for both stem form (14% to 9%; *Table 3*) and branch size 25% to 10%; *Table 3*).

Neither of the selection strategies studied here were expected to lead to a deterioration in any of the traits considered. This result is surprising given the fact that there was an adverse association between growth and branch size. For example, DEAN *et al.* (1983) and DEAN *et al.* (1986) have found that it is not possible to simultaneously improve two adversely associated traits in one population. In this case, however, selection should be quite straightforward. *E. globulus* is being planted in Tasmania primarily for pulp and paper production, therefore, until more is known about wood quality traits, improvement in growth is likely to be the main concern of the breeding program, at least in the first generation. Since it appears that substantial improvements can be made in growth whilst suffering no deterioration in stem form or branch size such a strategy should be easily implemented.

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Genetic Parameter Estimates for Pinus caribaea var. hondurensis in Coastal Queensland, Australia

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Summary

Nineteen open pollinated progeny trials, comprising about 32 000 trees of *Pinus caribaea* var. *hondurensis* in Queensland, Australia, were assessed for growth and stem straightness at about five years after planting, and for windfirmness following cyclone damage. Mean weighted narrow-sense heritabilities on an individual tree basis were 0.30 for diameter, 0.20 for height, 0.24 for straightness, and 0.08 for windfirmness. The magnitudes of heritability estimates were independent of site quality. Mean weighted genetic correlations were 0.82 between diameter and height, 0.21 between diameter and straightness, −0.15 between height and straightness, and 0.21, −0.10 and 0.18 between windfirmness and each of diameter, height and straightness, respectively. Selection for volume should not adversely affect windfirmness, which might best be improved by selection on family mean values at wind damaged sites.

Key words: Pinus caribaea, heritability, genetic correlation, growth, stem straightness, windfirmness.

Introduction

Genetic improvement of *Pinus caribaea* MORELET var. *hondurensis* BARRETT and GOLFARI (Pch) in Queensland, Australia, has been undertaken by the Queensland Department of Forestry (QDF) since the early 1960s. In the past decade, Pch has become the exotic plantation species of greatest importance in Queensland, with annual plantings currently approximating 4 500 ha. Some 40 000 ha, concentrated in three discrete coastal regions around latitudes 18° S, 22° S and 27° S, were established by 1987 (Queensland Department of Forestry, 1987). Much greater areas of Pch have been planted elsewhere in the tropics. Reliable estimates are difficult to obtain: DAVIDSON (1988) estimated that 456500 ha were established by 1980, and NIKLES (1979) suggested an annual planting rate of about 90 000 ha. Trials in Queensland currently represent one of

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the major sources of genetic information for the species worldwide.

The Pch genetic improvement program in Queensland, summarized by Nikles (1973, 1984, 1986), has been based on the assumption that economically important traits were heritable. It has long been recognized that efficient advanced-generation improvement relies upon accurate estimates of heritabilities and genetic correlations. Knowledge of these genetic parameters enables selection responses to be predicted and breeding strategies to be evaluated. Reliable parameter estimates also facilitate the development of optimal selection indices and best linear prediction of breeding values (e.g. Cotterill and Dean, in press; White *et al.*, 1986). Experiments to determine these parameters for Pch in Queensland were first established in 1972, and estimates from them have been reported by Eisemann (1981), Dran *et al.* (1986) and Kanowski (1986). In both 1986 reports, the trials from which estimates were made are located at Cardwell, the northernmost major plantation region. Further estimates, based on subsequent trials of a much broader range of genetic material and sites, are reported in this paper.

Experience in Queensland has been that sites of higher growth rate provide better separation of family means (Eisemann and Nikles, 1983). The trials considered here also allow the opportunity to investigate the extent to which parameter estimates are influenced by site quality.

Materials and Methods

Genetic Material

The progeny trials from which parameters were estimated are part of the QDF Experiment 567 series, which involves a total of 210 open pollinated Pch families. In some cases, the seed was collected from ortets standing in natural forest or from superior trees selected in exotic plantations; in others, the seed was collected from grafted ramets in seed orchards or clone banks. These ramets were of superior trees selected in exotic plantations. For analytical purposes, the assumption was made that the members of individual families were, in all cases, half-sibs. This assumption should be reasonable for seed collected from ortets in exotic plantations and from ramets, but may be more tenuous for seed collected from ortets in natural stands. In any case, parameters derived under this assumption can be readily transformed to satisfy alternative assumptions (Cotterill and Zed, 1980).

Families in the experimental series may be classified by origin into eight populations of diverse origin, as detailed in *table 1*. For ease of management in the field, populations were allocated to the three sets identified in *table 1*. The sets were planted as separate, adjacent, trials at each site. Sets 1 and 3 each comprised four populations of families from ortet seed, and set 2 comprised two populations of families from ramet seed. Not all families were necessarily represented at each site.

Experimental Sites

Because of the latitudinal range of plantation establishment in Queensland and the consequent possibility of important genotype-environment interaction, and because of the risk of loss from cyclonic winds, QDF standard practice is to replicate progeny tests across regions. The Experiment 567 series was established in eight regions of coastal Queensland in 1980, ranging from latitudes 18° S to 27° S. Defining each set within each region as a separate trial, a total of 25 trials was established. Nineteen of these were sufficiently developed by 1985 to be included in analyses. Details of the trials are summarized in *table 2*.

Experimental Design

Each trial was established in a randomised complete block design. Blocks comprised six units, in each of which one tree of each entry was represented as a single tree plot. Alternatively, blocks may be considered as comprising non-contiguous plots of six trees of each entry.

Planting at the Glasshouse Ridge site was restricted to four blocks, for a total of 24 trees of each entry. At all other sites, eight blocks were established, for a total of 48 trees of each entry. Trees were planted at the then operational spacing of 3.0 m × 3.4 m; the trials were unthinned when assessed.

Trial Measurement and Assessment

The ages at which each trial was assessed for the relevant traits are detailed in table 3. Not all blocks of each trial were necessarily assessed on each occasion. The final pooled data set comprised about 32 000 trees across the 19 trials.

Although many traits were assessed, we have concentrated here on reporting parameters for growth and stem straightness at around five to six years after planting, and windfirmness following cyclone damage. Improvement of yield, straightness and windfirmness are the

Table 1. — Genetic material in the progeny trials.

Population	Seed source	Origin	Total number of families in set		
			1	2	3
1	ortet	Queensland plantations	37	-	25
2	ortet	Culmi, Honduras	18	-	-
3	ortet	Rus Rus, Honduras	9	-	-
4	ortet	Fijian and New Caledonian plantations	23	-	21
5	ramet	Queensland plantations	-	24	-
6	ramet	Congo plantations	-	24	-
7	ortet	Sikalanka, Honduras	-	-	10
8	ortet	Congo plantations	-	-	8

Table 2. — Details of selected progeny trials in the series.

Site name	Site abbreviation and set representation	Latitude and longitude	Elevation a.s.l. (m)	Annual rainfall (mm)	Establishment date
Cardwell Ridge	cr 1, 2, 3	18°15' S 145°55' E	20	2122	February 1980
Byfield Ridge	br 1, 2	22°50' S 150°45' E	50	1625	March 1980
Byfield Swamp	bs 1, 2	22°50' S 150°45' E	50	1625	March 1980
Wongi Swamp	ws 1, 2	25°27' S 152°35' E	35	986	March 1980
Tuan Swamp	ts 1	25°38' S 152°47' E	20	1393	March 1980
Toolara Ridge	tr 1, 2, 3	25°53' S 152°50' E	50	1369	April 1980
Glasshouse Swamp	gs 1, 2, 3	26°48' S 153°05' E	10	1590	July 1980
Glasshouse Ridge	gr 1, 2, 3	27°05' S 153°05' E	20	1537	May 1980

major objectives of the local breeding program. Stem diameter overbark at 1.3 m and height were measured by girth tape and height sticks, respectively. Straightness of the basal 6 m was assessed on a subjective five or seven point scale, as specified in *table 3*. The most crooked trees were scored as category one. Windfirmness, expressed as resistance to stem lean, was assessed subjectively on a four point scale. The most windblown trees were scored as category one.

Table 3. — Age (months) at assessment of the trials.

Trial	Diameter	Height	Straightness (no. of classes)	Windfirmness
br1	66	66	66 (5)	19
br2	68	68	68 (5)	19
bs1	66	66	66 (5)	
bs2	66	66	71 (5)	
cr1	74		74 (7)	74
cr2	74		74 (7)	74
cr3	74		74 (7)	74
gr1	56	56	57 (5)	
gr2	56	56	57 (5)	
gr3	56	56	57 (5)	
gs1	63	63	63 (7)	
gs2	63	63	63 (7)	
gs3	63	63	63 (7)	
tr1	62	62	63 (5)	39
tr2	62	62		
tr3	62	62		
ts1	78	78		
ws1	88	88	78 (7)	78
ws2	88	88	78 (7)	78

Statistical Methods

Preliminary analyses were carried out on the populations within each trial, as defined in *table 1*, using the method of least squares (Harvey, 1960). In the case of windfirmness data, and several other instances for populations 7 and 8, data sets were too small to yield reliable estimates and were not analysed separately, but were included in subsequent pooled analyses. The model fitted for each population is described by equation (1).

$$Y_{jkl} = \mu + f_j + b_k + (fb)_{jk} + e_{jkl} \qquad (1)$$

Where μ is the overall mean;
Y_{jkl} is the observation on stem 1 of family j in block k;
f_j is the effect of family j;
b_k is the effect of block k;
$(fb)_{jk}$ is the interaction of family j and block k;
e_{jkl} is the normally and independently distributed random deviation of stem 1 of family j in block k, with a mean of zero.

Variance components were estimated from the analyses of variance by equating the appropriate mean squares to the expectations shown in *table 4*. The k coefficients of the variance components, shown in *tables 4* and *5*, were computed using the direct approach of Harvey (1960). The model described by equation (1) was fitted to each population in each trial, and resultant mean squares were tested for homogeneity of variance using Bartlett's test (Snedecor and Cochran, 1981). Data from populations within each set were subsequently pooled, and re-analysed according to the model described by equation (2).

$$Y_{ijkl} = \mu + p_i + f_j + b_k + (pb)_{ik} + (fb)_{jk} + e_{ijkl} \qquad (2)$$

Where μ ist the overall mean;

Y_{ijkl} is the observation on stem l of family j within population i and in block k;
p_i is the effect of population i;
f_j is the effect of family j within population i;
b_k is the effect of block k;
$(pb)_{ik}$ is the interaction of population i and block k;
$(fb)_{ik}$ is the interaction of family j and block k;
e_{ijkl} is the normally and independently distributed random deviation of stem l of family j within population i and in block k, with a mean of zero.

The expectations of the relevant mean squares are shown in *table 5*. Variance components were estimated by equating the appropriate mean squares to the expectations shown in *table 5*.

As the progeny within each family were assumed to be half-sibs, narrow sense heritabilities on an individual tree basis (h^2) were estimated according to equation (3).

$$h^2 = 4\sigma^2_f / (\sigma^2_f + \sigma^2_{fb} + \sigma^2_e) \quad (3)$$

Note that the component σ^2_b does not appear in the denominator of equation (3), implying that the heritability estimates derived are appropriate to selection within blocks, or on block-adjusted data, as explained by Cotterill (1987). Standard errors were estimated according to Swiger *et al.* (1964). Genetic correlations were estimated from additive genetic variances and covariances according to Hazel *et al.* (1943), and the standard errors of these correlations according to Tallis (1959).

Weighted mean heritability estimates across sites were calculated following Cunningham *et al.* (1977), with each estimate weighted by the inverse of its variance as in equation (4).

$$\hat{h}^2 = \Sigma_i z_i h_i^2 \quad (4)$$

Where $z_i = (1/v_i)/\sum_i(1/v_i)$
h_i^2 is the ith heritability estimate
v_i is the variance of the ith estimate;

and the variance of the weighted mean heritability estimate,

$$\hat{v} = \Sigma_i z_i^2 v_i \quad (5)$$

Estimates of genetic correlations for each site were similarly pooled to derive weighted means.

Results

The overall means and standard deviations of diameter, height, straightness and windfirmness at each site, and the appropriate k values as defined in *table 5*, are presented in *table 6*. Mean annual increments of height and diameter in each trial were also calculated. Increments assume an initial diameter of zero and an initial height of 0.2 m.

In is apparent from *table 6* that families originating from ramet seed collected in clone banks and seed orchards (set 2) were, on average and almost universally, straighter and more vigorous than those originating from ortet seed (sets 1 and 3). This superiority is due to two factors. One is the superior genetic quality of the pollen cloud in clone banks and seed orchards. The other is that the ortets in exotic plantations, from which the ramets derive, were a generation advanced over those selected in natural stands.

Table 4. — Expected mean squares for analyses of variance and covariance of each population.

Source of variation	Degrees of freedom	Expected mean squares
Family	$f - 1$	$\sigma^2_e + k_2\sigma^2_{fb} + k_3\sigma^2_f$
Block	$b - 1$	Not relevant to parameter estimation
Family x block	$(f - 1)(b - 1)$	$\sigma^2_e + k_1\sigma^2_{fb}$
Within-plot error	$N - \Sigma_j\Sigma_k n_{jk}$	σ^2_e

Where σ^2_f is the variance component due to families
σ^2_{fb} is due to family × block interactions
σ^2_e is due to random error
f is the number of families
b is the number of blocks
N is the number of observations
n_{jk} is the number of trees of the jth family in the kth block
k_1, k_2 and k_3 are the appropriate coefficients as described by Harvey (1960)

Table 5. — Expected mean squares for analysis of variance and covariance of data pooled across populations.

Source of variation	Degrees of freedom	Expected mean squares
Population	$p - 1$	Not relevant to parameter estimation
Family within population	$f - p$	$\sigma^2_e + k_2\sigma^2_{fb} + k_3\sigma^2_f$
Block	$b - 1$	Not relevant to parameter estimation
Population x block	$(p - 1)(b - 1)$	Not relevant to parameter estimation
Family x block	$(f - p)(b - 1)$	$\sigma^2_e + k_1\sigma^2_{fb}$
Within-plot error	$N - \Sigma_j\Sigma_k n_{jk}$	σ^2_e

Where p is the number of populations and other terms are as defined in *Table 4*.

Table 6. — Average growth increments and overall means, associated standard deviations and k values for diameter (cm), height (m), straightness and windfirmness scores.

Trial	k coefficient k_1	k_2	k_3	Diameter (cm/month) mean	s.d.	increment	Height (m/month) mean	s.d.	increment	Straightness mean	s.d.	Windfirmness mean	s.d.
br1	4.66	4.86	18.79	14.4	2.1	0.218	9.7	1.2	0.144	2.1	0.9		
bs1	5.86	5.87	23.44	16.6	2.4	0.252	10.7	1.3	0.159	1.5	0.7		
cr1	4.89	5.06	29.50	17.3	3.3	0.234				3.4	1.3	3.9	0.3
gr1	5.73	5.78	22.99	13.7	2.0	0.245	8.0	1.1	0.139	1.9	0.7		
gs1	5.58	5.66	27.99	16.7	1.9	0.265	9.7	1.1	0.151	2.0	1.2		
tr1	5.66	5.71	28.33	14.1	1.8	0.227	9.4	1.0	0.148	1.1	0.3	3.8	0.4 *
ts1	5.93	5.97	47.44	15.0	3.0	0.192	9.7	1.9	0.122				
ws1	5.91	5.92	35.47	16.0	2.0	0.182	11.3	1.1	0.126	2.9	0.8	3.9	0.3
br2	5.04	5.20	20.34	14.5	2.7	0.213	9.9	1.5	0.143	2.5	0.9		
bs2	5.13	5.26	20.65	17.7	2.1	0.268	11.3	1.3	0.168	2.5	0.9		
cr2	4.60	4.85	27.73	17.9	3.9	0.242				3.6	1.3	4.0	0.2
gr2	5.86	5.89	23.48	15.1	2.1	0.268	8.7	1.2	0.152	2.2	0.9		
gs2	5.64	5.69	28.25	17.3	2.1	0.275	10.1	1.2	0.157	3.2	1.7		
tr2	5.87	5.90	47.01	13.9	2.2	0.224	9.1	1.2	0.144				
ws2	5.86	5.89	35.21	17.1	2.0	0.194	12.0	1.2	0.134	3.1	1.0	4.0	0.1
cr3	4.91	5.18	29.73	17.1	3.4	0.231				3.7	1.3	4.0	0.2
gr3	5.51	5.58	16.61	12.7	2.6	0.227	7.3	1.4	0.127	2.0	0.8		
gs3	5.22	5.40	26.26	16.7	2.3	0.265	9.5	1.3	0.148	2.8	1.6		
tr3	5.72	5.76	45.79	14.0	2.4	0.226	9.2	1.3	0.145				
Mean - set1#				15.4		0.243	9.0		0.146	2.4			
Mean - set2#				16.0		0.252	9.3		0.151	3.0			
Mean - set3#				15.2		0.237	8.7		0.140	2.8			

* k_1 = 5.84, k_2 = 5.86 and k_3 = 23.37 for windfirmness
\# means calculated for common sites only

Parameter Estimates

Preliminary analyses within each population, fitting the model described by Equation (1), involved about 170 analyses of variance; they, and parameter estimates from them, are available from the authors but not detailed here. Weighted mean parameter estimates for each population are presented in *table 7*. Weighted mean heritability estimates for diameter varied from 0.13 to 0.39; for height from 0.06 to 0.23; and for straightness from 0.06 to 0.34. Phenotypic correlations between diameter and height ranged from 0.60 to 0.76; between diameter and straightness from 0.12 to 0.37 and between straightness and height from 0.11 to 0.24. Genetic correlations were more variable, ranging from 0.41 to 0.82 between diameter and height; from −0.40 to 1.00 between diameter and straightness; and from −0.25 to 0.47 between straightness and height.

Detailed results of the pooled analyses of variance are also available from the authors. Heterogeneity of within-population variances was not found to be an important or consistent feature, indicating that pooling data within sites was a valid procedure. A possible exception occurred with straightness of the set 1 populations, where significant heterogeneity of between-family variance occurred at three of the seven sites. Straightness scores at these three sites showed positive kurtosis, a condition under which Bartlett's test is known to return erroneous judgements of heterogeneity (Snedecor and Cochran, 1981). For simplicity, we elected to pool the raw data and interpret the results with due caution. Heritability estimates and associated standard errors from the pooled analyses are presented in *table 8*, genetic correlations in *table 9*, and phenotypic correlations in *table 10*.

Weighted mean heritabilities from pooled analyses were 0.30 for diameter, 0.20 for height, 0.24 for straightness and 0.08 for windfirmness with estimates ranging between 0.17 and 0.72, 0.10 and 0.39, 0.16 and 0.41, and 0.03 and 0.13, respectively. Weighted mean genetic correlations were highly positive between diameter and height, moderately positive between diameter and straightness and moderately negative between height and straightness, with magnitudes of 0.82, 0.21 and −0.15, and ranges of 0.34 to 1.00, −0.39 to 0.46 and −0·33 and 0.28, respectively. Phenotypic correlations were similar to genetic correlations with the exception of those between height and straightness, where phenotypic correlations were positive in all cases with an average of 0.16. Genetic correlations involving windfirmness were 0.21 with diameter, −0.10 with height, and 0.18 with straightness. Phenotypic correlations with windfirmness were all close to zero.

The Effect of Site Quality on Parameter Estimates

It is apparent from *table 6* that growth has differed markedly between sites: for example, mean diameter ranged from 12.7 cm at Glasshouse Ridge to 17.9 cm at Cardwell Ridge. However, these differences are due not only to variation in site quality but also to differences in age at measurement (*Table 3*). Site quality *per se* is better defined by mean annual increment in diameter and height, as listed in *table 6*. On this approximate basis, the poorest growth rates were at Tuan Swamp and Wongi Swamp, and the best at Byfield Swamp and Glasshouse Swamp.

Heritability estimates from each trial are plotted against corresponding diameter and height increment in *figure 1*. In both cases, correlations between growth increment and

Table 7. — Weighted mean heritabilities and genetic correlations, mean phenotypic correlations, and their ranges, from preliminary analyses of each population.

Heritabilities

Population	Diameter mean	Diameter range	Height mean	Height range	Straightness mean	Straightness range
1	0.26	(0.08, 0.71)	0.17	(0.05, 0.28)	0.21	(0.14, 0.39)
2	0.15	(0.06, 0.42)	0.10	(0.03, 0.35)	0.23	(0.08, 0.20)
3	0.13	(0.06, 0.57)	0.10	(0.04, 0.51)	0.25	(0.11, 0.47)
4	0.39	(0.21, 0.72)	0.23	(0.11, 0.60)	0.21	(0.05, 0.48)
5	0.31	(0.24, 0.63)	0.12	(0.04, 0.36)	0.34	(0.27, 0.52)
6	0.24	(0.15, 0.80)	0.17	(0.11, 0.40)	0.19	(0.11, 0.31)
7	0.30	(0.29, 0.34)	0.06		0.06	
8	0.24		0.07			

Genetic correlations

Population	Diameter and Height mean	Diameter and Height range	Diameter and Straightness mean	Diameter and Straightness range	Straightness and Height mean	Straightness and Height range
1	0.61	(0.13, 1.00)	0.51	(0.18, 0.72)	-0.16	(-0.60, 0.47)
2	0.80	(0.74, 1.00)	-0.40	(-1.00, 0.10)	-0.10	(-0.75,-0.19)
3	0.76	(0.01, 1.00)	0.14	(-0.22, 1.00)	-0.25	(-0.46, 1.00)
4	0.71	(0.19, 0.87)	0.33	(-0.57, 0.76)	0.11	(-0.43, 0.59)
5	0.71	(0.24, 0.87)	-0.24	(-0.92, 0.09)	-0.10	(-0.38, 0.11)
6	0.81	(0.40, 1.00)	0.29	(-0.11, 0.47)	0.47	(-0.33, 0.80)
7	0.82		1.00			
8	0.41					

Phenotypic correlations

Population	Diameter and Height mean	Diameter and Height range	Diameter and Straightness mean	Diameter and Straightness range	Straightness and Height mean	Straightness and Height range
1	0.63	(0.48, 0.74)	0.17	(-0.04, 0.37)	0.15	(0.07, 0.23)
2	0.65	(0.51, 0.76)	0.16	(-0.06, 0.19)	0.11	(0.02, 0.23)
3	0.66	(0.57, 0.75)	0.20	(0.01, 0.41)	0.21	(0.09, 0.41)
4	0.64	(0.51, 0.81)	0.14	(-0.02, 0.35)	0.16	(0.06, 0.39)
5	0.60	(0.51, 0.78)	0.13	(0.02, 0.19)	0.19	(0.05, 0.26)
6	0.64	(0.56, 0.78)	0.12	(0.01, 0.19)	0.24	(0.14, 0.29)
7	0.76		0.37			
8	0.69					

heritability were low and non-significant ($p > 0.05$). There is, therefore, little indication of a relationship between the heritability estimate and growth rate of the trial from which it derives.

Discussion

Parameter estimates for populations 2, 3, 7, and 8 must be treated cautiously because of the limited number of families in each. Given the relatively large sampling variances and range of estimates for each population at each site, there is little difference in heritability estimates between populations. The more intensively selected populations (5 and 6) have not yielded consistently higher or lower estimates than the less intensively or un- selected populations (1, 4 and 8; 2, 3 and 7, respectively). The estimates of heritabilities and genetic correlations from pooled data generally agree with those of Eisemann (1981) and Dran *et al.* (1986). Kanowski's (1986) results are more narrowly based and less comparable.

There appears to be some degree of genetic control over windfirmness, confirming earlier observational evidence (Queensland Dept. of Forestry, 1981). The relatively low heritability of windfirmness and its variable correlations with other traits may be a consequence of the limited scale used to assess this trait (e.g. Raymond and Cotterill, in press), and/or variation in the incidence and severity of cyclone damage. A trait such as windfirmness tends to be binomially distributed, and as such its heritability will

Table 8. — Estimates of heritabilities (h^2) and associated standard errors (s. e.) from pooled analyses of stem diameter, height, straightness and windfirmness.

Trial	Diameter h^2	± s.e.	Height h^2	± s.e.	Straightness h^2	± s.e.	Windfirmness h^2	± s.e.
br1	0.30	0.09	0.31	0.09	0.24	0.08		
bs1	0.19	0.07	0.24	0.08	0.16	0.06		
cr1	0.51	0.11			0.29	0.08	0.03	0.03
gr1	0.38	0.09	0.29	0.08	0.24	0.07		
gs1	0.36	0.09	0.24	0.07	0.36	0.09		
tr1	0.41	0.09	0.29	0.07	0.18	0.06	0.13	0.05
ts1	0.17	0.04	0.11	0.03				
ws1	0.46	0.08	0.38	0.07	0.20	0.05	0.10	0.03
br2	0.29	0.11	0.17	0.08	0.23	0.09		
bs2	0.29	0.11	0.10	0.07	0.29	0.11		
cr2	0.72	0.16			0.31	0.10	0.10	0.05
gr2	0.32	0.10	0.32	0.10	0.32	0.10		
gs2	0.22	0.08	0.11	0.06	0.23	0.08		
tr2	0.21	0.06	0.20	0.06				
ws2	0.35	0.10	0.39	0.10	0.41	0.11	0.13	0.05
cr3	0.61	0.15			0.39	0.11		
gr3	0.45	0.13	0.29	0.10	0.30	0.10		
gs3	0.23	0.10	0.18	0.08	0.35	0.12		
tr3	0.40	0.09	0.20	0.05				
Mean	0.30	0.02	0.20	0.02	0.24	0.06	0.08	0.02

Table 10. — Phenotypic correlations (r_p) from pooled analyses.

Trial	Diameter and Height	Diameter and Straightness	Straightness and Height	Windfirmness and Diameter	Windfirmness and Height	Windfirmness and Straightness
br1	0.67	0.20	0.21			
bs1	0.62	0.13	0.16			
cr1		0.31		0.11		0.03
gr1	0.68	-0.03	0.07			
gs1	0.49	0.10	0.09			
tr1	0.52	0.07	0.07	-0.02	0.02	0.05
ts1	0.75					
ws1	0.63	0.15	0.15	-0.05	-0.05	0.02
br2	0.78	0.04	0.10			
bs2	0.48	0.08	0.32			
cr2		0.24		0.06		0.07
gr2	0.60	0.04	0.17			
gs2	0.54	0.17	0.27			
tr2	0.70					
ws2	0.59	0.19	0.22	0.01	-0.01	0.02
cr3		0.36		0.19		0.16
gr3	0.79	0.05	0.14			
gs3	0.55	0.12	0.19			
tr3	0.70					
Mean	0.63	0.14	0.16	0.00	-0.01	0.04

depend on the mean and incidence in the population (Hill and Smith, 1977). An example of such a dependency was demonstrated by McGuirk and Atkins (1984), who found that the highest estimates of heritability for fleece rot in sheep were obtained when its intensity was at an intermediate level. On this basis, one would expect to make maximum genetic improvement in windfirmness from results obtained when wind damage is at an intermediate level.

A more realistic and desirable approach would be to base selection for windfirmness on a genetically correlated trait which is both normally distributed and expressed in the absence of wind damage. Correlations presented in *table 9* suggest that windfirmness would be improved by selecting shorter, plumper, straighter trees. However, as diameter and height have a strong positive genetic association (r_g = 0.82), such a strategy is likely to severely limit genetic gain in volume. Also, it is a matter of conjecture whether shorter families would remain more windfirm if grown as a monoculture. Until a more reliable indicator trait can be identified, it appears that the best method of simultaneously improving volume, straightness and windfirmness is to use indices which combine family information for windfirmness from a site with a moderate incidence of wind damage with individual tree and family data for volume and straightness from more protected sites.

Table 9. — Genetic correlations (r_g) and associated standard errors (s.e.) from pooled analyses.

Trial	Diameter and Height r_g	± s.e.	Diameter and Straightness r_g	± s.e.	Straightness and Height r_g	± s.e.	Windfirmness and Diameter r_g	± s.e.	Windfirmness and Height r_g	± s.e.	Windfirmness and Straightness r_g	± s.e.
br1	0.52	0.14	0.37	0.19	0.14	0.21						
bs1	0.47	0.18	0.27	0.24	-0.07	0.24						
cr1			0.43	0.14			0.41	0.31			0.59	0.35
gr1	0.69	0.10	0.14	0.19	-0.09	0.20						
gs1	0.34	0.17	0.31	0.17	-0.33	0.18						
tr1	0.48	0.13	0.23	0.18	0.02	0.20	0.35	0.22	-0.09	0.24	0.83	0.53
ts1	0.53	0.13										
ws1	0.61	0.09	0.24	0.14	-0.01	0.16	-0.05	0.18	-0.18	0.18	0.26	0.19
br2	0.89	0.08	-0.10	0.27	0.02	0.31						
bs2	0.36	0.3	-0.39	0.24	0.19	0.33						
cr2			0.21	0.18			0.25	0.25			0.20	0.28
gr2	0.74	0.11	0.05	0.22	-0.16	0.21						
gs2	0.58	0.19	0.01	0.24	-0.14	0.28						
tr2	0.59	0.13										
ws2	0.54	0.14	0.14	0.19	0.28	0.18	0.32	0.22	0.03	0.23	0.20	0.28
cr3			0.46	0.16								
gr3	1.00	0.03	-0.06	0.23	-0.20	0.24						
gs3	0.36	0.27	0.16	0.27	0.15	0.29						
tr3	0.67	0.09										
Mean	0.82	0.02	0.21	0.05	-0.15	0.10	0.21	0.10	-0.10	0.12	0.18	0.09

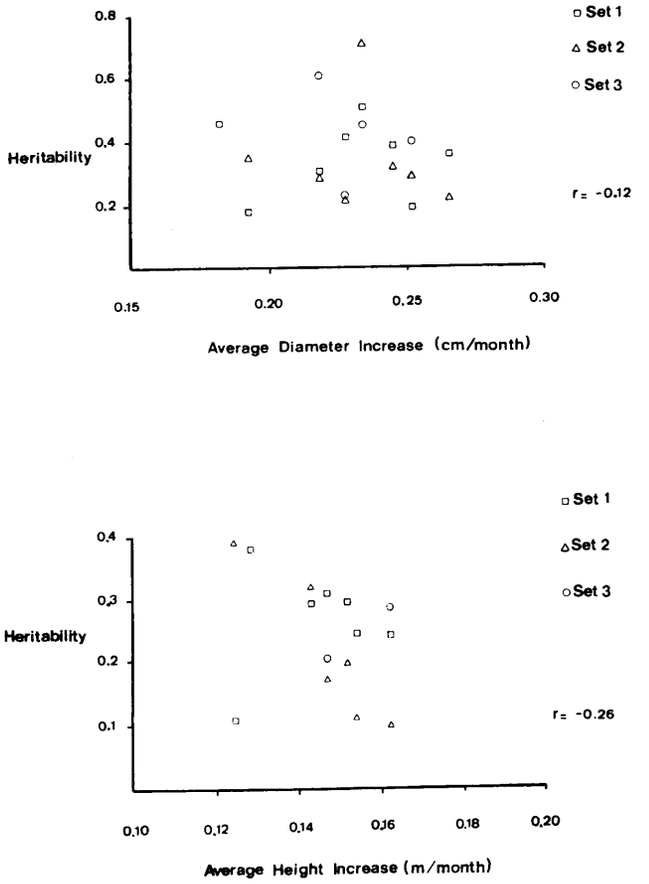

Figure 1. — Heritability estimates from each site plotted against corresponding average monthly diameter and height increments.

Although faster growth sites may result in greater differences between family means (EISEMANN and NIKLES, 1983), our results demonstrate that the accuracy of breeding value estimates does not necessarily increase on such sites. This implies that, as COTTERILL and DEAN (1988) found, increased phenotypic variance counteracts any advantages of increased additive genetic variance. Therefore, family rankings derived from faster growth sites may be no more reliable than those originating from slower growth sites. Although the fastest growth site does not necessarily provide higher heritability estimates, it may facilitate earlier selection and thereby reduce the generation interval.

Conclusions

For the populations tested in these trials, there are no apparent site effects on the magnitude of heritability estimates. Evidence from all sites tested suggests that selection in any of the populations should lead to genetic gain within that population. The parameters reported here are being used as the basis for index selection in the base population of Pch in Queensland. Further papers will report investigations of the magnitude of genotype- environment interactions and juvenile- mature correlations and their consequences for the breeding program.

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