GENETIC PARAMETERS FOR SLASH PINE (*PINUS ELLIOTTII*) GROWN IN SOUTH-EAST QUEENSLAND, AUSTRALIA: GROWTH, STEM STRAIGHTNESS AND CROWN DEFECTS

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ABSTRACT

Twelve wind-pollinated progeny tests of slash pine (*Pinus elliottii* var. *elliottii*) were measured at 6 to 11 years of age for growth, stem straightness and three crown defects (double leaders, ramicorn branches and basket whorls). Estimates of heritability (biased and unbiased), type B genetic correlations, and trait-trait/age-age genetic correlations are presented. Growth and stem straightness traits had moderate heritability estimates (0.15 to 0.3), and there appeared to be a weak negative genetic correlation between growth and stem straightness. The crown defects were assessed as binomial, presence/absence traits and the observed heritability estimates were modelled as a function of the average incidence of the traits and were transformed to the underlying normal scale. The average heritability estimates of the crown defects when transformed to the normal scale were of a similar magnitude to those for growth and stem straightness. Adverse genetic correlations were detected between the crown defects and growth traits, but favourable genetic correlations were found between crown defects and stem straightness. The negative genetic correlation between growth and crown defects was strong, and will limit the concurrent improvement of these traits. No evidence was found of any strong genotype-by-environment interaction across a range of sites in south-east Queensland: type B genetic correlations exceeded 0.78 for all traits. Implications for the future breeding of the species is discussed in relation to the development of superior inter-specific hybrids.

Keywords: *Pinus elliottii*, REML, variance components, heritability, type B genetic correlation, binomial traits

INTRODUCTION

In Queensland, slash pine (*Pinus elliottii* Engelm. var. *elliottii*) has been grown in commercial plantations for over five decades. More than 250,000 $m^3 \cdot year^{-1}$ of logs are currently being harvested from mature slash pine plantations, with the annual harvest expected to peak at around one million cubic metres by the year 2010. Although slash pine is a very important timber crop in Queensland, this species is no longer planted commercially; all commercial plantations in the coastal areas of south-east Queensland are now planted with hybrids between slash pine and *Pinus caribaea* Morelet var. *hondurensis* Barrett and Golfari (hereafter referred to as Caribbean pine). These hybrids combine the higher wood density, better stem straightness and wind-firmness of slash pine, with the superior growth rate and finer branching of Caribbean pine. Therefore, even though slash pine is no longer planted, the continued genetic improvement of slash pine is required in order to improve the genetic value of parents used to produce F_1 hybrids with Caribbean pine.

Throughout the last 45 years slash pine has been the subject of intensive, although somewhat sporadic, tree improvement activities in Queensland: changes in the intensity of the breeding program reflected the changing importance of the species for commercial use in Queensland. In the early 1950s approximately 70 plus-trees were intensively selected in plantations; the best 35 of these trees were grafted into a seed orchard in 1953, and a second orchard was established in 1958 using only the best 14 clones. These (±70) first-generation plus-trees were subsequently inter-mated and progeny tested. However, by the early 1970s it was realised that the genetic base was too narrow to support a sustained breeding program, and approximately 100 new plus-trees were selected. In 1975 a third seed orchard was established which incorporated the ±100 new first-generation plus-trees as well as 20 advanced-generation selections. Wind-pollinated seed collected from the ortets of these 100 new trees was used to establish progeny tests in 1976, 1977 and 1978. The data reported in this paper were collected from these progeny tests between 1982 and 1988, when the tests were between 6 and 11 years of age.

This paper aims to summarise information on the genetic parameters (heritability, type B genetic correlations, and age-age genetic correlations) for growth, stem straightness and crown defects (double leaders, ramicorn branches, and basket whorls) of slash pine grown in south-east Queensland. These results will be compared with published genetic parameter estimates from slash pine breeding programs in the USA and Africa, and discussed in relation to their implications for future breeding activities with slash pine.

MATERIALS AND METHODS

Test locations and design

A series of twelve wind-pollinated progeny tests were established over a three-year period (1976–1978), with four tests planted per year. The seed for the tests was collected from the ortets of first-generation plus-trees that were selected in commercial plantations located in south-east Queensland. All test sites were located on the coastal plain (less than 40m above sea level) between Brisbane and Maryborough in south-east Queensland (Table 1). Nine of the twelve sites had soil types that were subject to some degree of impeded drainage, while the soil types of the remaining three sites were well drained (Table 1). Overall, 97 different half-sib families were represented in these tests, with 49, 32 and 36 families represented in the tests planted in 1976, 1977 and 1978 respectively. Although four families were planted on all twelve sites, a given family was usually only included in the four tests that were planted in the one year.

All twelve tests were established using a randomised complete block design, with each family represented in eight blocks. In the 1976 and 1978 plantings each block contained a 6-tree non-contiguous plot of each family, while in the 1977 plantings 8-tree non-contiguous plots were used. Data were collected from a total of just under 23,000 individual trees.

Measure and assessment details

The tests were usually measured and assessed at six and ten years of age; however, data collection was sometimes delayed one or two years. The following traits were measured in some or all of the tests:

- diameter over bark (DB) at 1.3 m and tree height (HT) at 6, 8, 10 and 11 years (DB6, HT6, DB8 etc.),
- stem straightness using a 4-point scale (ST), a 7-point scale (STR), or the method advocated by BARNES and GIBSON (1986),
- utilisation potential at 6 years of age: a 3-point scale (1 = pulp, 2 = pulp and sawlog, and 3 = sawlog) which reflected stem straightness, tree size and branching defects such as double leaders and ramicorns, and
- the presence (score = 1) or absence (score = 0) of three serious crown defects – double leaders (DL), ramicorn branches (RM) and basket whorls (BW).

The presence/absence of double leaders (DL) and ramicorns (RM) was assessed at 6–8 years and 10–11 years of age, and the two assessment times were treated as different traits (DL1 and RM1 at 6–8 years, DL2 and RM2 at 10–11 years). Where both diameter and height

Table 1 Progeny test locations and soil types

Test	Planting month/year	Location		Latitude (°S)	Longitude (°E)	Site Type†	Soil Type‡
A	06/76	1B	Magnolia, Tuan	25°40'	152°46'	ID	Solodic planosol
B	07/76	10	Ulirraba, Toolara	25°55'	152°49'	WD	Ferric luvisol
C	07/76	30	Round, Toolara	26°08'	152°57'	ID	Humic podosol
D	08/76	1B	Storrs, Beerburrum	26°58'	153°01'	ID	Gleyic acrisol
E	07/77	27	Melaleuca, Tuan	25°37'	152°45'	ID	Humic planosol
F	07/77	29	Boronia, Tuan	25°44'	152°51'	WD	Feric luvisol
G	07/77	42	Round, Toolara	26°07'	152°55'	ID	Humic podosol
H	07/77	10B	Tripconys, Beerburrum	26°58'	153°02'	ID	Gleyic acrisol
I	07/78	30	Green Ridge, Tuan	25°37'	152°45'	ID	Humic planosol
J	07/78	26	Ulirraba, Toolara	25°53'	152°48'	WD	Ferric luvisol
K	07/78	55	Round, Toolara	26°53'	152°53'	ID	Humic podosol
L	07/78	3	Bribie, Beerburrum	27°03'	153°02'	ID	Gleyic acrisol

† ID = Impeded drainage, WD = Well drained site
‡ Soil types were classified according to FAO-UNESCO (1974) "Soil Map of the World".

were measured, individual tree volumes (VOL6, VOL8, VOL10) were calculated in cubic decimetres (VANCLAY 1980). For stem straightness assessed using the BARNES and GIBSON, 1986, (BG) method the six individual straightness scores assigned to each of the six 1-metre sections in the butt log were either:

i. assigned equal weights by summing the individual scores, to give a composite score ranging from 6 to 36 (BG1), or
ii. the individual scores for the 0–4 metre portion of the stem were multiplied by 0.2, and the scores for the remaining 4–6 metre section were multiplied by 0.1, and then weighted scores were summed together, thereby giving the bottom four 1-metre sections twice as much weight as the top two sections, and produced a composite score ranging from 1 to 6 (BG2).

Estimation of variance components and genetic parameters

The 12 progeny tests were analysed individually, and all possible pairs of tests within each planting year were analysed using PROC VARCOMP (SAS Institute Inc. 1989) to obtain Restricted Maximum Likelihood (REML) estimates of the variance components (PATTERSON & THOMPSON 1971). The statistical model used for the pair-wise analyses was:

$$Y_{ijkl}=\mu+T_i+B_{j(i)}+F_k+FT_{ik}+P_{ijk}+W_{ijkl}$$

Where Y_{ijkl} is the lth tree within the kth wind-pollinated family, in the jth block within the ith test environment, μ is the overall mean, E_i is the random effect of the ith test environment ($E[E_i] = 0$, $Var[E_i] = \sigma^2_t$), $B_{i(j)}$ is the random effect of the jth block within the ith test environment, ($E[B_{i(j)}] = 0$, $Var[B_{i(j)}] = \sigma^2_b$), F_k is the random effect of the kth wind-pollinated family ($E[F_k] = 0$, $Var[F_k] = \sigma^2_f$), FE_{ik} is the random effect of the interaction between the kth family and the ith test environment, ($E[FE_{ik}] = 0$, $Var[FE_{ik}] = \sigma^2_{fe}$), P_{ijk} is the random effect of the interaction between the kth family and the jth block within the ith test environment ($E[P_{ijk}] = 0$, $Var[P_{ijk}] = \sigma^2_p$), and W_{ijkl} is the random variation due to the lth tree within the ijkth plot ($E[W_{ijkl}] = 0$, $Var[W_{ijkl}] = \sigma^2_w$).

For the single-site analyses, the statistical model used was a special case of that described above (i.e. where the number of test locations equals one), and is obtained by dropping all terms relating to test location. The variance components for the family, plot and within-plot effects obtained from the single-site analyses will be referred to as σ^2_F, σ^2_P and σ^2_W respectively.

In order to remove scale effects (FALCONER 1989), the within-plot variance estimated from the single-site analyses (σ^2_w) was used to standardise the growth data before any paired-site analyses were conducted. The growth traits (diameter, height and volume) of each tree were divided by the square root of the within-plot variance, and produced a transformed variable with a within-plot variance of unity.

The wind-pollinated families were assumed to be half-sib families; hence the variance component for families, σ^2_f, obtained from across-site analyses can be interpreted as an estimate of one quarter of the additive genetic variance (σ^2_A). However, the corresponding estimate of the variance among families obtained from single-site analyses (σ^2_F) is upwardly biased due to the confounding effects of genotype-by-environment interaction (COMSTOCK & MOLL 1963), and is actually an estimate of one quarter of the additive variance plus one quarter of the additive-by-environment interaction (σ^2_{AE}). Further σ^2_{fe} obtained from the paired-site analyses was interpreted as an estimate of one quarter of σ^2_{AE}.

Biased and unbiased heritabilities, and type B genetic correlations (BURDON 1977) between the same trait measured in two different environments, were estimated using these variance components in the following manner:

Biased heritability: $$h^2_b = \frac{4\sigma^2_F}{\sigma^2_F + \sigma^2_P + \sigma^2_W}$$

Unbiased heritability: $$h^2 = \frac{4\sigma^2_f}{\sigma^2_f + \sigma^2_{fe} + \sigma^2_p + \sigma^2_w}$$

Type B genetic correlation: $$r_{gB} = \frac{\sigma^2_f}{\sigma^2_f + \sigma^2_{fe}}$$

From the equation for the type B genetic correlation, it can be seen that this parameter is a measure of genotype-by-environment interaction (G×E); when G×E is large, then r_{gB} approaches zero, however when G×E is small, r_{gB} approaches unity. As a rule of thumb, it has been suggested that unless the variance due to G×E was at least half the size of the additive variance (i.e. r_{gB} exceeds 0.67) then G×E is of no importance (SHELBOURNE 1972).

Standard errors for heritability and type B genetic (same trait) correlations were estimated by assuming that the denominator was a known constant rather than a random variable, as proposed by DICKERSON (1969) for heritability estimates. DIETERS *et al.* (1995b) showed that the approximate standard errors of heritability estimates calculated in this manner are similar to, but slightly more conservative than standard error estimates

based on a Taylor series approximation (*e.g.* TALLIS 1959).

Type B genetic correlations between two different traits (i.e. the same trait measured at different ages, or two different traits) measured in different environments, were estimated using the following equation:

$$r_g = \frac{\frac{1}{2}\left[Cov_A(X_1,Y_2) + Cov_A(Y_1,X_2)\right]}{\sqrt{V_A(X_{1.2})\cdot V_A(Y_{1.2})}}$$

where $Cov_A(X_1, Y_2)$ is the additive genetic covariance between two traits X and Y, that was estimated by calculating the covariance between the family means from sites 1 and 2. Similarly, $V_A(X_{1.2})$ and $V_A(Y_{1.2})$, are the additive genetic variances of traits X and Y estimated from the paired-site analyses of tests 1 and 2.

Average parameter estimates were calculated across tests and test-pairs. All tests were of similar size and precision, therefore there was no need to weight the parameter estimates in any manner.

Heritability of binomial traits

There is a substantial amount of literature dealing with the estimation of heritability from binomial data (ROBERTSON & LERNER 1949, DEMPSTER & LERNER 1950, VAN VLECK 1972, HILL and SMITH 1977, and a more recent review by MCGUIRK 1989). The theory treats binomial characters as threshold traits, with an underlying normal distribution of genetic and environmental values, which are not expressed until a certain threshold value is reached on the underlying normal scale (DEMPSTER & LERNER 1950). Further, the theory suggests that there is a simple linear relationship between heritability on the normal scale, and heritability estimated on the observed binomial scale:

$$h^2_{0/1} = \frac{h^2_n z^2}{p(1-p)},$$

where $h^2_{0/1}$ is the heritability estimated on the binomial (0/1) scale, h^2_n is the heritability on the underlying normal scale, z is the height of the ordinate of the normal distribution at the threshold point which corresponds to the observed incidence of the trait (p).

This transformation was applied to single- and paired-site estimates of the heritability for double leaders, ramicorns and basket whorls. For paired-site analyses the average incidence of the trait in the two sites was used as an estimate of p. Linear regression was used to investigate the relationship between average incidence of the traits and the observed variance components and heritability estimates.

RESULTS AND DISCUSSION

Growth and stem straightness

The heritability estimates for growth traits were moderate: estimates of biased heritability ranged between 0.19 and 0.33, while unbiased estimates were slightly lower and ranged between 0.20 and 0.24 (Table 2). There was no apparent age-related trend in the size of the heritability estimates for growth traits, and estimates remained fairly constant between 6 and 11 years of age (Figure 1, Table 2). The type B genetic correlations all exceeded 0.75, indicating that there was relatively little G×E in growth traits of slash pine in south-east Queensland.

The four methods that were used to assess stem straightness produced different heritability estimates for this trait (Table 2). Of the methods applied, the simplest methods (ST and STR) gave the highest heritability estimates, while the most complex method (BG1 and BG2) had the lowest heritability estimates. Also it should be noted that the different weights used in the BARNES and GIBSON (1986) assessment technique did not affect the parameter estimates (Tables 2 and 3). The type B genetic correlations for the different straightness assessment methods were all high, with a minimum of 0.78 for ST and a maximum of 0.95 for BG1 (Table 2). Hence, it appears that straightness was not affected by G×E interaction. Overall, the 7-point straightness assessment method (STR) seemed to be the most useful under local conditions; this method is simple to apply, had average heritability estimates exceeding 0.25, and a type B genetic correlation over 0.9 (Table 2).

No relationship was found between site type (Table 1) and the estimates of heritability and type B genetic correlation for growth traits or stem straightness. Estimates derived from tests of the same site type were not significantly different to estimates from different site types. In fact, average heritability and type B genetic correlation estimates from well-drained /impeded-drainage pairs often slightly exceeded those from pairs of sites with impeded drainage.

The type B genetic correlations (estimated between the same trait measured at different ages and between different traits) indicate that there were strong genetic relationships between the growth traits (Table 3). Some of the genetic correlations exceed the theoretical maximum of |1.0| (Tables 3 and 5); however, the errors associated with estimates of the additive genetic covariance are often large (FALCONER 1989), hence when the genetic relationship between two traits is very strong, estimates exceeding |1.0| can be expected. The relationship between six-year traits (DB6, HT6 and

VOL6) and volume at 10 years of age (VOL10) was very strong; all genetic correlations exceeded 0.87, indicating that six-year-old performance was a good indicator of growth to 10 years of age.

The four straightness assessment methods were also strongly correlated with one another, with genetic correlations approaching 1.0 (Table 3). Therefore all methods assessed essentially the same trait. However, the genetic correlations between stem straightness and the growth traits differed substantially amongst the four methods. The BARNES and GIBSON (1986) method (BG1 and BG2) appeared to have a moderate positive correlation with growth traits, while the remaining three methods (ST, STR and UP) were either slightly negatively correlated or uncorrelated with growth traits (Table 3). PSWARAYI *et al.* (in press) also reported only a weak association between growth traits and an 8–point visual assessment of straightness. These differences in the genetic correlations reflect inherent differences between the BARNES and GIBSON (1986) approach to the assessment of stem straightness, and other more subjective methods of assessing stem straightness. When the BARNES and GIBSON (1986) method was applied in these slash pine tests, straightness was determined in relation to stem diameter at the point of the bend. Thus a bend of a certain, absolute severity would be judged less significant if it occurred in a large tree when compared with the same bend in a small tree. By contrast, the other assessment methods (ST, STR and UP) appear to have scored large trees somewhat more critically than small trees.

When these parameter estimates are compared with published genetic parameter estimates for growth and stem straightness of slash pine in other parts of the FALKENHAGEN 1989, HODGE & WHITE 1992, and PSWARAYI *et al.* (in press)), the heritability estimates from this study are toward the upper end of the spectrum (Figure 1). Further, heritability estimates for volume in slash pine reported for tests located outside the natural range of the species, i.e. in Africa and Australia, were substantially higher than estimates from

Table 2 Average heritability and type B genetic correlation estimates (± standard errors) for growth and stem straightness traits in slash pine. (Number of tests or test–pairs indicated in parentheses.) Diameter, height and volume were measured in cm, m and dm^3 respectively, straightness was scored visually, and crown defects (basket whorls, ramicorn branches, and double leaders) were binomial presence/absence scores

Trait	Age (yrs.)	Biased heritability (h^2_b)	Unbiased heritability (h^2)	Type B genetic correlation (r_{gB})
Diameter (DB6)	6	0.246 ± 0.079 (11)	0.200 ± 0.005 (15)	0.790 ± 0.063 (15)
Diameter (DB8)	8	0.314 ± 0.090 (2)	–	–
Diameter (DB10)	10–11	0.269 ± 0.082 (9)	0.198 ± 0.004 (10)	0.780 ± 0.125 (10)
Height (HT6)	6	0.244 ± 0.076 (11)	0.220 ± 0.005 (15)	0.904 ± 0.110 (15)
Height (HT8)	8	0.188 ± 0.061 (2)	–	–
Height (HT10)	10–11	0.241 ± 0.067 (4)	0.221 ± 0.003 (6)	0.907 ± 0.091 (6)
Volume (VOL6)	6	0.288 ± 0.088 (11)	0.239 ± 0.006 (15)	0.824 ± 0.113 (15)
Volume (VOL8)	8	0.332 ± 0.094 (2)	–	–
Volume (VOL10)	10–11	0.280 ± 0.076 (4)	0.225 ± 0.004 (6)	0.807 ± 0.102 (6)
Straightness (ST)	6–7	0.204 ± 0.066 (7)	0.166 ± 0.003 (9)	0.780 ± 0.112 (9)
Straightness (STR)	7–11	0.300 ± 0.096 (6)	0.284 ± 0.007 (6)	0.913 ± 0.076 (9)
Utilisation Potential (UP)	6–7	0.154 ± 0.056 (7)	0.136 ± 0.002 (9)	0.863 ± 0.115 (9)
Barnes & Gibson (BG1)†	10	0.121 ± 0.072 (3)	0.131 ± 0.003 (3)	0.949 ± 0.080 (3)
Barnes & Gibson (BG2)‡	10	0.125 ± 0.073 (3)	0.131 ± 0.003 (3)	0.933 ± 0.082 (3)
Basket Whorls (BW)	7–11	0.052 ± 0.040 (6)	0.053 ± 0.001 (4)	0.801 ± 0.275 (4)
Double Leaders (DL1)	6–8	0.108 ± 0.050 (10)	0.084 ± 0.001 (12)	0.789 ± 0.179 (12)
Double Leaders (DL2)	10–11	0.128 ± 0.066 (6)	0.138 ± 0.008 (6)	0.933 ± 0.119 (6)
Ramicorns (RM1)	6–8	0.107 ± 0.049 (10)	0.101 ± 0.001 (12)	0.872 ± 0.138 (12)
Ramicorns (RM2)	10–11	0.101 ± 0.058 (6)	0.104 ± 0.005 (6)	0.921 ± 0.139 (6)

† Each 1-metre stem section was assigned an equal weight: composite scores ranged from 6 to 36.

‡ The lower four 1-metre sections were assigned 2× the weight of the top two 1-metre sections: composite scores ranged from 1 to 6.

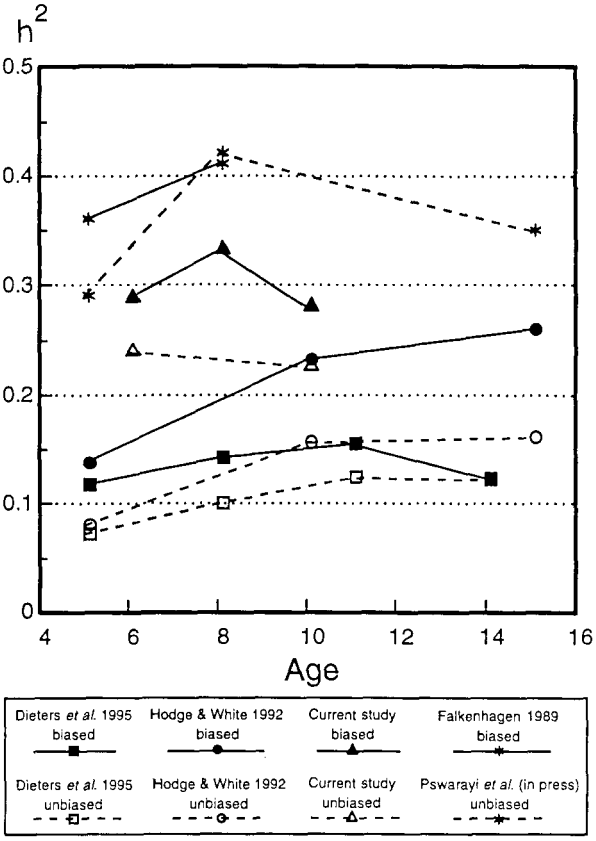

Figure 1 Published biased (single-site) and unbiased (multiple-site) heritability estimates for volume in slash pine

world (COTTERILL *et al.* 1987, DIETERS *et al.* 1995a, the south-eastern USA (Figure 1). The absence of fusiform rust (*Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme*) in these 'exotic' test locations may be contributing to the higher observed heritabilities – fusiform rust leads to differing levels of mortality within families, and so it is likely to increase the phenotypic variance of growth traits as a consequence of unequal inter–tree competition. In the tests reported by DIETERS *et al.* (1995a), on average just over 30% of all trees were infected by fusiform rust, and survival varied from 35% to 98%. By contrast, eleven of the tests reported in this study had survivals in excess of 97%, while the other test had a survival of 93%. Nevertheless, DIETERS *et al.* (1995a) indicated that there was no evidence to suggest that tests with high rust infection levels were unsuitable for estimating the genetic parameters of growth traits.

Relatively few published estimates of heritability for stem straightness in slash pine are available: COTTERILL *et al.* (1987) report a heritability of 0.15 ± 0.09 at eight years of age from one test in South Africa; FALKENHAGEN (1989) provided estimates averaging 0.20 ± 0.12 and 0.21 ± 0.15 at five and eight years of age respectively, from up to 15 tests in South Africa; and PSWARAYI *et al.* (in press) estimate that the heritability of stem straightness, from two tests in Zimbabwe, declines from 0.12 ± 0.05 at five years of age to 0.04 ± 0.04 at 15 years of age. Estimates reported by COTTERILL *et al.* (1987) and FALKENHAGEN (1989) are of a similar magnitude to those in this study, but estimates reported by PSWARAYI *et al.* (in press) are considerably lower. The latter suggest that the low heritability estimates obtained for stem straightness in their study may reflect the use of an absolute scale rather than a site-specific scale (COTTERILL & DEAN 1990). ST, STR and UP in the current study were visual assessments of an absolute straightness scale, and so this explanation alone is not sufficient to account for the observed differences in heritability. However, if the frequency distribution of scores does not approximate a normal distribution, especially when only a small number of scores are used, the amount of phenotypic variation is reduced and heritability estimates obtained from the data can be low (COTTERILL & DEAN 1990, RAYMOND & COTTERILL 1990).

Crown defects – double leaders, ramicorns and basket whorls

The heritability estimates for crown defects on the observed, binomial scale were quite low, with only small differences between the biased and unbiased estimates of heritability, and all type B genetic correlations were not significantly different from 1.0 (Table 2). Heritability estimates of this magnitude have been commonly reported for crown defects in radiata pine (COTTERILL & ZED 1980, SHELBOURNE & LOW 1980, MATHESON & RAYMOND 1984, CARSON 1986, COTTERILL & DEAN 1990, RAYMOND & COTTERILL 1990) and PSWARAYI *et al.* (in press) report heritability estimates for branch diameter and branch count for slash pine that are of a similar size.

There is a fairly common presupposition that crown defects have a low heritability in many forest tree species, and therefore can not be manipulated easily via selection and breeding. However, in the radiata pine experiments referred to above, where binomial (presence/absence) scores were recorded, heritability estimates were not transformed to the underlying normal scale. Hence, the reported heritability estimates were influenced by the incidence of the trait. The remaining heritability estimates for crown defects are mostly based

Table 3 Average trait-trait type B genetic correlations (± standard errors) for growth and stem straightness of slash pine in Queensland. (The number of test pairs that contributed to each average is indicated in parentheses.)

	DB10	HT6	HT10	VOL6	VOL10
DB6	0.964 ± 0.032 (5)	0.724 ± 0.071(11)	0.467 ± 0.040 (2)	0.963 ± 0.012(11)	0.873 ± 0.005 (2)
DB10		0.781 ± 0.177 (5)	0.604 ± 0.009 (5)	0.911 ± 0.002 (5)	0.937 ± 0.016 (4)
HT6			1.310 ± 0.404 (2)	0.897 ± 0.082(11)	1.230 ± 0.446 (2)
HT10				0.582 ± 0.076 (2)	0.720 ± 0.012 (4)
VOL6					0.926 ± 0.012 (2)
	BG1	BG2	UP	ST	STR
DB6	0.351 ± 0.100 (2)	0.330 ± 0.104 (2)	−0.094 ± 0.093 (6)	−0.153 ± 0.082 (6)	0.058 ± 0.120 (3)
DB10	0.258 ± 0.087 (2)	0.232 ± 0.104 (2)	−0.227 ± 0.156 (4)	−0.168 ± 0.133 (6)	−0.187 ± 0.108 (3)
HT6	0.534 ± 0.088 (2)	0.536 ± 0.084 (2)	0.093 ± 0.106 (6)	−0.004 ± 0.073 (6)	0.208 ± 0.047 (3)
HT10	– (0)	– (0)	−0.312 ± 0.102 (2)	−0.189 ± 0.001 (2)	−0.206 ± 0.001 (2)
VOL6	0.478 ± 0.061 (2)	0.463 ± 0.064 (2)	0.027 ± 0.088 (6)	−0.760 ± 0.076 (6)	0.163 ± 0.079 (3)
VOL10	– (0)	– (0)	−0.363 ± 0.174 (2)	−0.318 ± 0.068 (2)	−0.104 ± 0.056 (2)
BG1		1.10 ± 0.050 (2)	0.862 ± 0.023 (2)	0.823 ± 0.047 (2)	–
BG2			0.884 ± 0.040 (2)	0.832 ± 0.058 (2)	–
UP				1.084 ± 0.036 (6)	0.998 (1)
ST					0.933 (1)

Table 4 Average single-site biased (h^2_b) and paired-site (h^2) heritability estimates (± standard error) for double leaders, ramicorns and basket whorls, that have been adjusted to an underlying normal scale, based on the incidence of the trait

Trait	Single-site analyses		Paired-site analyses	
	Incidence	Adjusted h^2	Average incidence	Adjusted h^2
Basket Whorls (BW)	0.096	0.248‡ ± 0.154 (6)	0.112	0.169 ± 0.022 (4)
Double Leaders (DL1)	0.172	0.247 ± 0.049 (10)	0.180	0.191 ± 0.024 (12)
Double Leaders (DL2)	0.172	0.296 ± 0.033 (6)	0.172	0.316 ± 0.042 (6)
Ramicorns (RM1)	0.437	0.170 ± 0.019 (10)	0.439	0.161 ± 0.015 (12)
Ramicorns (RM2)	0.529	0.176 ± 0.038 (6)	0.529	0.177 ± 0.011 (6)

† The average incidence of the trait in each pair of tests.
‡ The average includes one estimate of 1.8, well outside the theoretical upper limit, that was arbitrarily set to 1.0.

on some form of 'malformation index' (CARSON 1986), which combines a number of different characteristics into a single trait. COTTERILL and DEAN (1990) and RAYMOND and COTTERILL (1990) argue against the use of this type of integrated assessment procedure because a) they are difficult to apply, b) of the potential for assessor bias, and c) the component traits can be integrated more accurately using a selection index.

When the incidence of the three binomial traits was investigated, it was found that each trait occurred over a relatively narrow range of mean incidence levels (Figure 2). Basket whorls, double leaders and ramicorns had mean incidence levels of 0.10, 0.17, and 0.44/0.53 respectively (Table 4). Therefore the heritability estimates for each trait are really only repeated observations of the heritability at a fixed incidence level. Consequently, it was impossible to model the heritability of each trait (separately) as a function of incidence, and average heritability estimates were calculated after transforming the estimates to the underlying normal scale. The average heritability estimates on the underlying normal scale (Table 4) are considerably higher than those on the binomial scale, and are similar to the heritability estimates for growth and stem straightness traits. Heritability estimates of this magnitude are more in line with observations of the first and second genera-

tion progeny of slash pine in Queensland where certain parents will consistently produce progeny with a substantially higher incidence of ramicorns and double leaders. Therefore, crown defects appear to be under a moderate level of genetic control in slash pine.

Double leaders and ramicorns showed moderate, positive (*i.e.* adverse) genetic correlations with growth traits (0.2 to 0.6), negative (*i.e.* favourable) genetic correlations of –0.2 to –0.6 with stem straightness, and strong, positive genetic correlations (0.6 to 1.0) with each other (Table 5). Unfortunately, it was not possible to estimate trait–trait genetic correlations involving basket whorls because this trait was not regularly assessed across sites and planting years.

The high genetic correlations between two assessment times of ramicorns and double leaders (Table 5) indicate that these traits can be assessed reliably at 6–8 years of age. Further, the strong genetic relationship observed between double leaders and ramicorns (Table 5) was expected, because both traits reflect a lack of apical dominance. Stem straightness may also reflect the degree of apical dominance: straight trees having stronger apical dominance than more crooked trees. If this is true, then it provides a reasonable explanation for the observed favourable correlation between straightness and double leaders/ramicorns. The adverse association between growth traits and crown defects it will make the concurrent improvement of both traits difficult.

Modelling the heritability of crown defects

It was not possible to model the heritability of basket whorls, double leaders and ramicorns as separate traits due to the limited range of mean incidence levels at which each trait was observed. However, when the total phenotypic variance ($\sigma^2_T = \sigma^2_F + \sigma^2_P + \sigma^2_W$) and the additive variance ($4\sigma^2_F = \sigma^2_A$) estimated from single-site analyses (on the binomial scale) were plotted against the mean incidence of the trait (p) at the site multiplied by ($1-p$), good relationships were evident across the three traits (Figure 2). The high genetic correlations between double leaders and ramicorns (Table 5) suggest that there were many common genes controlling the expression of these two traits, although the trait–trait genetic correlations involving basket whorls was unknown. It therefore seemed reasonable to model these three traits together.

The following simple, linear relationships were found between additive and phenotypic variance with ($p(1-p)$) across the three traits:

Total phenotypic variance:

$\sigma^2_T = -0.0012 + 0.995(p(1-p))$ $\quad R^2 = 0.996$

Additive variance:

$\sigma^2_A = -0.0001 + 0.111(p(1-p))$ $\quad R^2 = 0.482$

When attempts were made to model the heritability as a function of incidence, the highest R^2 value obtained was 0.14. Nevertheless, these two models imply a constant heritability (biased, on the binomial scale) for any level of incidence equivalent to 0.111/0.995 = 0.11 (if the intercept terms are considered to be equivalent to zero). This predicted heritability is very similar to those reported in Table 2. Also, if this constant heritability was adjusted to the underlying normal scale using the average incidence levels (Table 4), the estimated heritabilities of basket whorls, double leaders (DL1 and DL2) and ramicorns (RM1 and RM2) were 0.33, 0.24 and 0.17 respectively. Although the adjusted heritability estimates for double leaders and ramicorns were very similar to those for biased heritability, the estimate for

Table 5 Average trait-trait type B genetic correlations (± standard errors) for double leaders, ramicorns and basket whorls of slash pine in Queensland. (The number of test pairs that contributed to each average is indicated in parentheses.)

	RM1	RM2	DL1	DL2
DB6	0.375 ± 0.110 (8)	0.096 ± 0.262 (3)	0.335 ± 0.110 (8)	0.360 ± 0.059 (3)
DB10	0.465 ± 0.134 (4)	0.218 ± 0.199 (4)	0.575 ± 0.028 (4)	0.390 ± 0.051 (4)
HT6	0.214 ± 0.103 (8)	0.326 ± 0.365 (3)	0.200 ± 0.114 (8)	0.534 ± 0.232 (3)
HT10	0.330 ± 0.095 (2)	0.495 ± 0.074 (2)	0.428 ± 0.045 (2)	0.596 ± 0.026 (2)
VOL6	0.303 ± 0.091 (8)	0.083 ± 0.229 (3)	0.264 ± 0.114 (8)	0.340 ± 0.057 (3)
VOL10	0.420 ± 0.003 (2)	0.503 ± 0.026 (2)	0.480 ± 0.031 (2)	0.417 ± 0.091 (2)
BG1	–0.450 ± 0.019 (2)	–0.735 ± 0.077 (2)	–0.417 ± 0.295 (2)	–0.497 ± 0.021 (2)
BG2	–0.402 ± 0.039 (2)	–0.685 ± 0.101 (2)	–0.392 ± 0.304 (2)	–0.466 ± 0.001 (2)
UP	–0.567 ± 0.074 (3)	–0.630 ± 0.057 (6)	–0.314 ± 0.119 (6)	–0.308 ± 0.101 (3)
ST	–0.496 ± 0.086 (3)	–0.540 ± 0.102 (2)	–0.355 ± 0.010 (6)	–0.365 ± 0.053 (3)
STR	–0.477 ± 0.056 (3)	–0.624 ± 0.043 (2)	–0.338 ± 0.223 (3)	–0.478 ± 0.044 (2)
RM1		0.943 ± 0.075 (3)	0.711 ± 0.050 (8)	0.687 ± 0.202 (3)
RM2			0.663 ± 0.117 (3)	0.659 ± 0.047 (4)
DL1				1.183 ± 0.091 (3)

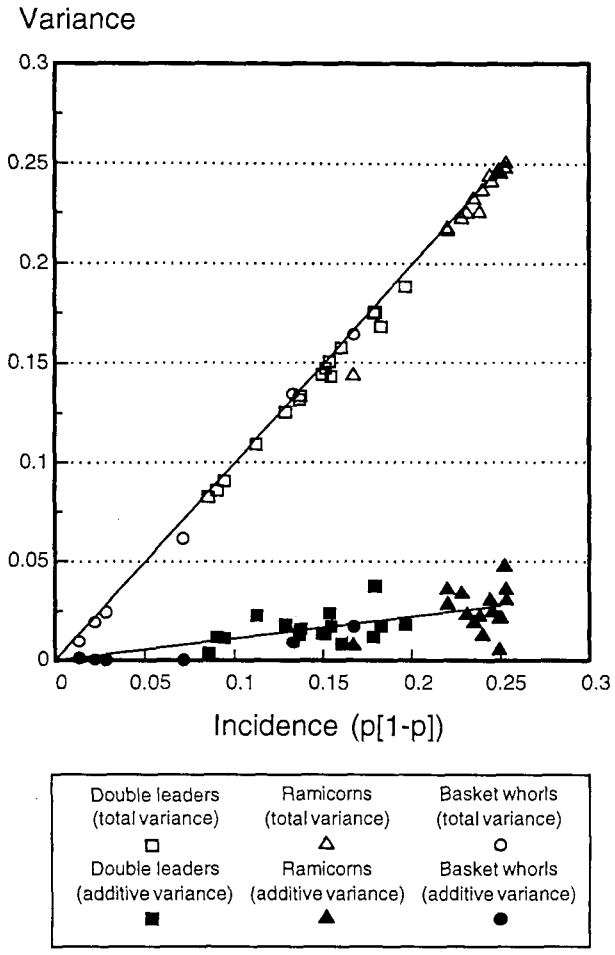

Figure 2 The relationship between mean incidence of basket whorls, double leaders and ramicorns, and the additive genetic and total phenotypic variance of these traits estimated from individual progeny tests of slash pine in south-east Queensland. (R^2 values are 0.996 and 0.483 for the total phenotypic and additive variances respectively.)

basket whorls from these two simple models was considerably higher than the average (Table 4). Therefore it appears that this model is not appropriate for basket whorls. When a linear model was fitted to the data for basket whorls separately, the r-squared value increased to 0.84, and implied a constant heritability on the binomial scale of 0.099; the adjusted heritability on the underlying normal scale was reduced only slightly to 0.29.

Implications for future breeding activities

The results presented indicate that growth, stem straightness and crown defect traits of slash pine grown in Queensland are all under a moderate level of genetic control with heritabilities around 0.15 to 0.3. Therefore, this species offers good opportunities for the further genetic improvement of all traits investigated. However, there may be a weak, adverse genetic correlation between the preferred method of straightness assessment (*i.e.* STR) and growth traits, as well as adverse genetic correlations between crown defects and growth traits. The adverse association between growth traits and crown defects appears to be the most serious, while the other correlations may be an artefact of the assessment procedure and/or were relatively weak with large standard errors so that they are probably close to zero.

Unpublished data indicate that incidence of double leaders and ramicorn branching is considerably lower in the Queensland breeding population of Caribbean pine than in the slash pine population. The F_1 hybrid between slash and Caribbean pines is usually intermediate between the two parental populations for these traits. Therefore, reduction in the incidence of crown defects in the F_1 hybrid is likely to be achieved most readily by selection against these traits in the slash pine breeding program. The favourable correlation between crown defects and stem straightness should mean that concurrent improvement in these traits will be relatively simple. However, generally adverse correlations between growth traits and both stem straightness and crown defects will mean that some trade-offs are necessary. In the absence of real economic weights it is difficult to determine the most appropriate emphasis to place on adversely correlated traits. A detailed sawing study is currently being undertaken in Queensland using slash and Caribbean pines, that aims to define breeding objectives and determine true economic weights for these species. However, in the interim breeding of slash pine in Queensland will aim to reduce the incidence of crown defects, at least maintain stem straightness, while attempting to improve growth.

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