GENETIC PARAMETER ESTIMATES FOR *PINUS RADIATA* IN BASQUE COUNTRY, NORTHERN SPAIN

S. ESPINEL and A. ARAGONÉS

CIMA,
Apartado 46, Vitoria-Gasteiz, 01080 Spain

(Received for publication 27 February 1997; revision 7 November 1997)

ABSTRACT

Genetic parameters were estimated for growth and form traits in a 7-year-old progeny trial containing 28 open-pollinated families of *Pinus radiata* D.Don selected for the Basque Country breeding programme of the species. Observed individual heritabilities were moderate for height ($\hat{h}^2 = 0.20$), stem diameter ($\hat{h}^2 = 0.22$), branch size ($\hat{h}^2 = 0.14$), and branch angle ($\hat{h}^2 = 0.15$) and negligible for stem straightness. Stem diameter, height, and branch angle were positively correlated. Branch size had an adverse genetic correlation with growth traits. Genetic gains under index selection strategies were examined. Results from this small-scale trial suggest that is not possible to achieve simultaneous improvements in both growth and branch size.

Keywords: heritability; genetic correlation; growth; form traits; *Pinus radiata.*

INTRODUCTION

Pinus radiata was introduced in the Basque Country (northern Spain) at the end of the last century, and now occupies 162 000 ha distributed mainly in the coastal area of the region. Recent studies of field performance of natural provenances and of the local population (Espinel *et al.* 1995) as well as data from RAPD analysis (Aragonés *et al.* 1997) have demonstrated that the local population descends most probably from the Año Nuevo provenance. Genetic improvement of *P. radiata* has been undertaken by the CIMA (Centro de Investigación y Mejora Agraria) Department of Forestry since 1984. The breeding objectives were focused mainly on improving growth traits (height and diameter). Part of the breeding programme was supported by the Basque Forest Ownership Association.

Small private owners (owning 85% of the forested area of the species) have opted for "traditional management regimes". This approach involves control over branch size through management of stand density, facilitated by the integration of smallwood marketing into the management system, and an average final-crop tree diameter of 40 cm in a rotation of 35 years. However, in the last few years there has been a substantial swing towards adoption of intensive regimes for new plantings based on New Zealand schedules (Sutton 1984).

New Zealand Journal of Forestry Science 27(3): 272–279 (1997)

Knowledge of genetic parameters such as estimates of heritabilities and genetic correlations enables selection responses to be predicted and breeding strategies to be evaluated (Woolaston *et al.* 1990). The value of genetic parameters in applied and theoretical tree breeding has been well documented (Cotterill & Zed 1980; Shelbourne & Low 1980; Carson 1991; Hodge & White 1992). Reliable parameter estimates also facilitate the development of optimal selection indices and best linear prediction of breeding values (White & Hodge 1988).

The aim of this paper is to present estimates of a set of genetic parameters for growth and form traits of a 7-year-old *P. radiata* trial. The data were from progenies of 28 half-sib families.

MATERIAL AND METHODS

Trial Site and Design

The trial was established in November 1989 with 1/0 seedlings on a moderately fertile site near Luyando village in Basque Country, northern Spain (lat. 43° 07′ N, long. 3° 01′ W, alt. 230 m). The site previously supported *P. radiata* plantation. Preparation and silviculture were as usual: the cleared site was ploughed and ridged before planting and weeds were manually eliminated in the first 2 years. This region experiences a moderate temperate climate with an average annual rainfall of 1200 mm.

Progenies were grown in 1987 from open-pollinated seeds obtained from 28 clones in naturalised stands in the coastal area of the Basque Country. All parent clones were selected for superior growth and form as part of a first-generation breeding population. Therefore, the genetic estimates determined from their progeny performance refer only to improved stock in this region (Cotterill & Zed 1980).

The design was a randomised complete block design with 31 replications of single-tree plots arranged in 4 × 7 blocks with 3 × 3 m spacing.

Measurements

After 7 years, survival was 92%. Of the surviving trees, 5% were discarded because of severe damage caused by snow.

All trees were measured for growth and form traits in September 1996 when the trial was 7 years from planting. Growth traits included total height (cm) measured with a pole, and diameter over bark (cm) at 1.3 m, measured with a calliper. Components of tree form were assessed visually following Raymond & Cotterill (1990) on a six-point scale: stem straightness, 1 = crooked to 6 = straight; branch diameter, with 1 = very thick branches to 6 = very thin branches; branch angle, 1 = steep branching to 6 = branches at a flat angle). The trees were assessed by the same team of two assessors. Before starting the assessment, the team walked around the trial arriving at a consensus about the subjective score for each tree.

Data Analysis

Statistical analysis

Individual tree data were analysed using PROC GLM in SAS (SAS Institute Inc. 1985) with the following random model:

$Yijk = m + fi + bj + eijk$
where $Yijk$ = value of the kth tree in the ith family, jth block.
m = experimental mean.
fi = effect of the ith half-sib family.
bj = effect of the jth block.
$eijk$ = error.

Variance components were estimated using SAS Varcomp Method Type 1 (Spector & Goodnight 1985).

Genetic parameters

The offspring of an open-pollinated family were assumed to be half-sib and therefore the individual heritabilities (h_i^2) were estimated as :
h_i^2 = additive variance / variance of individual phenotypes $= 4\sigma^2_f/(\sigma^2_f + \sigma^2_e)$
where σ^2_f = component of variance due to family
σ^2_e = component of variance due to within-plot error

Approximate standard errors of individual heritabilities (σ_h)were estimated according to Wright (1976):
$\sigma_h = (1-h_i^2/4)[1+(NB-1)h_i^2/4] / [(NB/2)(NB-1)(F-1)]^{1/2}$
being: h_i^2 = heritability
N = number of trees per plot
B = number of replications
F = number of families

Family-mean heritabilities were estimated as (Johnson & Burdon 1990):
$h_{fm} = \sigma_f/[\sigma^2_f + \sigma^2_e/k]$
where k is the harmonic mean of trees per family.

Genetic correlations were calculated from estimates of additive genetic variances and covariances (Falconer 1989) using the option MANOVA in the GLM procedure of SAS:
$r_g = cov(x,y) /\sigma_x*\sigma_y$
where cov(x,y) is the family covariance component between traits x and y, and σ_x,σ_y are the square root of family variance components for the two traits respectively. Approximate standard errors of the genetic correlations were calculated according to Falconer (1989, Equation 19.4).

Phenotypic correlations were estimated as correlation coefficients.

Index selection

Selection indices were used to select plus-trees from existing progeny test populations and to predict the genetic gains that could be expected from this index selection (Dean *et al.* 1983).

Height, diameter, and branch size were combined in the linear equation:
$I = b_1P_1 + b_2P_2 + b_3P_3$
where I is the index, b_i values are the index coefficients, and P_1, P_2, and P_3 the phenotypic values of individual trees at 7 years for height, diameter, and branch size. The *b* coefficients were calculated solving the set of equations described by Falconer (1989) :

$$b^*P = G^*a$$

where G and P are the genetic and phenotypic variance-covariance matrices, and *a* is the column vector of economic weights (the relative economic values assigned to each trait by the breeder).

Two sets of economic weights have been used for the index construction. The first set was based on *equal emphasis weighting* (Cotterill & Jackson 1985) which is defined as the inverse of the phenotypic standard deviation of the trait. The second set involved more realistic economic weights for the traits nowadays in Basque Country, giving diameter twice the importance of height and four times that of branch size (i.e., $a1 = 1$, $a2 = 2$, and $a3 = 0.5$ for height, diameter, and branch size respectively). Stem straightness was not included in the index. Branch angle is considered of little economic value in the Basque Country, so this trait has been omitted from index selection.

Expected gains for these traits were calculated following Falconer (1989) with two individual selection intensities, one in every 100 and five in every 100, giving selection indices of $i = 2.06$ and $i = 2.66$ (Zobel & Talbert 1984).

RESULTS AND DISCUSSION

Overall means and their standard deviations for all trees are given in Table 1. Mean square of variance of traits are shown in Table 2 and individual and family heritabilities (with their standard errors) in Table 3. Phenotypic and genotypic correlations (with standard errors) are presented in Table 4.

Differences among families were statistically significant for all traits investigated except for stem straightness (*see* Table 2). Average tree heights ranged between 8.7 m for the best

TABLE 1–Overall means and standard deviations of traits of individual trees measured in the 7-year-old progeny test of *Pinus radiata* in Luyando.

Trait	Mean ± s.d.
Height (m)	7.85 ± 1.18
Diameter (cm)	10.96 ± 2.32
Stem straightness (1–6 score)	4.58 ± 1.26
Branch size (1–6 score)	3.69 ± 0.99
Branch angle (1–6 score)	4.21 ± 0.85

TABLE 2–Family, block, and residual mean squares for the analysis of variance of five traits measured in the Luyando progeny test.

Source of var.	d.f.	Height	Diameter	Stem str. score	Branch size score	Branch angle score
Family	27	2.773 **	11.145 **	1.786 ns	1.586 *	1.346 *
Block	30	6.111 **	26.416 *	2.782 *	4.349 **	1.317 *
Error	700	1.146	4.328	1.534	0.903	0.819

* significant at 1% level
** significant at 0.01% level
ns not significant

TABLE 3—Individual and family heritabilities and their standard errors for the traits measured in the Luyando progeny test.

Trait	Individual	Family
Height	0.200 ± 0.085	0.588 ± 0.117
Diameter	0.221 ± 0.089	0.613 ± 0.123
Stem straightness	0.024 ± 0.041	0.142 ± 0.060
Branch size	0.137 ± 0.069	0.489 ± 0.097
Branch angle	0.145 ± 0.072	0.505 ± 0.101

TABLE 4—Genotypic correlations with standard errors (above the diagonal) and phenotypic correlations (below the diagonal) for all traits in the Luyando progeny test.

Trait	Height	Diameter	Branch size score	Branch angle score
Height		0.79±0.15	–0.49±0.25	0.39±0.28
Diameter	0.73		–0.89±0.07	0.13±0.30
Branch size score	–0.23	–0.52		0.07±0.35
Branch angle score	0.11	–0.09	0.48	

family and 7.3 m for the worst one; in a similar fashion values for diameter, stem straightness, branch size, and branch angle varied between 12.5 and 9.8 cm, 5.0 and 4.1 (score), 4.2 and 3.3 (score), and 4.6 and 3.8 (score) respectively.

Individual heritabilities of growth traits were low to moderate with low standard errors. Values ranged from $h^2 = 0.20 \pm 0.085$ for height to $h^2 = 0.221 \pm 0.089$ for diameter (Table 3). These results are consistent with other studies of *P. radiata*. The values estimated by Dean *et al.* (1983) for two sites with trees of similar age in Eastern Victoria were 0.16 for height and 0.23 for diameter. Cotteril & Zed (1980) observed a range of 0.18–0.45 and 0.07–0.39 respectively for four sites in South Australia, and Burdon (1992) gave 0.2 for height and 0.1–0.3 for stem diameter. These heritabilities suggest that substantial genetic gains should follow individual selections for growth traits in Basque Country.

Stem straightness had no detectable genetic variation among trees. There are two possible explanations for this finding, but the most likely would be a combination of both. One reason could be a deficiency in trait estimation by the two operators, although the distribution of the scores was approximately normal and the complete range of the six-point score was used. Alternatively, the heavy snow fall in Luyando during 1996 badly knocked down bent trees (approximately 5% of the total trees). This is a very frequent phenomenon in the winters of Basque Country at altitudes over 200 m, apparently masking genetic variation in stem straightness, at least in Luyando trials. In another 5-year progeny trial sited in the coastal downland (less than 125 m altitude) more genetic variation in stem straightness was found, with a heritability estimate of 0.13 for the trait (Espinel & Aragonés 1997).

The other form traits presented moderate to low individual heritabilities with values of $h^2 = 0.135 \pm 0.069$ for branch size score and $h^2 = 0.145 \pm 0.072$ for branch angle score. These results are lower that those (0.30 and 0.34 respectively) found by Raymond & Cotterill

(1990) and (0.2 for branch size) by Burdon (1992) but closer to those cited by Dean *et al.* (1983) and Cotterill & Zed (1980) for branch quality (including both traits together)—0.18 for the first authors and 0.21 for the second.

Strong genetic (r_a= 0.79±0.15) and phenotypic (r_p= 0.73) correlations were found between height and stem diameters with relatively low standard error (Table 4). Selection in one trait would lead to a strong and positive response in the other.

Branch size had a strong adverse genetic correlation with both height and diameter (r_a = –0.49±0.25 and r_a = –0.89±0.07 respectively). Its phenotypic correlation was also negative with height (r_p = –0.23) and strongly negative with diameter (r_p = –0.51). These genetic correlations suggest that selection for both growth characteristics and fine branching patterns is not feasible in the *P. radiata* population of the Basque Country. Low positive genetic correlation was found for branch angle and growth traits and no correlation between branch angle and branch size (r_a = 0.07±0.35), suggesting little genetic relationship among traits but a moderate phenotypic effect.

Gains Expected from Index Selection

Relatively large gains in growth traits, especially with 1% selection, were at the cost of increased branch size in all examples studied here. With the second set of economic weights and 1% selection in the units measured at age 7, it could be possible to achieve 8.8% and 11.6% gains for height and diameter respectively (Table 5) but at a reduction of 9.8% in branch size scores.

Results obtained in this small-scale trial in northern Spain show that for juvenile *P. radiata* moderate genetic gains would be expected for the second selection generation in height and stem diameter. These results agree with breeding programmes carried out in Australia and New Zealand (Dean *et al.* 1983; Johnson & Burdon 1990). However, a strong adverse genetic association was found between growth traits and branch diameter, and so simultaneous improvements probably cannot be achieved for growth and branch size using multi-trait selection. Obviously, it is necessary to confirm and extend the results with more trials already established in Basque Country to ensure the selection patterns and the possible

TABLE 5–Percentage expected genetic gains from index selection in *Pinus radiata* in Basque Country (northern Spain) with varying economic weights for height, diameter, and branch size. The calculations are for individual selection of superior trees at intensities of five trees in every 100 (5%, i = 2.06) and one tree in every 100 (1%, i = 2.66). Gains are expressed in units of measurement and as percentage change in trait means (in parentheses).

Economic weight			Expected gains					
Height	Diameter	Branch size score	5% selection			1% selection		
			Height (m)	Diam. (cm)	Branch size score	Height (m)	Diam. (cm)	Branch size score
0.76	0.47	1.09	0.55 (7.0)	0.82 (7.5)	–0.19 (–5.1)	0.72 (9.2)	1.06 (9.7)	–0.25 (–6.8)
1	2	0.5	0.50 (6.4)	0.98 (8.9)	–0.28 (–7.5)	0.68 (8.8)	1.27 (11.6)	–0.36 (–9.8)

genotype-environment interaction, taking into account the different soil types present in Basque Country. Although Matheson & Raymond (1984) and Carson (1991) reported two studies in Australia and New Zealand respectively where no coherent pattern of genotype-environment interaction was evident for *P. radiata*, other authors obtained indications of a much more coherent pattern for the same species (Johnson & Burdon 1990).

ACKNOWLEDGEMENTS

We are grateful to Dr Ricardo Alía for his helpful comments on the manuscript and to Enrique Barrena for linguistic advice and critical review.

REFERENCES

ARAGONÉS, A.; BARRENA, I.; ESPINEL, S.; HERRAN, A.; RITTER, E. 1997: Origin of Basque populations of radiata pine inferred from RAPD data. *Annales des Sciences Forestières 54(8)*: 697–703.

BURDON, R.D. 1992: Genetic survey of *Pinus radiata*. 9: General discussion and implications for genetic management. *New Zealand Journal of Forestry Science 22(2/3)*: 274–298.

CARSON, S.D. 1991: Genotype × environment interaction and optimal number of progeny test sites for improving *Pinus radiata* in New Zealand. *New Zealand Journal of Forestry Science* 21(1): 32–49.

COTTERILL, P.P.; JACKSON, N. 1985: On index selection. I. Methods of determining economic weight. *Silvae Genetica 34(2–3)*: 56–63.

COTTERILL, P.P.; ZED, P.G. 1980: Estimates of genetic parameters for growth and form traits in four *Pinus radiata* D.Don progeny tests in South Australia. *Australian Forest Research 10*: 155–167.

DEAN, C.A.; COTTERILL, P.P.; CAMERON, J.N. 1983: Genetic parameters and gains expected from multiple trait selection of radiata pine in Eastern Victoria. *Australian Forest Research 13*: 271–278.

ESPINEL, S.; ARAGONÉS, A. 1997: Estado actual de la mejora genética de *Pinus radiata* D.Don en el País Vasco. *Actas del II Congreso Forestal Español 3*: 195–200.

ESPINEL, S.; ARAGONÉS, A.; RITTER, E. 1995: Performance of different provenances and of the local population of the Monterey pine (*Pinus radiata* D. Don) in northern Spain. *Annales des Sciences Forestière 52*: 515–519.

FALCONER, D.S. 1989: "Introduction to Quantitative Genetics". 3rd edition. Longman Harlow, United Kingdom.

HODGE, G.R.; WHITE, T.L. 1992: Genetic parameter estimates for growth traits at different ages in slash pine and some implications for breeding. *Silvae Genetica 41(4–5)*: 252–262.

JOHNSON, G.R.; BURDON, R.D. 1990: Family-site interaction in *Pinus radiata*: Implications for progeny testing strategy and regionalised breeding in New Zealand. *Silvae Genetica 39*: 55–62.

MATHESON, A.C.; RAYMOND C.A. 1984: The impact of genotype × environment interactions on Australian *Pinus radiata* breeding programmes. *Australian Forest Research 14*: 11–25.

RAYMOND, C.A.; COTTERILL, P.P. 1990: Methods of assessing crown form of *Pinus radiata*. *Silvae Genetica 39(2)*: 67–71.

SAS INSTITUTE 1985: "SAS User's Guide: Statistics". Version 5 edition. SAS institute Inc. Box 8000, Cary, NC 27511-8000.

SHELBOURNE, C.J.A.; LOW, C.B. 1980: Multi-trait index selection and associated genetic gains of *Pinus radiata* at five sites. *New Zealand Journal of Forestry Science 10*: 307–324.

SPECTOR, P.C.; GOODNIGHT, J.H. 1985: The VARCOMP procedure. *In* "SAS User's Guide: Basic". Version 5 edition. SAS Institute Inc. Cary, N.C.

SUTTON, W.R.J. 1984: New Zealand experience with radiata pine. 34th H.R.McMillan Lecture, February, University of British Columbia, Vancouver.

WHITE, T.L.; HODGE, G.R. 1988: Best linear prediction of breeding values in a forest tree improvement program. *Theoretical and Applied Genetics 76*: 719–727.

WOOLASTON, R.R.; KANOWSKI, P.J.; NIKLES, D.G. 1990: Genetic parameter estimates for *Pinus caribaea* var. *hondurensis* in coastal Queensland, Australia. *Silvae Genetica 39(1)*: 22–28.

WRIGHT, J.W. 1976: "Introduction to Forest Genetics". Academic Press, Inc. New York.

ZOBEL, B.; TALBERT, J. 1984: "Applied Forest Tree Improvement". John Wiley & Sons, Inc. New York. 505 p.