted June 8, 2004

ABSTRACT

One hundred and seven half-sib families of *Pinus pinaster* planted at four sites in Galicia (NW Spain) were evaluated at age 8 for growth (height, diameter, volume and mean internode length), stem form (straightness, leaning, forking) and branching characteristics (branch diameter, angle and number and total number of whorls). The analyzed half-sib families were obtained from first-generation plus trees selected for the coastal area breeding programme in Galicia. Estimates of individual and family heritabilities and genetic correlation among traits are presented. Total height, average internode length, number of whorls and branch angle had moderate individual heritability estimates (0.11–0.37). Family heritabilities were moderate to high for almost all traits. Unfavourable genetic correlations were detected between growth and stem form traits and between polycyclism and growth. The average internode length appeared to be an interesting selection trait. It combines both polycyclism pattern and growth, shows moderate individual heritabilities (0.21–0.27) and high family heritabilities (0.67–0.74), and was favourably genetically correlated with other interesting traits. The results are compared with published data and discussed in relation to their implications in the breeding activities.

Key words: genetic variance, heritability, *Pinus pinaster*, progeny trial, half-sibs, genetic correlation.

INTRODUCTION

Maritime pine (*Pinus pinaster* Ait.) is the most important forest species in Galicia (NW Spain). It occupies near 400,000 ha (27 % of the Galician wooded area) with an annual volume increment estimated around $3 \cdot 10^6 \text{ m}^3 \cdot \text{year}^{-1}$ (XUNTA-DE-GALICIA 2001). The *P. pinaster* population in Galicia is included within the Atlantic NW provenance (ALÍA *et al.* 1996), characterized by good growth and intermediate stem form in relation to other Spanish provenances (MOLINA 1965, ALIA *et al.* 1995, ALÍA *et al.* 2001), and a relatively low level of genetic diversity (SALVADOR *et al.* 2000).

Genetic improvement of *P. pinaster* in the coastal area of Galicia was initiated in 1985 and has included phenotypic mass selection in wild stands and use of this material for seed production in clonal seed orchards (VEGA *et al.* 1993). Progeny tests of the phenotypic selections were established to select genetically superior families for further breeding purposes and roguing clonal seed orchards. As in other countries, tree breeding objectives were focused mainly on improving growth traits (height and diameter), stem form and branch quality. Variability of these important economic traits is expressed both within (COTTERILL *et al.* 1987, KREMER & LASCoux 1988, SIERRA DE GRADO *et al.* 1997, KUSNANDAR *et al.* 1998) and among populations

(MOLINA 1965, ALIA *et al.* 1995, ALÍA *et al.* 2001).

The degree and type of genetic control over important traits affect both strategies for breeding and for commercial propagation. Knowledge of genetic parameters is used to design efficient progeny testing and to estimate gain from selection strategies (NAMKOONG 1979). Additionally, genetic and phenotypic relationships among different traits are useful to develop optimal selection indices (DIETERS 1996).

The aim of this paper is to present estimates of a set of genetic parameters (heritability and genetic correlation) for growth, stem form and branch traits of *Pinus pinaster* in the coastal area of Galicia. The data were collected from 8-yr-old *Pinus pinaster* half-sib families tested across four environments. The results were compared with published genetic parameter estimates from other breeding programs and discussed in relation to their implications for future breeding activities.

MATERIAL AND METHODS

Genetic material and test sites

The study material consists of half sib families obtained from 107 selected plus trees represented in the *Sergude* clonal seed orchard (Figure 1). All plus trees were selected for superior growth, stem form and branch characteristics as part of a first-generation breeding

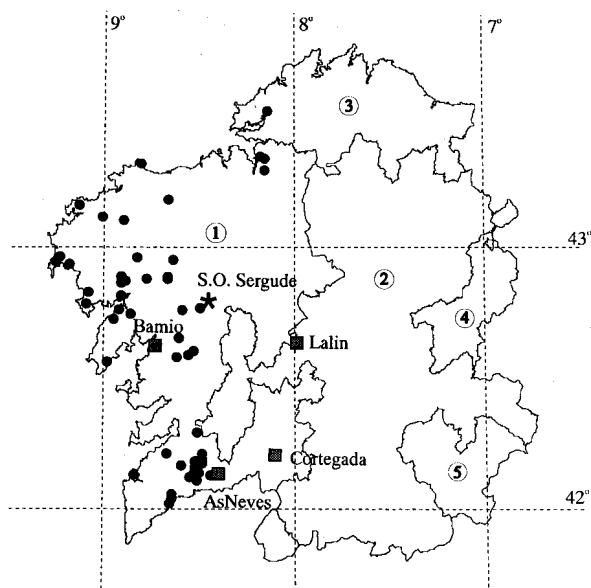


Figure 1. Location of the *Pinus pinaster* plus trees (black dots), the clonal seed orchard (black star) and the four progeny tests (grey squares). Encircled numbers indicated the number of the 'Identification and Utilization Regions' (RIUs) of forest reproductive material (GARCÍA *et al.* 2001).

population. The selection was carried out within the provenance "1a, Noroeste Litoral" (ALÍA *et al.* 1996).

Containerized seedlings of these 107 half-sib families were planted at four sites in 1994 and 1995. Site characteristics are presented in Table 1. Sites were within the RIU (Region of Identification and Utilization of forest reproductive material (GARCÍA *et al.* 2001)) number 1 which constitute, a priori, the breeding area for the selected material (Figure 1). The sites have Atlantic climate characterized by relative high annual precipitation, low summer drought and very low annual temperature oscillation. Cortegada and Lalin sites show a slight Mediterranean influence with lower annual and summer precipitation (Table 1). All sites have acid and coarse textured soils with relatively low levels of nutrients.

All four plantations follow a randomized complete block design with 10 replications of 5 tree-row-plots with 3 × 3 m spacing. A different subset of the 107 families was planted at each site. Fifty-eight, 13 and 36 out of the 107 families were represented in 4, 3 and 2 sites, respectively.

Assessments

All trees of each site were assessed for growth, stem form and branch characteristics at age 8 from planting, except those dead, dying or badly suppressed. Growth traits included total height (*HT*) measured with a pole and diameter at breast height (*DBH*) measured with a

caliper. A volume index was calculate for each tree as $V = HT \cdot DBH^2$. Stem form and branch traits were assessed following GALERA *et al.* (1997). Stem form of each tree was evaluated by a straightness score (*STR*: 1 = straight to 6 = very crooked), a forking score (*FOR*: 1 = no fork, 2 = single fork at the top to 4 = single fork at the bottom of the stem) and a stem leaning score (*LEN*: 1 = vertical to 4 = severe lean). Four traits were considered in relation to branch characteristics: the number of branches in the whorl nearest to the breast height (1.3 m) (*BRN*), the diameter of the thickest branch in this whorl (*BRD*), the number of whorls (*WH*) and a branch angle score (*ANG*: 1 = branches at a flat angle to 3 = steep branching). Additionally, the mean height increment between successive whorls was calculated as $\Delta H = HT / WH$.

Statistical analyses

Plot mean data for each trait and test was analysed using the SAS GLM procedure (SAS-INSTITUTE 1999) and the following random model:

$$Y_{ij} = \mu + F_i + B_j + e_{ij}$$

where Y_{ij} is the plot mean value of family i at block j , μ is the overall mean, F_i is the random effect of the i^{th} family, B_j is the random effect of the j^{th} block and e_{ij} is the random error term. Variance components (σ_f^2 , σ_b^2 , σ_e^2) were estimated equating the type III mean squares in the ANOVA table to their expected values and solving the resulting equations (WRIGHT 1976). Because analyses were based on plot means, within plot variances were estimated separately and included as residual variance (STONECYPHER 1992, p. 202). Individual (h_i^2) and family (h_f^2) heritabilities were estimated as:

$$h_i^2 = \frac{\sigma_A^2}{\sigma_{wp}^2 + \sigma_{pp}^2 + \sigma_f^2} \quad [1]$$

$$h_f^2 = \frac{\sigma_f^2}{\frac{\sigma_{wp}^2 + \sigma_{pp}^2}{NB} + \sigma_f^2} \quad [2]$$

where σ_A^2 is the additive variance which was assumed to be $\sigma_A^2 = 4 \cdot \sigma_f^2$, σ_{wp}^2 is the within plot variance and σ_{pp}^2 is the plot to plot variance estimated as $\sigma_{pp}^2 = \sigma_e^2 - \sigma_{wp}^2 / N$ (STONECYPHER 1992, p. 208), N is the harmonic mean of the number of trees per plot, B is the number of blocks and σ_f^2 and σ_e^2 are the variance components estimated from the analysis of variance.

Table 1. Details of *Pinus pinaster* progeny trials.

	AsNeves	Bamio	Cortegada	Lalin
No of families	82	73	95	93
Altitude	525	300	530	700
Aspect	E	N	S	S
Slope (%)	24.9	26.8	5.2	17.6
Parental origin	Granite	Granite	Schist	Schist
Average soil depth (cm)	84	47	61	59
Annual precipitation (mm)	1760	1730	1106	1202
Summer precipitation (mm)	143	186	118	93
Annual mean temperature (°C)	12.6	13.1	12.6	11.3
Plot size	5	5	5	5
Number of replications	10	10	10	10
Spacing	3 × 3	3 × 3	3 × 3	3 × 3
Plantation date	Nov. 94	Oct. 94	Nov. 95	Nov. 95
Seedlings age at planting (years)	1	1	2	2

Approximate standard errors of individual and family heritabilities were estimated according to WRIGHT (1976, p. 244).

A joint analysis including all sites was also performed using a mixed model with sites considered as a fixed effect:

$$Y_{ijk} = \mu + F_i + S_j + FS_{ij} + B_k(S_j) + e_{ijk}$$

where S_j is the fixed effect of site j and F_i , FS_{ij} and $B_k(S_j)$ are the random effects of the family i , the interaction between family i and site j , and the block k within site j , respectively. To analyze this highly unbalanced mixed model (not all the progenies represented in all environments) the SAS MIXED procedure was used (SAS-INSTITUTE 1999). This procedure estimates the variance components based on mixed model equations and the restricted maximum likelihood (REML) method, and gives the best unbiased predictors (BLUP) of the random effects (SAS-INSTITUTE 1999).

Individual and family heritabilities were estimated as (same nomenclature as before):

$$h_i^2 = \frac{4 \cdot \sigma_A^2}{\sigma_{wp}^2 + \sigma_{pp}^2 + \sigma_f^2 + \sigma_{fs}^2} \quad [3]$$

$$h_f^2 = \frac{\sigma_f^2}{\frac{\sigma_{wp}^2 + \sigma_{pp}^2}{NBS} + \frac{\sigma_{fs}^2}{S} + \sigma_f^2} \quad [4]$$

where S is the number of sites and σ_{fs}^2 is the variance component of the family × site interaction.

Heritability estimates of dichotomous characters (e.g. survival) were adjusted by the method described by DEMPSTER and LERNER (1950). This method assumes an underlying continuous normal variable, which at a given threshold point changes the outward observable variable into a yes or no response. The following equation relates the heritability of the outward scale (h_{01}^2) to the heritability of the continuous underlying scale (h^2):

$$h_{01}^2 = \frac{h^2 \cdot z^2}{\Phi \cdot (1 - \Phi)} \quad [5]$$

where z is the height of the ordinate of the normal distribution at the threshold point which correspond to the observed incidence of the trait (Φ). This transformation was applied to the estimates of heritability based on raw tree data instead of plot means.

Genetic correlations between different traits were calculated from estimates of additive genetic variances and covariances from the joint analysis (FALCONER 1989) using the option MANOVA in the GLM procedure of SAS (SAS-INSTITUTE 1999):

$$r_g = \frac{cov_A(x,y)}{\sigma_x \cdot \sigma_y} \quad [6]$$

where $COV_A(x,y)$ is the family covariance component between traits x and y , and s_x and s_y are the square root of family variance components for the two traits. The standard errors of genetic correlations were estimated as in FALCONER (1989, p. 317). Phenotypic correlations were estimated as Pearson correlation coefficients between plot means.

Table 2. Overall means and standard errors of traits measured at age 8 in the four *Pinus pinaster* progeny tests.

Trait	Code	AsNeves	Bamio	Cortegada	Lalín
Growth traits					
Height (cm)	HT	510.6±2.8	489.0±3.5	558.1±3.1	440.9±2.1
Diameter at breast height (cm)	DBH	10.09±0.07	9.20±0.08	9.96±0.08	7.71±0.05
Volume (dm ³)	V	60.5±1.02	50.5±1.08	65.9±1.23	30.1±0.52
Mean height between whorls (cm)	ΔH	48.71±0.24	49.48±0.35	54.9±0.26	46.21±0.21
Stem form traits					
Stem straightness (score 1 to 6)	STR	2.28±0.02	2.98±0.03	2.24±0.02	2.28±0.01
Fork score (1-4)	FOR	1.41±0.01	1.27±0.01	1.49±0.02	1.18±0.01
Leaning score (1-4)	LEN	1.41±0.01	1.61±0.01	1.70±0.01	2.07±0.01
Branch characteristics					
Number of branches	BRN	4.54±0.02	4.29±0.02	4.74±0.02	4.61±0.02
Diameter of the thickest branch (cm)	BRD	2.92±0.02	3.22±0.03	2.93±0.03	2.12±0.02
Branch angle (1-3)	ANG	1.78±0.01	1.91±0.01	1.78±0.01	1.78±0.01
Number of whorls	WH	10.69±0.05	10.02±0.04	10.3±0.04	9.79±0.04
Survival (%)	SUR	85.0±0.66	79.5±0.88	79.8±0.63	88.9±0.56

RESULTS AND DISCUSSION

Overall means

Table 2 gives overall means for all traits calculated as the average of all plot means in each site. Slight differences can be observed between sites. In relation to growth traits, Cortegada is the best site whereas Lalín is the worst. Survival shows the opposite trend.

The proportion of polycyclic trees in the test sites was relatively high (in all sites, more than half of the trees showed two growth cycles in at least one year). The number of whorls (*WH*) was relatively high in all sites (Table 2), especially in AsNeves, with maximum individual data as high as 20, indicating that some years more than two growth cycles must have occurred. The high humidity and precipitation in these Atlantic sites may have favoured the ability to express polycyclic growth (ALIA *et al.* 1997).

Bad stem forms were observed with relatively high frequencies at all sites. *P. pinaster* has a remarkable tendency for sinuosity. The stem form in *P. pinaster* is influenced by the sensitivity to different external factors (wind, frost, etc) and the ability to straighten following a deviation from the vertical line (SIERRA DE GRADO *et al.* 1997). A long nursery period of the containerized seedlings may have led to root deformations and hence, to a bad anchorage at the field that may have increased the instability of the trees (CIFUENTES *et al.* 2001). Since 1999, many young *P. pinaster* plantations in Galicia have shown instability problems that have been associated with root deformities (CIFUENTES *et al.* 2001).

Heritability estimates

Growth traits

Growth traits showed significant ($p < 0.05$) family effects in all sites with the exception of diameter and volume in Bamio and Lalín (Table 3). Individual heritability for height ranged from 0.11 to 0.17, similar to those found by other authors (COTTERILL *et al.* 1987, KUSNANDAR *et al.* 1998) but lower than those found by KREMER and LASCoux (1988) in France at similar ages. Heritability for height was always higher than for diameter as observed by COTTERILL *et al.* (1987). Other authors have reported the opposite, i.e., higher genetic control of diameter (COSTA & DUREL 1996, KUSNANDAR *et al.* 1998). Diameter is more affected by microenvironment effects and competition between trees than height and could be under rather different genetic control (COSTA & DUREL 1996). The relatively low quality of the test sites may have influenced the diameter growth and thus, affected the estimates of heritabilities. In fact, the family effect was not significant for diameter in those sites with lower mean *DBH* (Table 2 and Table 3).

Survival

Survival showed no differences among families except in Cortegada (Table 3), which was the site with higher mortality (Table 2). Heritabilities were very low in all cases. Survival is a binomial variable with variance dependent on means, and thereby violates a fundamental requirement of variance analysis. The analyses based on plot means reduced but did not eliminate these

Table 3. Significance levels of family effect (F), individual (h_i^2) and family (h_f^2) heritabilities and their standard errors estimated at each site independently.

Trait ¹	AsNaves			Bamio			Cortegada			Lalin		
	F	h_i^2	h_f^2	F	h_i^2	h_f^2	F	h_i^2	h_f^2	F	h_i^2	h_f^2
HT	**	0.17±0.04	0.63±0.06	*	0.11±0.03	0.50±0.05	**	0.13±0.04	0.54±0.06	**	0.14±0.04	0.59±0.06
DBH	**	0.11±0.03	0.52±0.05		0.03±0.02	0.22±0.03	**	0.11±0.04	0.52±0.05		0.04±0.02	0.31±0.04
V	**	0.10±0.03	0.50±0.05		0.04±0.02	0.27±0.03	**	0.10±0.03	0.49±0.05		0.05±0.02	0.34±0.04
ΔH	***	0.23±0.04	0.71±0.07	***	0.27±0.05	0.71±0.08	***	0.21±0.05	0.67±0.08	***	0.26±0.05	0.74±0.08
STR	***	0.13±0.03	0.56±0.05	*	0.10±0.03	0.46±0.04	**	0.09±0.03	0.45±0.05		0.04±0.02	0.28±0.03
FOR	**	0.09±0.03	0.46±0.04		0.05±0.02	0.30±0.04		0.03±0.02	0.21±0.03	**	0.08±0.03	0.45±0.04
LEN	*	0.07±0.02	0.40±0.04	**	0.11±0.03	0.48±0.05	**	0.10±0.03	0.48±0.05	**	0.09±0.03	0.48±0.05
BRN	*	0.05±0.02	0.34±0.04	**	0.10±0.03	0.47±0.05		0.04±0.02	0.26±0.04	*	0.05±0.02	0.32±0.04
BRD		0.03±0.02	0.23±0.03		0.05±0.02	0.31±0.04	**	0.08±0.03	0.43±0.05		0.00±0.02	0.00±0.02
ANG	***	0.15±0.04	0.61±0.06	***	0.22±0.05	0.66±0.07	***	0.13±0.04	0.55±0.06	**	0.09±0.03	0.47±0.05
WH	***	0.31±0.06	0.77±0.09	***	0.29±0.05	0.73±0.08	***	0.28±0.06	0.73±0.09	***	0.37±0.07	0.81±0.11
SUR		0.03±0.02	0.24±0.03		0.04±0.02	0.26±0.03	0	0.04±0.02	0.25±0.04		0.03±0.02	0.22±0.03

¹ See Table 2 for codification of variables. Significance levels: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

problems, and neither improvement was obtained by transforming the dependent variable. Adjusted individual heritabilities for survival (DEMPSTER & LERNER 1950) were relatively higher than those estimated in Table 3 but remained low (around 0.07 for all sites).

Stem form traits

Significant family effects were observed for stem form traits (*STR*, *LEN*, *FOR*) in some sites (Table 3) and in all sites together (Table 4). However, individual heritabilities were low in all cases. Improving straightness is one of the principal goals of maritime pine breeding programs (BUTCHER & HOPKINS 1993, SIERRA DE GRADO *et al.* 1997, POT *et al.* 2002). However, in our case, little genetic gain can be expected through individual selection on these traits. Similar results have been reported in other breeding programs (COTTERILL *et al.* 1987, HOPKINS & BUTCHER 1994). However, reports on the genetic control of the stem straightness show great variability (SIERRA DE GRADO *et al.* 1997) and some authors have reported high heritabilities for *P. pinaster* (SIERRA DE GRADO *et al.* 1997). Differences in age, material and environments among these studies may be influencing but, the method used to evaluate the stem straightness is probably the most critical factor affecting the genetic parameter estimates (COTTERILL *et al.* 1987, RAYMOND & COTTERILL 1990, SIERRA DE GRADO *et al.* 1997). Nevertheless, the moderate family heritability estimates for all the three stem form traits (Table 3, Table 4) suggests that family selection can be considered and genetic gain can be expected through roguing the clonal seed orchard or through selective seeds harvesting.

Leaning is a trait closely related to straightness and both traits are difficult to evaluate independently (Table 5). A leaning tree (motivated for example by a poor root system and a wind episode) may be more likely to cause curvatures in the stem because of its trend to reorientation to the vertical position. Some authors evaluate straightness as the departure from the vertical (*e.g.* POT *et al.* 2002) equivalent to our leaning index definition (GALERA *et al.* 1997). However, straightness (sinuosity) and leaning may be controlled by different genes and their man

Table 4. Significance levels of fixed effects, variance components of random effects and estimates of individual and family heritabilities and their standard errors for all sites together.

Trait ¹	Fixed effect	Variance components (%)				Heritabilities	
		S	σ_f^2	σ_{sf}^2	$\sigma_{b(s)}^2$	σ_e^2	h_i^2
HT	***	2.23***	1.40*	47.6***	48.8	0.09±0.02	0.69±0.05
DBH	***	1.51**	1.15*	40.0***	57.4	0.05±0.01	0.57±0.03
V	**	1.07*	1.37*	46.1***	51.5	0.04±0.01	0.49±0.03
ΔH	***	7.29***	2.83***	28.5***	61.4	0.17±0.03	0.80±0.08
STR	***	2.53**	3.12**	13.2***	81.1	0.04±0.01	0.53±0.03
FOR	***	3.14***	0.99	11.6***	84.3	0.04±0.01	0.59±0.03
LEN	***	3.24***	1.67*	19.5***	75.5	0.06±0.01	0.64±0.04
BRN	***	4.01***	0.37	4.07***	91.6	0.05±0.01	0.65±0.03
BRD	***	2.74***	0.04	17.1***	80.1	0.05±0.01	0.66±0.03
ANG	***	8.49***	1.55	5.07***	84.9	0.13±0.02	0.80±0.06
WH	*	9.92***	5.23***	19.5***	65.4	0.20±0.03	0.80±0.09
SUR	**	0.05	2.75**	10.2***	87.0	0.00±0.00	0.02±0.01

¹ See Table 2 for codification of variables. Significance levels: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

agement as a pool may lead to confusing results (SIERRA DE GRADO *et al.* 1997). Nevertheless, as in the case of straightness, leaning showed low individual heritabilities but moderate to high family heritabilities (Table 3, Table 4) suggesting a high gain in this trait through family selection.

Forking (*FOR*) showed significant ($p < 0.05$) family effects in only two sites, with low individual heritabilities in all cases (Table 3 and Table 4). To assess the forking score we have used an unusual score (GALERA *et al.* 1997) which give worse values to forks in the lower part of the stem because of its higher economic value. In order to compare with published data, a binomial trait was determined for each assessed tree (0 = no fork, 1 = forked). Heritability of this trait was estimated based on raw tree data and then transformed following the methodology described for binomial data (DEMPSTER & LERNER 1950). The adjusted heritabilities for this binomial trait were clearly higher than those presented in Table 3 and Table 4, and ranged from 0.10 to 0.22, indicating that this trait may be subject to individual selection. These values were near those found by DIETERS (1996) in Slash pine (*Pinus elliottii*) and clearly higher than those found by COTTERILL and ZED (1980) and RAYMOND and COTTERILL (1990) for radiata pine. However, as pointed out by DIETERS (1996), in the radiata experiments referred above, heritability estimates were not transformed to the underlying scale and, hence, the reported values were influenced by the incidence of the trait.

Branch traits

Branch size, angle, number and distribution are other major factors in determining the quality of the

resultant timber (BUTCHER & HOPKINS 1993). In the present study the branch angle and the number of whorls showed a high genetic control with moderate individual and high family heritabilities (Table 3, Table 4). Conversely the number of branches and the diameter of the thickest branch showed lower levels of heritabilities. Polycyclism has been shown to be under strong genetic control in *P. pinaster* (KREMER 1981, KREMER & LASCoux 1988, ALIA *et al.* 1997). The ability to express a second growth and the length of this second shoot are the usual traits used to assess polycyclism (KREMER & LASCoux 1988). Frequency of polycyclic trees has been shown to be more heritable than the length of the second growth (KREMER 1981, KREMER & LASCoux 1988). In order to compare with these studies, the ability to express a second growth at least once was determined by a binomial trait that was set to one if the number of whorls exceeded 9. The heritability of this trait, (estimated on a raw tree data basis and transformed as described before (DEMPSTER & LERNER 1950)) ranged between 0.15 and 0.32, slightly lower than those found by KREMER and LASCoux (1988) for single year estimations. In our case, the total number of whorls seems to be a better way to assess the polycyclism because of its higher heritability and easy measurement.

The branch angle was also moderately heritable (Table 3, Table 4) as observed previously in *Pinus pinaster* (BUTCHER & HOPKINS 1993). RAYMOND and COTTERILL (1990) suggest a 1–6 scale to assess both diameter and angle of branches. Here, we have initially used a 1–3 scale to assess branch angle but it was seen that more scores can be easily distinguished so intermediate scores (1.5 and 2.5) were allowed.

Table 5. Genetic correlations and their standard errors (above diagonal) and phenotypic correlation (below diagonal, $N = 3372$) between traits.

	Growth traits					Stem form traits					Branching traits				
	HT	DBH	V	ΔH	STR	FOR	LEN	BRN	BRD	ANG	WH	SUR			
Growth	HT	0.59	0.85	0.48	0.35 (0.12)	0.08 (0.14)	0.31 (0.12)	0.02 (0.13)	-0.18 (0.13)	0.09 (0.12)	0.21 (0.11)	0.52 (0.54)			
	DB	(0.09)	(0.04)	(0.09)	0.35 (0.13)	0.50 (0.11)	0.36 (0.13)	0.23 (0.14)	0.28 (0.14)	-0.13 (0.13)	0.21 (0.12)	1.00 (0.00)			
	H	0.90	0.95	0.23	0.39 (0.14)	0.38 (0.14)	0.36 (0.13)	0.21 (0.15)	0.03 (0.16)	-0.21 (0.13)	0.20 (0.13)	1.85 (2.06)			
	V	0.73	(0.02)	(0.12)	0.47 (0.10)	0.00 (0.13)	0.37 (0.11)	0.04 (0.12)	0.10 (0.12)	-0.28 (0.10)	-0.76 (0.04)	-0.03 (0.68)			
	ΔH	0.55	0.58	(0.11)											
Stem form	STR	-0.04	0.04	-0.05	0.18 (0.15)	0.91 (0.02)	0.24 (0.14)	0.14 (0.15)	-0.07 (0.13)	-0.26 (0.12)	0.49 (0.62)				
	FOR	0.32	0.35	0.19	0.03	0.24 (0.14)	-0.53 (0.11)	0.42 (0.12)	0.40 (0.11)	0.09 (0.13)	-0.82 (0.27)				
	LEN	-0.04	-0.07	-0.01	0.36	0.01	0.06 (0.14)	0.08 (0.14)	0.21 (0.12)	-0.17 (0.12)	-2.43 (3.80)				
Branching	BRN	0.15	0.13	0.16	-0.09	0.01	0.04	0.17 (0.14)	-0.29 (0.12)	-0.04 (0.12)	0.73 (0.37)				
	BRD	0.48	0.64	0.35	0.20	0.29	-0.15	-0.04	-0.01 (0.13)	-0.22 (0.12)	2.26 (3.28)				
	AN	0.06	0.08	0.07	0.10	-0.01	-0.06	0.19	0.24 (0.10)	0.70 (0.36)					
	G	0.50	0.56	-0.21	0.00	0.18	-0.03	0.23	0.01		0.51 (0.50)				
	WH														
Survival	SUR	-0.04	-0.07	-0.03	-0.09	-0.02	-0.01	-0.04	-0.12	0.02	-0.01				

The number of branches (*BRN*) and the diameter of the thickest branch (*BRD*) were under low genetic control and showed low individual heritabilities (Table 3, Table 4). We observed a high variability both within and between whorls (data not presented) and thus, the number of branches in one whorl and the diameter of the thickest branch may be not good indicators of the branch number and the branch size of the tree as a whole. Another problem is the relation between the stem diameter (*DBH*) and the branch diameter (Table 5): thickest trees have thickest branches and viceversa, so the absolute value of the branch diameter may not reflect the relative importance of knots in the timber quality. The ratio *BRD/DBH* may be a better indicative of this relative importance. Individual heritability of this trait range from 0.00 to 0.14 (data not presented) for single-site analyses and was 0.06 ± 0.02 for the joint analyses. Branch size and number should be further investigated and the low heritabilities of these characteristics should be confirmed with other assessment protocols such as a 6 point score as suggested by RAYMOND and COTTERILL (1990).

Family heritabilities for growth, form and branch traits were of much greater magnitude than individual heritabilities (Table 3, Table 4) reflecting the greater reliability of progeny performance as a guide to the breeding value of an individual. From the results presented in this paper it is clear that significant gains can be expected from family selection for almost all the traits studied. However, as COTTERILL and ZED (1980) pointed out, it would be wrong to conclude that progeny selection should always be preferred to individual selection. Absolute responses from family selection cannot be expected to be substantially greater than those from individual selection until individual heritabilities fall below 0.20 (FALCONER 1989) or even lower values if response per unit of time is considered. Therefore, total height, average internode length, number of whorls and branch angle should respond probably better to individual selection.

Individual heritabilities for each trait were relatively consistent across sites (Table 3) but values estimated from single-site analyses were generally higher than those obtained from the joint analyses (Table 4). These discrepancies can be explained because heritability

ty estimates from the single-site analyses may be biased due to the unidentified genotype \times environment interaction. $G \times E$ interaction reduced the genetic variance component in the joint analyses and thus, reduced heritability estimates. The analysis of the $G \times E$ interaction across the test sites will be presented elsewhere.

Genetic correlations

Genetic and phenotypic correlations are presented in Table 5. As observed elsewhere (e.g. COTTERILL *et al.* 1987) strong genetic and phenotypic correlation can be observed between all the growth traits indicating that selection in one trait would lead to a strong and positive response in the others.

Stem form traits were positively genetically correlated with growth. It must be noted that positive correlations here should be interpreted as unfavourable because stem form scores are higher for the worse forms. Reports on the genetic correlation between growth and stem forms show great variability. In other *Pinus pinaster* Atlantic provenances negative (unfavourable) genetic correlations between stem form and growth are common (BUTCHER & HOPKINS 1993, POT *et al.* 2002) but positive correlations (favourable) were also observed (COTTERILL *et al.* 1987). The results of the present study suggest that simultaneous improvements probably cannot be achieved for growth and stem form traits using multi-trait selection. Selections based on individual traits and crossing the two resulting lines may be a good alternative for further breeding.

As discussed previously, straightness and leaning were strongly correlated (Table 5). The high phenotypic correlation between both traits reflects the difficulty of an independent evaluation. As COTTERILL and ZED (1980) pointed out, operators may tend to assign a score which reflects an intermediate of both traits. Because of this and due the equivalent genetic pattern of these traits it is suggested that in future measurements both traits can be assessed as a whole.

Genetic correlations between survival and other traits must be handled with care because of the low family heritabilities for survival (Table 4). In fact, estimates of genetic correlations for this trait exceeded in some cases the theoretical range (-1 to 1) and showed high standard errors.

The relationship between branch size and growth traits (Table 5) has been mentioned before. HARFOUCHE *et al.* (1995) found height to be negatively correlated with branch diameter in *P. pinaster*. However, it is possible that the subjective assessment methods have scored large trees more critically than small trees (DIETERS 1996). In our case, branch number and size should be further studied because the assessed traits did

not reflect well the real number and size of the tree as a whole.

Another interesting relation is that between the number of whorls and the growth traits which showed moderate positive genetic and phenotypic correlation (Table 5). Polycyclic trees tend to grow more than monocyclic trees and thus selection for both growth and polycyclic pattern is not practical. Positive relationship between polycyclism and growth has been observed previously in *P. pinaster* (KREMER 1981). The average length of the internodes (ΔH), which integrates both growth and polycyclic pattern, appears to be an interesting trait for breeding purposes. It showed positive genetic correlation with growth traits and negative with the number of branch whorls (Table 5). Furthermore, the heritability of this trait was higher than that for growth traits (Table 4, Table 5).

All these unfavourable correlations should be considered when roguing the seed orchards or in individual selections within the progeny tests. Appropriate selection indices should consider the relative economic importance, the heritability and the genetic and phenotypic correlations between the different characters. The analysis of the specific combining ability between the best clones for different traits (growth, form and polycyclism) would be desirable for further breeding purposes.

CONCLUSIONS

1. Total height, average internode length, number of whorls and branch angle were the most interesting traits for breeding in this Galician *Pinus pinaster* population. All these traits may be subject to individual selection, although expected gains would be modest. Diameter, volume, stem straightness, stem leaning and forking would respond to family selection.

2. Stem form traits were unfavourably correlated with growth traits indicating that selection for both characteristics is not easy in this *Pinus pinaster* population. Polycyclism and growth were also unfavourably correlated.

3. The average length of the internodes (ΔH) was shown to be a good selection parameter. It combines both polycyclism pattern and growth and showed moderate individual heritability (0.21–0.27).

ACKNOWLEDGEMENTS

This study was supported by the INIA project RTA2-109. The series of trials was established by the co-ordination of G. Vega. Nursery and plantation was under the supervision of

Mariano Arnedo. We thank Ricardo Ferradás, Agustín Quintairós, Sonia Queimadelos, Marisa Blanco, Pilar Soto and Maribel Juncal of the C.I.F.A. Lourizán and the students David Díaz, Elías Cabrera and Marga García for field assessment.

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