Genetic Parameter Estimates for Radiata Pine in New Zealand and New South Wales: A Synthesis of Results

By K. J. S. Jayawickrama[1])

Forest Research, Private Bag 3020, Rotorua, New Zealand

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Abstract

This paper summarises genetic parameters for radiata pine, based on 1961 first-generation selections: 1660 tested in New Zealand and 301 tested in New South Wales. Three genetic parameters were estimated from analyses of pairs of sites: narrow-sense heritability (h^2_A), type B genetic correlation (r_B), and the genetic correlation between different traits (r_G). Within-site estimates of narrow-sense heritability (h^2_w) were also obtained. The traits were height, over-bark diameter at breast height (dbh), stem straightness score, branch cluster frequency score, malformation score, needle retention score, crop acceptability, wood density and grain spirality. The trees were assessed at between 5½ and 11 years from planting, with most of the trials assessed near age eight. Over 154,000 trees were assessed for growth and form, 6,200 for grain spirality and 6,700 for wood density.

A total of 172 estimates of h^2_A and r_B were obtained; these were unequally distributed across traits, from six estimates for spiral grain to 33 estimates each for dbh, branching and straightness. The mean h^2_w were higher than the pair-wise estimates; the discrepancy was greatest for height, malformation and needle retention score. The highest mean h^2, obtained by both approaches, was for branch cluster frequency. The overall mean h^2_A were: 0.11 (dbh), 0.13 (height), 0.19 (straightness score), 0.33 (branch cluster frequency score), 0.12 (needle retention score), 0.06 (acceptability) and 0.26 (spiral grain angle). The highest average r_B were for straightness, branch cluster frequency and spiral grain angle (0.89, 0.87 and 0.81 respectively). Based on 120 progenies on two sites, an h^2_A of 0.72 and a r_B of 0.99 were obtained for wood density.

A total of 711 r_G estimates were obtained, ranging for three estimates for spiral grain- acceptability to 66 estimates each for dbh-straightness and branching-straightness. Branch cluster frequency was positively correlated with height, dbh and straightness. Acceptability was strongly and positively correlated with straightness and malformation score. There appeared to be weak unfavourable correlations between dbh and grain spirality, and between dbh and density (the latter estimate based on two sites only).

Key words: Pinus radiata, heritability, genetic correlation, type B correlation, New Zealand, New South Wales, diameter, branch cluster frequency, straightness, malformation, spiral grain, wood density.

Introduction

Radiata pine is the main plantation forestry species in New Zealand, Australia and Chile. Starting in the 1950s (Thulin, 1957; Burdon, 1992b) there has been sustained work on the genetic improvement of this species in New Zealand. Key aspects of this programme have been described by Shelbourne et al. (1986, 1989), Carson et al. (1990), and Jayawickrama et al. (1997, 1998).

The selection of plus-trees in unimproved plantations was the starting point for the genetic improvement of radiata pine in New Zealand, as for other conifer tree improvement programmes world-wide. This selection was begun by the Forest Research Institute in 1949 and continued through to 1973, followed by another round of plus-tree selection between 1985 and 1988. Over 4,100 first-generation plus-trees were selected in all; details on these selection programmes are given in Shelbourne et al. (1986), Jayawickrama et al. (1997) and Jayawickrama and Low (1999). Large-scale progeny testing of first-generation plus-trees started in 1969 and continued to 1989 (Shelbourne et al., 1986; Jayawickrama et al., 1997). The New Zealand Radiata Pine Breeding Co-operative (NZRPBC) was formed in 1987. One of the members was an Australian corporation that had planted several open-pollinated progeny trials of first-generation selections between 1985 and 1987. This programme is described by Johnson (1987).

Many of the progeny trials listed above had the features recommended by White (1996) for the estimation of genetic parameters: half-sib mating designs, large numbers of families, single-tree-plot designs and replication over several sites. This contrasts with many published estimates of heritabilities and correlations for important conifer species, which have been from small groups of trials or even single trials, with few parents represented. The results from first-generation trials are also different from later generations, in that the genetic variance is expected to be at its highest in the first generation (Falconer and Mackay, 1996) and it is often possible to assume that the selections are unrelated. It will be assumed that first-generation selections made within the New Zealand landrace are unrelated to each other, and that the same applies to the Australian landrace.

The data from radiata pine progeny trials have been used internally in New Zealand and have played a key role in developing strategies for breeding. While some estimates are available (Bannister, 1969 and 1979; Wilcox et al., 1975; Shelbourne and Low, 1980; Johnson and Burdon, 1990; Carson, 1991; Burdon, 1992; Burdon and Low, 1992; Burdon et al., 1992 a,b,c; King and Burdon, 1991; King et al., 1998; Jayawickrama and Low, 1999), genetic parameter estimates from several important trials ("885", "887", NSW 1986, NSW 1987; see *Table 1* for descriptions) are unpublished and unavailable to the international tree breeding community. These four trials contained nearly 1,000 first-generation selections. The "885" and "887" trials in particular are well-suited for the estimation of genetic parameters (large number of families, multiple sites, single tree plot designs) and were planted at a time when New Zealand breeders had gained years of experience in progeny testing. In contrast, some of the earlier estimates were based on small populations (Bannister, 1969 and 1979; Wilcox et al., 1975; Carson, 1991). A recent development has been the large-scale screening for grain spirality (using the bark window technique), a trait for which few genetic estimates have been published for radiata pine. Neither has a comprehensive synthesis of data from the full database been attempted. Such summary parameters would be useful for purposes such as predicting gain, the choice of breeding and testing strategies,

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[1]) Current address: Department of Forest Science, Oregon State University, Corvallis, OR 97331-5752, USA

and in modelling. Given that radiata pine is a conifer species of commercial value, and in some ways a model species, there is a wealth of information that could interest a broader audience.

Since 1992 several summaries on major conifer species have come available, each based on a reasonable number of trials. These have been for: *Pinus patula* SCHIEDE and DEPPE (by BARNES et al., 1992), slash pine (*P. taeda* L.; by HODGE and WHITE, 1992 and DIETERS et al., 1995), longleaf pine (*P. palustris* MILL; by ADAMS et al., 1994), loblolly pine (*P. taeda* L.; by LI et al., 1996), *P. tecunumanii* (HODGE and DVORAK, 1999) and Douglas-fir (*Pseudotsuga menziesii* (MIRB) FRANCO; by STONECYPHER et al., 1996). In keeping with the progress in these species, and for the reasons given in the previous paragraph, a comparable synthesis for *P. radiata* is timely.

This paper was therefore written to present a summary of genetic parameters for radiata pine, based on 1961 first-generation selections of this species; 1660 tested in New Zealand and 301 tested in New South Wales.

Material and Methods

Selection of Trials for the Synthesis of Parameters

A subset of the first-generation New Zealand and Australian trials, each with a minimum of 100 half-sib families and planted on two or more sites, was selected for the purpose of this synthesis and is presented in *table 1.* With one exception (the "850" polycross), they were raised from open-pollinated seed collected from the parent ortets. A high proportion of the New Zealand trials were from the North Island; many of these were from the volcanic plateau in the centre of the island, for reasons explained below. The earliest of the trials selected for this synthesis deserves special mention: this was the "268" series trial planted in 1969, the largest progeny test planted in New Zealand (and perhaps in the world). It had 580 open-pollinated families plus controls on three sites, with 50 trees per family per site (SHELBOURNE et al., 1986), giving a total of over 90,000 trees planted. The New Zealand trials selected were planted as single tree plots or non-contiguous plots, with the exception of the "268" series trial which was planted as 10-tree row-plots. The Australian trials included in this synthesis were planted as 5-tree row-plots with up to 6 replications per site; no data were available from single-tree-plot trials.

Much of the testing in New Zealand has been in the central North Island. This has been due to five factors: the importance of this region for plantation forestry, the availability of suitable trial sites, good expression of phenotypic variability, rapid growth and the proximity to the Forest Research Institute in Rotorua. Several trials have also been planted on sandy soils in the northern North Island (the Auckland sands), a region characterised by high heritabilities but a smaller range of phenotypic variation than the central North Island. Some regions tend to have important limiting factors, such as high micro-site variability, frequent strong winds, earthslips, waterlogged soils, heavy weed pressure and slow growth. These factors resulted in having a high proportion of the New Zealand trials from the central North Island or the Auckland sands. The Australian trials included in this synthesis are of plus-trees selected in New South Wales and tested in the same state.

Table 1. – Description of first-generation trials used for genetic parameter estimation.

Series	Mating design	No. of progenies	No. of sites	Year planted	Plot design[1]	No. of replicates at individual sites	Age when individual sites were assessed (years)	No. of trees assessed for	
								Growth and Form	Spiral Grain (SPG) or Wood Density (WD)
In New Zealand									
"268"	O.P.	580[2]	3	1969	10-tree row plots	5	10[2]	39,176	5,950[2] (WD)
"850"	Poly-cross	109	6	1975	5 non-contiguous trees/ family/ replicate for 3 sets, an average of 3.5 for the fourth set	10	8 ½	22,652	–
"885"	O.P.	468	3	1987	Single-tree plots	25	8 ½, 8 ½, 6 ½	30,334	2,027 (SPG)
"887"	O.P.	224	3	1988	Single-tree plots	33, 32, 32	8 ½, 8 ½, 6 ½	16,973	2,937 (SPG) 732 (WD)
"888"	O.P.	279	3	1989	Single-tree plots	32	8 ½, 7 ½, 6 ½	24,236	–
In Australia (New South Wales)									
NSW 1986	O.P.	176	3	1986	5-tree row plots	6	9, 10	13,861	746 (SPG)
NSW 1987	O.P.	125	3	1987	5-tree row plots	6	9, 9, 11	7,227	485 (SPG)
TOTAL		***1961***	***24***					***154,279***	***6,195 (SPG)*** ***6,682 (WD)***

No. = Number, O.P. = Open Pollinated

1) All the New Zealand trials were established according to a Sets-in-Replications design, a variant of the Randomized Complete Block Design.

2) Height, dbh, straightness and density data also available on a subset of 120 progenies, on two of the three sites, at age 5 ½ years.

Field Assessments

Traits Assessed in New Zealand and the Associated Objectives

A number of traits are routinely assessed in radiata pine progeny trials and clonal trials in New Zealand. They are diameter at breast height over bark (dbh), straightness, branch cluster frequency, malformation, needle retention, acceptability, spiral grain angle and wood density (*Table 2*). The first five have been routinely assessed since 1983 while routine assessment of the two wood properties started around 1995; there was, however, a large screening effort on wood density in 1975. The relevance of these traits is outlined below, with more details available in Low (1991), King and Burdon (1991), Sorensson et al. (1997), Jayawickrama et al. (1997) and Jayawickrama and Low (1999).

Table 2. – Details of the traits assessed, and the assessment methods.

TRAITS	**Assessment criteria / method**
Diameter (dbh)	In millimetres, over bark, at breast height (1.4 m)
Straightness	Subjective 1-9 scale (1= very crooked , 9 = very straight)
Branch cluster frequency	Subjective 1-9 scale (1=one whorl per year, 9= several whorls per year)
Malformation	Subjective 1-9 scale (1= multiple forking, 9= no malformation)
Needle retention	Subjective 1 – 9 scale (1-3= up to 100% current year's foliage, 4-6= up to 100% current and previous year's foliage, 7-9= up to 100% current, 1-and 2-year old foliage)
Acceptability (ac1)	Acceptability = 1 if tree is subjectively judged likely to develop into an acceptable crop tree, = 0 if judged unacceptable
Wood density	Assessed using the water displacement method, on a bark-to-bark core of 5 mm diameter, taken at breast height
Spiral grain angle	Two measurements taken on opposite sides of the tree, at mid-whorl (as close as possible to breast height) avoiding grain deviations associated with branches, using the bark window method

Large, straight stems, free of malformation such as forks, bring more value to growers. Measurement of stem diameter at breast height (dbh) is much faster and often more accurate than measurement of total height under New Zealand conditions. The trees are often 16 meters in height at the age of assessment and seeing the tip may be difficult; the terrain is often steep. Consequently diameter has been measured in preference to height as an indication of vigour. Assessing branch cluster frequency score is a cost-effective way to rank entries for internode length, which in turn influences the yield of clearwood from unpruned stems (Jayawickrama et al., 1997). Needle retention is assessed mainly to rank entries for resistance to needle cast caused by *Cyclaneusma minus* (Butin) DiCosmo *et al.,* since needle loss at ages 6-10 tends to affect growth later in the rotation (Low, 1991; King and Burdon, 1991). Dothistroma needle blight, caused by *Dothistroma pini* Hulbary, is another disease that reduces crop productivity if left unchecked; this trait is assessed on sites with a high incidence of *Dothistroma* (Carson, 1989). High spiral grain angles in radiata pine are associated with lumber distortion on drying (Sorensson et al., 1997), while denser wood is usually stiffer and stronger and gives higher pulp yields.

Assessment Age

The first major assessment of a progeny trial, the "268" trial, was at age five years. Selection around eight years of age was later shown to give optimum genetic gains per unit time for radiata pine in New Zealand (King and Burdon, 1991). Since the 1980s the practice has been a single assessment around age 8. On a typical plantation site in New Zealand trees would average about 200 mm in diameter at this age. Sites such as the Auckland sands, which usually result in slower tree growth, tend to be assessed slightly later and very fertile sites are assessed slightly earlier. This results in data from trees of a fairly uniform size and state of development. The trials are now planted as single-tree plots; given that stands are often thinned by age 12 or earlier the trials are not designed to yield balanced data beyond this age.

Wood properties are usually assessed after the assessment of growth of form, and usually on a subset of progenies with good growth and form. This usually takes place around age 10 years.

Data in the Analysis

The data available for each group can be inferred from *table 3*. Height data were only available for the "268" and "850" series, while neither acceptability or spiral grain angle were assessed in these two series. Needle retention was not assessed on sites on which most of the trees showed very healthy foliage, or where *Cyclaneusma* was clearly not the agent causing needle loss.

Spiral grain or wood density data were used only where 50 or more progenies had been assessed for the given trait. This led to the selection of eight sites for spiral grain (with between 50 and 58 progenies assessed per site) and three sites for wood density (56 progenies on one site, and 120 progenies assessed on two sites).

Statistical Analysis

Within-site Analyses

Within-site (single-site) genetic parameters are convenient to calculate, and are used routinely to estimate heritabilities (e.g. Cotterill et al., 1987; Matheson et al., 1994; Hylen, 1997; Mugasha et al., 1997; Soria and Borralho, 1997). They are routinely used in the New Zealand radiata pine breeding programme, and were therefore estimated as the first step in this synthesis. The following linear models were used for statistical analyses:

Trait = mean + replicate(site) + family + error
in trials with single-tree plots, or

Trait = mean + replicate(site) + family + replicate*family + error
in trials with multiple-tree plots

where trait = diameter, straightness etc. Replicate, family and replicate*family were considered random effects. Variance components were estimated using the Reml option in PROC VARCOMP (SAS Institute Inc., 1988). Within-site narrow-sense heritabilities (h^2_w) were estimated as conventionally for half-sib families, namely:

$h^2_w = 4\ s^2_{fw} / s^2_{pw} = 4\ s^2_{fw} / [s^2_{fw} + s^2_e]$ in trials with single-tree plots, or

$= 4s^2_{fw} / [s^2_{fw} + s^2_{rf} + s^2_e]$ in trials with multiple-tree plots

with s^2_{fw} = within-site family variance,
s^2_{pw} = within-site phenotypic variance,
s^2_{rf} = within-site replicate*family variance,
s^2_e = within-site error variance

Across-site Analyses

Estimates based on a single location can be upwardly biased if there is significant genotype x environment interaction. The upward bias occurs when estimates of family variance within sites are greater than the estimate obtained across sites. This can happen when genetic effects are specific to some sites and not to others. The use of pooled across-site analyses avoids bias (White, 1996) and has been used by Hodge and White (1992), Adams et al. (1994) and Dieters et al. (1995). The procedure used in this study was as in Hodge and White (1992), namely:

Table 3. – Estimated within-site heritabilities, by series and site, for radiata pine in New Zealand and New South Wales. (Approximate standard errors of the estimates are given in parentheses).

Series	Site	Height	Dbh	Straightness score	Branch cluster frequency score	Malformation score	Needle retention score	% Acceptable stems	Spiral grain angle	Wood Density
268 (Age 5 ½)	Kaingaroa	0.25 (0.02)	0.29 (0.02)	0.20 (0.02)	•	•	•	•	•	0.65 (0.09)
	Waimihia	0.19 (0.02)	0.24 (.002)	0.20 (0.02)	•	•	•	•	•	0.82 (0.10)
268	Kaingaroa	•	0.29 (0.03)	0.34 (0.03)	0.38 (0.03)	•	•	•	•	•
	Waimihia	•	0.26 (0.02)	0.24 (0.02)	0.29 (0.03)	•	•	•	•	•
	Gwavas	•	0.16 (0.02)	0.22 (0.02)	0.27 (0.03)	•	•	•	•	•
850	Woodhill	0.39[1] (0.06)	0.24 (0.05)	0.18 (0.04)	0.50 (0.07)	0.06 (0.03)	•	•	•	•
	Maramarua	0.10[1] (0.03)	0.07 (0.02)	0.14 (0.03)	0.26 (0.05)	0.05 (0.02)	0.12 (0.03)	•	•	•
	Kaingaroa	0.21[1] (0.04)	0.36 (0.05)	0.33 (0.05)	0.59 (0.07)	0.17 (0.03)	0.21 (0.04)	•	•	•
	Golden Downs	0.27[1] (0.05)	0.16 (0.04)	0.27 (0.05)	0.46 (0.06)	0.13 (0.03)	0.25 (0.05)	•	•	•
	Eyrewell	0.47[1] (0.07)	0.28 (0.05)	0.16 (0.04)	0.38 (0.06)	0.05 (0.02)	0.21 (0.04)	•	•	•
	Berwick	0.16[1] (0.04)	0.22 (0.04)	0.15 (0.04)	0.30 (0.05)	0.08 (0.03)	•	•	•	•
885	Pouto	•	0.11 (0.02)	0.22 (0.02)	0.29 (0.03)	0.06 (0.01)	0.06 (0.01)	0.12 (0.02)	0.35 (0.12)	•
	Kaingaroa	•	0.21(0.02)	0.21 (0.02)	0.33 (0.03)	0.08 (0.02)	0.32 (0.03)	0.10 (0.02)	0.23 (0.10)	•
	Kairara	•	0.22 (0.03)	0.21 (0.03)	0.36 (0.03)	0.11 (0.02)	0.28 (0.03)	•	0.59 (0.15)	•
887	Pouto	•	0.22 (0.03)	0.21 (0.02)	0.30 (0.03)	0.04 (0.02)	0.24 (0.03)	0.10 (0.02)	0.21 (0.08)	•
	Kinleith	•	0.18 (0.03)	0.22 (0.02)	0.29 (0.03)	0.05 (0.02)	•	0.08 (0.02)	0.26 (0.09)	0.72 (0.15)
	Paengaroa	•	0.13 (0.03)	0.17 (0.02)	0.35 (0.04)	0.10 (0.03)	0.20 (0.04)	0.09 (0.03)	0.26 (0.09)	•
888	Pouto	•	0.20 (0.02)	0.22 (0.03)	0.42 (0.04)	0.10 (0.02)	0.24 (0.03)	0.09 (0.02)	•	•
	Kinleith	•	0.20 (0.03)	0.24 (0.03)	0.42 (0.04)	0.08 (0.02)	0.36 (0.04)	0.11 (0.02)	•	•
	Kaingaroa	•	0.16 (0.02)	0.16 (0.02)	0.33 (0.04)	0.06 (0.02)	0.10 (0.02)	0.07 (0.02)	•	•
NSW 1986	Billapaloola	•	0.15 (0.03)	0.16 (0.03)	0.30 (0.05)	0.04 (0.02)	0.11 (0.03)	0.02 (0.02)	0.36 (0.11)	•
	Carabost	•	0.09 (0.02)	0.16 (0.03)	0.35 (0.05)	0.03 (0.02)	0.15 (0.03)	0.07 (0.02)	•	•
	Mt. David	•	0.15 (0.03)	0.21 (0.04)	0.08 (0.02)	0.09 (0.03)	•	0.05 (0.02)	•	•
NSW 1987	Bago	•	0.15 (0.04)	0.22 (0.05)	0.58 (0.09)	0.05 (0.03)	•	0.09 (0.03)	•	•
	Carabost	•	0.13 (0.05)	0.27 (0.07)	0.50 (0.09)	•	0.19 (0.06)	0.03 (0.04)	•	•
	Nundle	•	0.24 (0.05)	0.33 (0.07)	0.66 (0.10)	0.13 (0.04)	0.26 (0.06)	0.15 (0.04)	0.55 (0.17)	•

[1]) At age 6 years.

1. For each trait, estimate family variances (s^2_f) for each pair of sites within a trial series as a covariance of family means.

2. For each pair of traits, estimate family covariances (s_{ff*}) for each pair of sites within a trial series as a covariance of family means.

3. For each trait and site, estimate the within-site family variance ((2fw) and within-site phenotypic variance (s^2_{pw}).

4. For each trait and pair of sites, estimate a pooled family variance (s^2_F) and pooled phenotypic variance (s^2_P) as geometric means of the two within-site family variances and within-site phenotypic variances respectively.

5. Estimate narrow-sense heritability (h^2), Type B genetic correlation (r_B), and the genetic correlation between different traits (r_g) for each pair of sites as:

$$h^2_A = 4\, s^2_f / s^2_P,$$
$$r_B = s^2_f / s^2_F$$
$$r_g = (s_{f,f*}) / (s^2_f\, s^2_{f*})^{1/2}$$

Family means were obtained for each site, using PROC MEANS in SAS (SAS Institute Inc., 1990). The covariance of family means on different sites was estimated using PROC CORR in SAS. Approximate standard errors of the within-site heritabilities were estimated using the formula given by BECKER (1992, p. 48).

WHITE (1996) recommended standardizing data prior to running pooled analyses, a recommendation used in both ADAMS et al. (1994) and DIETERS et al. (1995). This step was found not to alter the estimates of h^2_A, r_B or r_g in the current study.

Means and standard deviations

For the current study unweighted means were calculated for h^2, r_B and r_g, and the variability of these parameters quantified through calculating their empirical standard deviations (i.e. the square roots of the sample variances of the estimates). In the process of calculating mean parameter estimates, the reason for assigning weights to different estimates is that they vary in their information content. This was the case for HODGE and WHITE (1992), for example, where a pair of tests could have as few as five families in common. In the current study, there were between 100 and 580 families in common for the growth traits, and 50 to 58 families for spiral grain angle. Further, while the "268" series had a field design which is less desirable for the accurate estimation of variance components, this was compensated for by a very large number of families.

It is recognized that variances for heritabilities and genetic correlations are difficult to specify (BURDON, 1977, HODGE and WHITE, 1992); the true nature of the distribution of these parameters is unclear. Since for most traits there were a substantial number of estimates, I chose rather to estimate empirical standard deviations.

Results

Within-site narrow-sense heritabilities (h^2_w) are given in *table 3*. The highest h^2_w estimates were obtained for density, spiral grain angle and branch cluster frequency score, and the lowest estimates for malformation and acceptability. Mean within-site and across-site h^2 are given in *table 4*; type B correlations are given in *table 5*. There were 172 pair-wise estimates of heritability and type B correlation. These were unequally distributed across traits, from six estimates for spiral grain to 33 estimates each for dbh, branching and straightness. The individual pair-wise h^2_A estimates (not shown) ranged from –0.02 to 0.62 while the individual type B correlations (not shown) ranged from –0.36 to 1.74. The mean h^2_w were higher than the pair-wise estimates; the discrepancy was greatest for malformation and needle retention score. One consistent pattern was that the highest mean h^2, obtained by both

Table 4. – Estimated mean narrow-sense heritabilities1) (obtained by within-site and by pairwise analyses), by series and overall, for radiata pine in New Zealand and New South Wales.

SERIES	Height	Dbh	Straightness score	Branch cluster frequency score	Malformation score	Needle retention score	% Acceptable stems	Wood density	Spiral grain angle
Within-site heritabilities									
268 (Age 5 ½)	0.22	0.27	0.20	—	—	—	—	0.73	—
268		0.24	0.27	0.31	—	—	—	—	—
850	0.27[2]	0.22	0.21	0.42	0.09	0.20	—	—	—
885		0.18	0.21	0.33	0.08	0.22	0.10	—	0.39
887		0.18	0.20	0.31	0.06	0.22	0.09	—	0.24
888		0.19	0.20	0.39	0.08	0.23	0.09	—	
NSW 1986		0.13	0.18	0.24	0.05	0.13	0.05	—	0.36
NSW 1987		0.17	0.27	0.58	0.09	0.23	0.09	—	0.55
OVERALL	*0.27[3]* *(0.14)*	*0.19[3]* *(0.07)*	*0.22[3]* *(0.06)*	*0.37* *(0.13)*	*0.10* *(0.06)*	*0.21* *(0.09)*	*0.08* *(0.03)*	—	*0.35* *(0.14)*
Across-site heritabilities									
268 (Age 5 ½)	0.17	0.25	0.14	—	—	—	—	0.72	—
268		0.17	0.33	0.25	—	—	—	—	—
850	0.13[2]	0.10	0.16	0.35	0.03	0.08	—	—	—
885		0.10	0.18	0.26	0.02	0.18	0.06	—	0.35
887		0.11	0.16	0.25	0.02	0.08	0.04	—	0.17
888		0.16	0.19	0.40	0.04	0.12	0.08	—	—
NSW 1986		0.06	0.14	0.19	0.03	0.12	0.02	—	—
NSW 1987		0.09	0.25	0.55	0.02	0.16	0.15	—	—
OVERALL[2]	*0.13[3]* *(.05)*	*0.11[3]* *(.05)*	*0.19[3]* *(.06)*	*0.33* *(.12)*	*0.03* *(.03)*	*0.12 (.06)*	*0.06* *(.04)*	—	*0.26* *(.11)*

1) Empirical standard deviations are given in parentheses.

2) At age 6 years.

3) Does not include the age 5 ½ "268" data.

Table 5. – Estimated mean Type B correlation[1] (obtained by pairwise analyses), by series and overall, for radiata pine in New Zealand and New South Wales.

SERIES	Height	Dbh	Straight-ness score	Branch cluster frequency score	Malforma-tion score	Needle retention score	% Accep-table stems	Wood density	Spiral grain angle
268 (Age 5 ½)	0.78 (3)	0.96 (3)	0.68 (3)	–	–	–	–	0.99 (1)	–
268		0.84 (3)	1.48 (3)	0.91 (3)	–	–	–	–	–
850	0.54[2] (15)	0.47 (15)	0.83 (15)	0.85 (15)	0.33 (15)	0.42 (6)	–	–	–
885		0.56 (3)	0.84 (3)	0.81 (3)	0.22 (3)	0.63 (3)	0.63 (1)	–	0.92 (3)
887		0.60 (3)	0.79 (3)	0.81 (3)	0.34 (3)	0.36 (1)	0.48 (1)	–	0.69 (3)
888		0.70 (3)	0.80 (3)	0.88 (3)	0.50 (3)	0.33 (3)	0.68 (3)	–	–
NSW 1986		0.48 (3)	0.83 (3)	0.90 (3)	0.66 (3)	0.85 (1)	0.61 (3)	–	–
NSW 1987		0.49 (3)	0.89 (3)	0.95 (3)	0.65 (3)	0.76 (1)	1.26 (1)	–	–
OVER ALL	*0.54[3] (.17)*	*0.55[3] (.19)*	*0.89[3] (.30)*	*0.87 (.12)*	*0.36 (.33)*	*0.49 (.32)*	*0.69 (.26)*	–	*0.81 (.22)*

[1] Numbers in parentheses are the number of site-site correlations for a trait within a series. In the case of the last line in the table (OVERALL), the numbers in parentheses are the empirical standard deviations.

[2] At age 6 years.

[3] Does not include the age 5 ½ "268" data.

approaches, was for branch cluster frequency. The highest mean across-site h^2 were for the NSW 1987, 888 and 850 series (0.55, 0.40 and 0.35 respectively). No h^2_A, r_B or r_g could be obtained for grain spirality for the NSW 1986 and NSW 1987 series, since this trait was only measured on one site in each series.

The r_g for the "268" trial were grouped separately since they were for age 5½ years, and because they included wood density (*Table 6*). A total of 711 r_g estimates were obtained from the assessments made on the other trials, ranging for three estimates for spiral grain: acceptability to 66 estimates for dbh: straightness and branching: straightness. The individual estimates (not shown) ranged from –2.92 to 5.79. Mean genetic correlations, by trait combination are given in *table 7*. Branch cluster frequency was positively correlated with height, dbh and straightness. Acceptability was strongly and positively correlated with straightness and malformation score.

Table 6. – Estimated mean genetic correlations (obtained by pairwise analyses), for two sites of the '268' series radiata pine trial at age 5 ½ years.

	Dbh	Straightness score	Wood density
Height	0.52 (6)	-0.43 (6)	0.22 (2)
Dbh		-0.41 (6)	-0.16 (2)
Straightness score			-0.26 (2)

The numbers in parentheses are the number of between-site correlations for a given pair of traits. Giving an example for clarity, the trait1, site A: trait2, site B correlation and the trait2, site A: trait1, site B correlation were considered two separate estimates of the same trait.

Discussion

The common trend reported to date, for genetic parameters, has been for h^2_A to be lower than h^2_w (Hodge and White, 1992; Adams et al., 1994; Dieters et al., 1995). The differences in the current study between h^2_A and h^2_w matched expectation for the most part, although the difference for height was large. This could be because the height data came from only one trial.

The mean across-site heritabilities in this summary generally fell in the range hypothesized by Burdon (1992): 0.13 for height (compared with 0.2), 0.11 for dbh (0.1 to 0.3), 0.19 for straightness score (0.1 to 0.3), 0.33 for branch cluster frequency score (0.3), 0.12 for needle retention score (0.1 to 0.35 for *Cyclaneusma* needle cast), 0.72 for wood density (0.7). Burdon's (1992) estimates were based largely on a trial with native populations, which would be expected to have a greater amount of genetic variation than between selections from the landrace. The striking exception is a grain spirality estimate of 0.26 compared with Burdon's prediction of 0.8 or higher.

The type B correlations in this summary were quite high for the important traits. This could be attributed to a number of reasons. They would increase as the covariances of family means (and hence s^2_f estimates) increase, in turn due to the ranking of families being consistent on different sites. Efficient trial designs that ranked families well would help, as would allowing the trees to reach similar sizes and states of development at different sites. Covariances of family means based on large numbers of families would tend to be more stable. Interestingly the "850" series, which had the widest range of sites (and therefore the highest potential for rank changes), did not stand out by having the lowest mean r_B values. One interpretation is that sites in New Zealand are relatively homogeneous;

Table 7. – Estimated mean genetic correlations[1] (obtained by pairwise analyses), by series and overall, for radiata pine in New Zealand and New South Wales.

	Dbh	Straightness score	Branch cluster frequency score	Malformation score	Needle retention score	% Acceptable stems	Spiral grain angle
Height	0.69 (0.31)	-0.19 (0.36)	0.31 (0.18)	-0.10 (0.75)	-0.07 (0.45)	–	–
Dbh		0.04 (0.30)	0.34 (0.27)	0.04 (1.15)	0.20 (0.52)	0.12 (0.37)	0.34 (0.53)
Straightness score			0.38 (0.24)	0.49 (0.71)	0.18 (0.25)	0.98 (0.24)	-0.38 (0.61)
Branch cluster frequency score				0.49 (0.88)	0.15 (0.30)	0.47 (0.54)	0.18 (0.29)
Malformation score					0.24 (0.76)	0.68 (0.51)	0.50 (0.86)
Needle retention score						0.31 (0.36)	0.35 (0.20)
% Acceptable stems							0.29 (0.45)

[1] Empirical standard deviations are given in parentheses.

another is that open-pollinated families from the New Zealand landrace are well-buffered against changes in environment from site to site.

The mean r_B were highest for density, straightness score, branch cluster frequency and spiral grain angle (*Table 5*). JAYAWICKRAMA and LOW (1999) found that branch cluster frequency had the highest across-site heritability; across-site heritabilities for dbh, malformation and needle retention were considerably lower than within-site heritabilities. JOHNSON and BURDON (1990) obtained higher r_B for straightness and branch cluster frequency than for dbh. Other analyses (unpublished) by the New Zealand radiata pine breeding programme have shown similar results and that ranks for wood density, grain spirality, straightness and branch cluster frequency are consistent across sites. With regards to needle retention, the causes for needle loss could vary from site to site; the cause could be a pathogen on one site and a nutrient deficiency on another site. This could account for large changes in rank from site to site and low r_B. It was no surprise that the r_B estimates for malformation score were lower than for the other traits; the previous experience has been that malformation is not under as strong a genetic control as straightness, branch cluster frequency or dbh.

The high heritability of branch cluster frequency has resulted in internode length being increased significantly in the Long Internode breed (JAYAWICKRAMA et al., 1998), and decreased, often indirectly, in the main production population. Branch cluster frequency increases (and internode length decreases) when selecting intensively for dbh and straightness, due to the modest positive correlations between branch cluster frequency, straightness and dbh (*Table 7*).

A possible cause for high mean h^2_w and h^2_A for branch cluster frequency in the NSW 1987, 850 and 888 series is that the parents tested in these series came from a population covering the full range for this trait. This issue is explored for the "850" and "888" series in greater detail by JAYAWICKRAMA and LOW (1999); both these series contained parents selected in diverse parts of New Zealand. The high r_B for needle retention observed in the two NSW series may be due to needle loss being controlled by the same agent across sites, resulting in a stable ranking of genotypes.

Acceptability was an unusual trait in that h^2_w and h^2_A were low, but at the same time r_B were as high as for dbh, and r_g with straightness and malformation were high. One interpretation is that most of the information in this trait is already contained in the scores for straightness and malformation. The unfavourable r_g observed between dbh and grain spirality and between dbh and density, though weak, are cause for some concern as they imply that faster-growing families tend to have more extreme spirality and lower density. The true correlations may be greater than the figures of 0.34 and 0.16 obtained, given that spirality and density tend to be assessed on families pre-selected for growth and form.

It is of interest that the r_g between dbh and straightness appeared to be negative (unfavourable) at age five years (*Table 6*) and close to zero at age eight (*Table 7*). There are some unpublished results which indicate the correlation then becomes positive when the trees are older. It has been hypothesised that faster growing trees may show sinuosity at early ages; they push their way above their peers and grow faster in diameter, and eventually fill up the curvature on the bole. This would indicate assessment of stem straightness earlier rather than later, since the consequences of sinuosity continue (in terms of grade recovery) even beyond the stage when the outside of the log shows evidence for it.

It is possible to impose bounds on the values of parameters that are considered acceptable, such as –1.3 and 1.3 for r_g, and –0.3 and 1.3 for r_B (HODGE and WHITE, 1992). This approach was not taken in the current study, and all estimates were accepted. Of the 711 estimates of r_g, 50 were greater than 1 and 5 were greater than 2. This can be compared with the distribution of a standard normal variable with mean 0 and variance 1, which would be expected (for a sample of 711) to have 113 observations greater than 1 and 16 observations greater than 2.

Genetic correlations between dbh, straightness score, branch cluster frequency score and malformation score have been relatively well estimated in this study in terms of the number of estimates obtained and the number of progenies assessed. By this standard, r_g involving spiral grain angle and wood density have been estimated based on relatively few pair-wise estimates. The best datasets existing for these two traits are based on 120 progenies on two sites (for wood density) and 58 progenies on three sites (for spiral grain angle). More definitive estimates of r_g involving these two traits are a priority for radiata pine improvement, and would entail including families that rank poorly for growth and form.

Sixteen of the 18 New Zealand sites were in the North Island. Given that about 30% of the plantation estate of radiata pine in New Zealand is in the South Island, the South Island was under-represented in the trial area. The reasons for concentrating trials in the central North Island have been explained previously. It should also be emphasised that these findings relate to the age for which the greatest volume of data is available, that is for the period between age six and 10 years. This is natural given that selection typically takes place at this age. A comparable volume of data are not available for radiata pine close to rotation age (which can be between 20 and 35 years), and it is unlikely that extensive data will be collected for rotation-age trees.

In addition to the six sites in New South Wales, there are several active breeding programmes and first-generation trials in other parts of Australia (Victoria, Tasmania, South and Western Australia). In some instances the inheritance of traits not discussed here have been studied, such as by Butcher et al. (1984). There are therefore more opportunities to summarise genetic parameters for radiata pine in Australia.

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Appendix 1. – Description of sites for trials involved in parameter estimation.

Group and Series	Site	Soil type	Elevation (m)	Latitude (South)	Previous use	Trees measured as % of trees planted
“268”	Kaingaroa	Volcanic ash	400	38° 35′	Manuka, scrub, bracken fern	45^1
	Waimihia	Volcanic	400	38° 50′	Manuka, bracken fern	47^1
	Gwavas	Yellow-brown earth	485	39° 44′	Abandoned farmland	43^1
“850” polycross	Woodhill	Sand	20	36° 20′	Sanddune	66
	Maramaura	Heavy clay	110	37° 19′	*P. nigra* stand	79
	Kaingaroa	Volcanic ash, pumice	560	38° 41′	Manuka	95
	Golden Downs	Gravel	670	41° 35′	Grazing land	71
	Eyrewell	Stony silt loam	180	43° 25′	*P. radiata* stand	87
	Berwick	Yellow-brown earth	400	45° 58′	Grazing land	66
“885”	Pouto	Yellow-brown sand	30	36° 22′	Sand	95
	Kairara	Clay, silty clay, silt loam	100	35° 48′	Grazing, farming	75
	Kaingaroa	White pumice	570	38° 30′	*P. nigra* stand	89
“887”	Pouto	Sand	30	36° 21′	Sand	96
	Kinleith	Pumice, organic topsoil	370	38° 17′	*P. radiata* stand	85
	Paengaroa	Pumice	60	37° 50′	Farmland	56
“888”	Pouto	Sand	30	36° 20′	Sanddune	98
	Kinleith	Pumice, organic topsoil	380	38° 16′	*P. radiata* stand	88
	Kaingaroa	Pumice, ash	400	38° 30′	*P. radiata* stand	83
NSW (1986)	Bilapaloola	NA	NA	35° 15′	NA	83
	Carabost	NA	NA	35° 40′	NA	93
	Mt. David	NA	NA	33° 45′	NA	87
NSW (1987)	Bago	NA	NA	35° 40′	NA	83
	Carabost	NA	NA	35° 40′	NA	47^1
	Nundle	NA	NA	31° 20′	NA	63

[1]) Trials were thinned before the assessment reported in this study. NA = information not a available.