

# BREEDING FOR WOOD QUALITY AND PROFIT IN *PINUS RADIATA*: A REVIEW OF GENETIC PARAMETER ESTIMATES AND IMPLICATIONS FOR BREEDING AND DEPLOYMENT\*

H. X. WU<sup>†</sup>, M. IVKOVIĆ, W. J. GAPARE, A. C. MATHESON,  
B. S. BALTUNIS,

CSIRO Forest Biosciences\*\*,  
P O Box E4008, Kingston, ACT 2604, Australia

M. B. POWELL, and T. A. McRAE

Southern Tree Breeding Association Inc.  
P O Box 1811, Mount Gambier, SA 5290, Australia

(Received for publication 1 August 2007; revision 20 September 2007)

## ABSTRACT

We surveyed 55 genetic studies published from 1960 to 2007 involving 11 growth-, form-, and wood-quality traits in *Pinus radiata* D. Don, including seedling and clonal trials. Estimated genetic parameters evidently varied according to populations, environments, and ages. Overall, estimated heritability for wood-quality traits (except shrinkage) was always higher than for growth and form traits. Wood density had the highest grand-mean of estimated heritability (0.63) among the six wood-quality traits, followed by microfibril angle (0.61), spiral grain (0.55), fibre (tracheid) length (0.54), stiffness (0.50), and shrinkage (0.20). Selective breeding for these wood-quality traits (except shrinkage) would be very effective. Among the five growth and form traits, branch cluster frequency had the highest heritability (0.35), followed by branch size (0.27), branch angle (0.25), diameter at breast height (0.23), and stem straightness (0.23). Broad-sense heritability estimates were higher than narrow-sense heritability, particularly for diameter at breast height (average 0.39 *versus* 0.21). This indicates there is considerable non-additive genetic variance that should be exploited in breeding and deployment programmes for *P. radiata*. There was a higher and more complex genotype by environment interaction ( $G \times E$ ) for diameter at breast height in Australian sites than in New Zealand sites. Growth rate (dbh) was adversely correlated with all wood-quality traits (for both density and mean stiffness  $rg = -0.48$ ).

\* Paper originally presented at the inaugural Australasian Forest Genetics Conference “Breeding for Wood Quality”, Hobart, 11–14 April 2007.

<sup>†</sup> Corresponding author: Harry.wu@csiro.au

\*\* Research carried out under the Ensis UJV

Breeding for overcoming or at least coping with adverse genetic correlations and effective utilisation of non-additive genetic variation are two of the most challenging issues in the advanced generations of *P. radiata* tree improvement and deployment programmes.

**Keywords:** genetics; tree breeding; genetic parameters; heritability; genetic correlation; *Pinus radiata*.

## INTRODUCTION

The importance of limitation in wood quality in *Pinus radiata* was recognised a long time ago in Australia. Jacobs (1938) recorded the occurrence and importance of spiral grain in *P. radiata* in the Australian Capital Territory. Genetic variation in wood-quality traits such as density, spiral grain, and tracheid length was reported by Fielding (1953), and heritability for wood density in Australian *P. radiata* was estimated as early as 1960 (Fielding & Brown 1960; Dadswell *et al.* 1961). In 1957, the first *P. radiata* seed orchard was established (Brown 1971). The 1960s and early 1970s saw increased studies on genetic variation of wood quality and their importance for tree improvement (Eldridge 1962; Nicholls *et al.* 1964; Nicholls 1967; Fielding 1967; Bannister 1969; Burdon & Harris 1973; Burdon 1975). These early genetic studies on *P. radiata* wood quality were reviewed by Nicholls (1978).

Although the significance of wood-quality traits in *P. radiata* breeding was recognised at the same time as *P. radiata* breeding programmes started more than 50 years ago, only in the last few years has concerted breeding for wood quality been applied. The first formal assessments of wood properties for *P. radiata* breeding started before 1960 (Nicholls & Dadswell 1965), and the initial concern about a possible adverse relationship between growth and wood density was raised in 1958 (Fielding 1958). Wood density was often cited as the single most-important wood-quality trait because it is easier to measure than other wood traits and it strongly correlates with timber strength and stiffness and with some pulp and paper properties (Harris 1976; Cown *et al.* 1992). Although wood density was measured for many of the early plus-trees, selection intensity for this trait (discarding about one in five) was far too small to be effective.

In the early 1990s, breeding values for wood density were predicted for 122 parents (from a total of 1213 first-generation selections) and 619 progenies (from a total of 1152 second-generation selections) in the Southern Tree Breeding Association (STBA) breeding population, but only about two dozen trees with wood density values were included in an index selection for the second-generation breeding population (White *et al.* 1999). Incorporation of wood density was seriously implemented only in the recent selection of the third-generation breeding population after optimal economic weights were worked out for breeding objective traits (Ivković, Wu, McRae, & Powell 2006). In New Zealand, early selection was

focused on “Growth and Form” (Thulin 1957; Shelbourne *et al.* 1986). In 1970, a “Long Internode” breed was instigated to produce knot-free lumber from unpruned trees (Jayawickrama *et al.* 1997). Ranking families for wood density (by Pilodyn penetrometer) started in 1975 in New Zealand, with two seed orchards established in the late 1970s and early 1980s containing clones with high wood density, but a formal breeding population was not formulated until 1988. To increase wood density, a “High Wood Density” breed was established in 1995 (Jayawickrama & Carson 2000).

There are several reasons for the 40-year delay between recognition of the importance of wood-quality traits and incorporation of wood density and other wood-quality traits into practical breeding programmes. For example:

- (1) There was no requirement or market push for improving wood density in the initial selection and breeding programme. The connection between wood quality and the sawing and processing properties of logs was not established at early stages of breeding. In Australia, wood stiffness of older logs was high enough and usually acceptable for structural timber. In New Zealand, harvesting of trees from the 1925–35 planting boom which had increased density due to tree age had deterred uptake of genetic improvement of wood properties.
- (2) Measuring large numbers of trees for wood density was too slow and expensive using hand-operated increment corers and, somewhat later, ancillary equipment such as the torsionmeter and Pilodyn penetrometer.
- (3) Advanced-generation breeding programmes were not started until the late 1970s in New Zealand and early 1980s in Australia, and breeding objectives were not well-defined for the first two generations.

Breeding for wood density and quality was more seriously recognised in recent years because of shorter rotations and the realisation that lengthening the rotation markedly increases the effective growing cost. This is due to a significant boost of growth rate through the first generation of genetic improvement and more aggressive silvicultural regimes applied to the new plantations. In Australia, realised genetic gains up to 33% were reported for volume at age 15 years from the first generation of selections (Matheson *et al.* 1986), and most first-generation trials measured at 10–15 years produced an average of 20–25% volume gain (Eldridge 1982; Johnson 1992). In New Zealand, volume gains increased 3–35% from the first generation of selection, with the majority of gains around 20% (Shelbourne *et al.* 1986; Carson *et al.* 1999). With such increases in growth rate, plantation rotations have become shorter. In New Zealand rotation length has been shortened from 37–40 years to 27 years in 1999 (Jayawickrama 2001) and to 20 years for some stands (Macalister 1997); in Australia, plantation rotations have been shortened from about 45 years to 30 years (Ivković, Wu, McRae, & Powell 2006). With such shortened rotations, the proportion of both corewood and juvenile wood (Burdon

*et al.* 2004) with unfavourable characteristics (Cown 1980; Walker & Butterfield 1996; Xu & Walker 2004) has increased greatly. This in turn affects grade outturn in sawmills (Ivković, Wu, McRae, & Powell 2006).

To breed for wood-quality traits alone would be effective because estimated heritabilities for wood-quality traits such as wood density, microfibril angle, and modulus of elasticity are usually high, and there is sizable genetic variation (Wu *et al.* 2007; Baltunis *et al.* 2007). The decline of wood density from faster-growing trees was attributed partly to negative genetic correlations and partly to negative environmental correlations (Zobel & Buijtenen 1989; Downes *et al.* 2002). Our biggest challenge is breeding against the negative genetic correlation (adverse relationship) between wood quantity and quality. This challenge has been raised by *P. radiata* breeders (Dean 1986) several times but has never been seriously addressed in breeding programmes. To overcome the adverse genetic correlation, we have adopted two approaches for Australian *P. radiata* breeding programmes:

- (1) In the short term, developing appropriate breeding objectives for structural timber products, and
- (2) In the long term, developing optimal breeding strategies to overcome or breed out the adverse relationship by dissecting the genetic basis of the adverse relationship between quantity and quality traits (or at least not to increase and possibly to decrease adverse correlations).

The economic breeding objectives were developed for Australian *P. radiata* structural timber production, by estimating optimal economic weights for breeding-objective traits (Ivković, Wu, McRae, & Powell 2006; Ivković, Wu, McRae, & Matheson 2006). The purpose for developing economic breeding objectives is to construct a merit index which maximises profit by weighting breeding-objective traits according to their relative economic importance. To estimate the economic weights precisely, five general steps were undertaken for structural wood production in *P. radiata*:

- (1) Specification of the breeding, production, and marketing systems;
- (2) Identification of sources of income and expense in the specified production and marketing systems;
- (3) Determination of biological traits influencing returns and costs of the production system (breeding-objective traits);
- (4) Definition of a profit equation (or bio-economical model) linking profit with biological traits; and
- (5) Derivation of the economic value of each breeding-objective trait.

Four breeding-objective traits were defined after an industry survey of *P. radiata* companies. These were mean annual increment, branch size, or branch index (BIX), stem sweep, and timber stiffness. A bio-economic model was constructed to link breeding-objective traits with each component of a production system and

used to estimate economic weights for such traits. Economic weights for the four breeding-objective traits reflect how the improvement in those traits impacts on the overall profitability of a forestry enterprise. An economic weight is formally defined as the expected change in overall profitability of an enterprise as a result of a unit increase in a given breeding-objective trait, and a selection index was developed that combines those economic weights and genetic parameters (heritabilities and correlations) (Ivković, Wu, McRae, & Powell 2006). Although an economic index is optimal for the current population, it does not necessarily diminish adverse correlation between traits (Sanchez *et al.* in press).

For a long-term solution to the adverse genetic correlation between quantity and quality of *P. radiata* wood production, understanding of the genetic basis is critical. To understand this and to improve corewood and juvenile wood of *P. radiata*, a research project called the Juvenile Wood Initiative was launched with the four objectives to:

- (1) Develop optimal methods for measuring juvenile wood (corewood);
- (2) Understand the quantitative genetics of juvenile wood traits;
- (3) Understand the molecular genetics of juvenile wood traits;
- (4) Develop strategies to improve juvenile wood.

Our current focuses are on integrating molecular information into quantitative genetics and breeding programmes, and developing strategies to deal with adverse genetic correlations between wood quantity and quality.

Both developing a breeding objective and addressing the adverse genetic correlations require understanding of the pattern of variation and inheritance of wood traits. In addressing breeding objectives for tree species, selection is usually conducted long before rotation age owing to the long generation interval. Breeding-objective traits are usually defined in terms of harvest (rotation)-age values, at around 30 years, but selection of genotypes for breeding purposes is usually done much earlier, based on the measurements at 6 or 7 years. To link selection criteria to breeding-objective traits for breeding purposes, good estimates of genetic and phenotypic covariances between traits at selection (early age) and rotation ages are among the necessary pieces of information.

To overcome the adverse genetic correlation between quantity and quality of wood and to develop an optimal strategy, an understanding of the genetic basis at both quantitative and molecular levels is essential.

In this study, genetic parameter estimates for 11 *P. radiata* traits were reviewed with a focus on wood-quality traits. Five growth and form traits were diameter at breast height (dbh), stem straightness (STS), branch size (BRS), branch angle (BRA), and branch cluster frequency (BRC). Six wood-quality traits were wood density (DEN), microfibril angle (MfA), wood stiffness or modulus of elasticity (MoE),

spiral grain (SPG), shrinkage (SHR), and fibre (tracheid) length (FBL). There are limited parameter estimates for some additional traits that are not addressed in this review and which is based only on published genetic parameters.

## METHODOLOGY

Several studies examined tree-to-tree variation for wood properties before the 1960s, but none of them estimated the ratio of genetic to environmental variation in *P. radiata*. Beginning with Fielding & Brown (1960), experiments were set up to study inheritance of wood density and other wood-quality traits. Since then, numerous heritabilities and genetic correlations among growth, tree-form, and wood-quality traits in *P. radiata* have been estimated. We have surveyed published *P. radiata* genetic studies involving 11 traits in a total of 55 publications from 1960 to 2007 (Appendix 1). These publications represent the most important inheritance estimates in *P. radiata*, and heritabilities and genetic correlations are summarised in the Findings and Discussion section.

The sample size varied widely among the publications and estimates, from a minimum of nine clones to a maximum of 580 families. Pedigrees used varied from clone (CI) to half-sib (Hs) or full-sib (Fs) families, or mixtures of half- and full-sib families in more recent studies. Ages of estimates ranged from year 1 up to harvest age of 30 years, or from ring 1 to ring 30 from pith. Also heritability was estimated based on broad-sense heritability (B), or tree-to-tree repeatability of clones and individual narrow-sense heritability (N). For stem straightness, branch size, and branch angle, a measurement score of 1–6 (or 5 and 9) was usually used in these publications, with high scores representing straight, small branch, and flat branch angle, respectively. For each trait, a total number of estimates, mean and median were assembled from published data. Due to large differences in numbers of estimates among publications, an arithmetic average estimate was calculated for each publication, and a grand mean was computed based on the arithmetic average of means for each publication. It is acknowledged that the estimates of both heritability and genetic correlations were not of equal precision, no attempt could be made to weight them for their relative value as most of the estimates were published without a standard error of the estimates.

## FINDINGS AND DISCUSSION

### Growth Rate

Growth rate was represented mainly as diameter at breast height (dbh), usually measured 1.3 m above ground level in Australia and 1.4 m in New Zealand. Diameter at breast height is the most commonly measured growth trait and has been the focus of numerous genetic studies to date (Table 1).



TABLE 1—continued

| Sample size        | Age(s)                    | Heritability |             | Genetic correlation $\diamond$ |       |       |       |      |     | Ref. No. <sup>‡</sup> |      |
|--------------------|---------------------------|--------------|-------------|--------------------------------|-------|-------|-------|------|-----|-----------------------|------|
|                    |                           | Aver. value  | No. estim's | STS                            | BRA   | BRS   | BRC   | MfA  | MoE |                       | SPG  |
| 10(Cl)             | Year 16                   | 0.51         | 2(B)        |                                |       |       |       |      |     |                       | 31   |
| 25(Hs)             | Year 13, 25               | 0.88         | 2(N)        |                                |       |       |       |      |     |                       | 32   |
| 73-467(Hs)         | Year 8 and 10             | 0.22         | 4(N)        |                                |       | 0.28  |       |      |     |                       | 34   |
| 28 (Hs)            | Year 7                    | 0.22         | 1(N)        |                                | 0.13  | -0.89 |       |      |     |                       | 35   |
| 154(Fs)            | Year 7                    | 0.14         | 4(N)        |                                |       |       |       |      |     |                       | 36   |
| 11(Fs)             | Year 10,12,14, 16,18      | 0.25         | 5(N)        |                                |       |       |       |      |     |                       | 37   |
| 11(Fs)             | Year 23                   | 0.16         | 1(N)        |                                |       |       |       |      |     |                       | 38   |
| 15-36(Fs)          | Year 5,5, 8,5, 15         | 0.28         | 4(N), 8(B)  |                                |       |       |       |      |     |                       | 39   |
| 125-580(Hs)        | Year 6-11                 | 0.20         | 26(N)       | 0.04                           |       |       | 0.34  |      |     | 0.34                  | 40   |
| 224(Hs)            | Year 12                   | 0.10         | 1(N)        | 0.26                           |       |       |       |      |     | -0.65                 | 42   |
| 29-72 (Hs)         | Year 7,8 10,11, 13,14, 15 | 0.18         | 4(N)        |                                |       |       |       |      |     |                       | 44   |
| 100-216(Fs)        | Year 9-10                 | 0.15         | 10(N)       | -0.02                          | 0.17  | -0.42 | -0.01 |      |     |                       | 45   |
| 30 (Hs)            | Year 1-26                 | 0.29         | 26(N)       |                                |       |       |       |      |     |                       | 47   |
| 19(Fs), 70(Hs)     | Year 7 and 10             | 0.30         | 6(N), 4(B)  |                                |       |       |       |      |     |                       | 50   |
| 30(Hs)             | Year 1-28 (30)            | 0.34         | 58(N)       |                                |       |       |       |      |     |                       | 51   |
| 110-250(Fs and Hs) | Ring 1-6                  | 0.15         | 2(N)        |                                |       |       |       | 0.26 |     | -0.5                  | 53   |
| Min                |                           | 0.03         |             | -0.02                          | -0.28 | -0.89 | -0.01 | 0.26 |     | -0.65                 | 0.34 |
| Max                |                           | 0.88         |             | 0.48                           | 0.37  | 0.37  | 0.43  | 0.26 |     | -0.30                 | 0.34 |
| Grand Mean         |                           | 0.23         |             | 0.22                           | 0.05  | -0.21 | 0.29  | 0.26 |     | -0.48                 | 0.34 |

$\diamond$  Genetic correlations: STS stem straightness; BRA branch angle; BRS branch size; BRC branch cluster frequency; MfA microfibril angle; MoE modulus of elasticity; SPG spiral grain

<sup>‡</sup> References listed in Appendix 1

<sup>‡</sup> Clone (CL), Half-sib (HS), Full-sib (Fs)

$\S$  Narrow-sense (N), Broad-sense (B)

$\P$  Six populations, each of 50 families

$\parallel$  Only general combining ability (GCA) was estimated

In several studies, sectional area, annual or accumulated ring width, or volume were used to represent growth. Heritability estimates were based either on measurements at a single age (or single ring width) in some studies, or several measurements at different ages in other studies (length of increment core).

If heritability estimates were reported both for core length and individual ring width, estimates for whole core length were usually used in this report. The majority of heritability estimates were based on narrow-sense using half- or full-sib progeny tests while others used clones for broad-sense heritability estimates.

Among the 38 studies, sample sizes varied from only 10 clones up to 580 half-sib and 216 full-sib families. Tree age varied from 1 to 30 years at breast height. There was an unusually high heritability estimate (the mean of the two estimates was 0.88) for radial growth from Shelbourne *et al.* (1997), possibly due to selection of 25 dispersed families for their study, and a total of 250 heritability estimates with a mean of 0.26 and a median of 0.22 (Fig. 1). The normal distribution fitted well with the data, showing a slight skewness of 1.08. The average heritability based on each publication varied from 0.03 to 0.88 among the 38 studies, with a grand mean of 0.23 for all studies (Table 1).

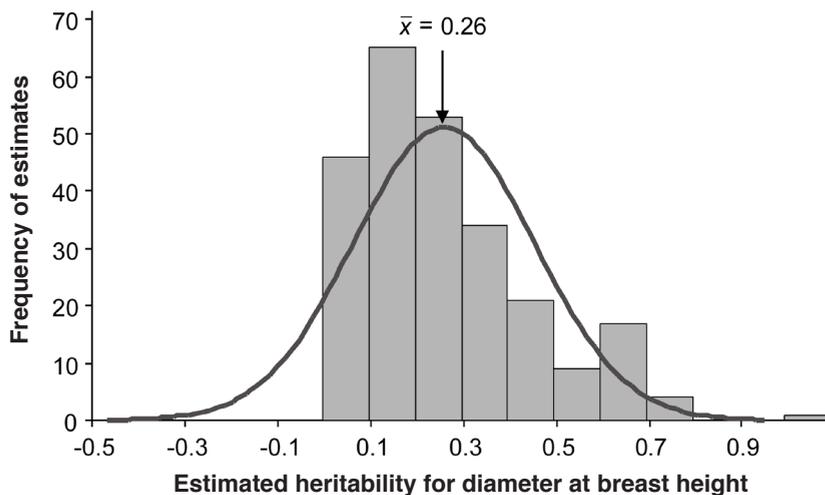


FIG. 1—Frequency distribution of heritability estimates for diameter at breast height (dbh).

The difference between broad- and narrow-sense heritability is more obvious than other factors such as site, generation, and population. For example, the average estimate of broad-sense heritability was 0.39, which is almost twice the average estimate for narrow-sense heritability (0.21). An examination of heritability estimates from these publications does not show a trend of reduction from the first-generation selection to the second-generation selections. However, heritability estimates

from native populations were generally higher than estimates from populations selected from Australian and New Zealand landraces, judging from three studies involving native populations (Burdon *et al.* 1992a,b, c). The higher heritability estimates from native populations were attributed to non-randomness of mating in native collections. Age trend of heritability for diameter at breast height from several recent publications showed a rise from very early ages, and then heritability flattened at around ages 11 to 15 years. Significant genotype by environment ( $G \times E$ ) interactions were reported in several publications, the  $G \times E$  interaction patterns being more complex in Australian sites than in New Zealand ones. In general,  $G \times E$  in Australia is usually larger and less predictable than in New Zealand where it is caused mainly by phosphorus level or soil type (pumice/clay sites); in Australia there were no clear patterns except that observed between elevation (coldness/snowiness) and genotypes (Wu & Matheson 2002). There were only a few publications with estimated specific combining ability (SCA) components for diameter at breast height. Variance ratio of specific combining ability to general combining ability (GCA) varied from 31% to 103% with an average of 57%, and relative importance of specific combining ability (SCA variance/(2 × GCA variance + SCA variance)) varied from 6% to 98% with an average around 45% .

Genetic correlations were also estimated between diameter at breast height and other traits in these publications. The estimated genetic correlation between diameter at breast height and stem straightness averaged 0.22 (favourable, ranging from -0.02 to 0.48). There were four positive and two negative correlation estimates ( $r_g$ ) between diameter at breast height and branch angle, with an average of 0.05. Values for  $r_g$  between diameter at breast height and branch size ranged from -0.89 to 0.37 with a mean of -0.21 (adverse). Estimated genetic correlations between diameter at breast height and branch cluster frequency were all positive except for one small negative estimate of -0.01 and the average was 0.29 (favourable). The positive correlation between diameter at breast height and branch cluster frequency would be favourable specifically to a short-internode ideotype. There was only one estimate each between diameter at breast height and microfibril angle (0.26, adverse) and between diameter at breast height and spiral grain (0.34, adverse). All three estimates of genetic correlations between diameter at breast height and modulus of elasticity were negative, ranging from -0.30 to -0.65 with an average of -0.48 (adverse).

### Wood Density

Considerable research on inheritance of wood density in *P. radiata* has been done in the last 3 decades. Wood density is the second most-studied trait in *P. radiata*, and there are 25 published reports listed in Table 2. Heritability estimated using the Pilodyn was not included. Heritability estimates for wood density were based



TABLE 2—Continued

| Sample size†           | Age(s)                      | Heritability |           | Genetic correlation‡ |       |      |      |      |       |       | Ref. No.§ |       |    |
|------------------------|-----------------------------|--------------|-----------|----------------------|-------|------|------|------|-------|-------|-----------|-------|----|
|                        |                             | Aver. value  | No. est.§ | dbh                  | STS   | BRA  | BRS  | BRC  | MfA   | MoE   |           | SHR   |    |
| 72(Hs)                 | Year 12                     | 0.7          | 1(N)      | -0.97                | -0.21 |      |      |      |       |       |           |       | 42 |
| 50(Hs)                 | Ring 5,10,30                | 0.6          | 6(N)      |                      |       |      |      |      |       |       |           |       | 43 |
| 29–72 (Hs)             | Year 7,8,10,11,<br>13,14,15 | 0.57         | 4(N)      | -0.33                |       |      |      |      |       |       |           |       | 44 |
| 30 (Hs)                | Year 1–26                   | 0.30         | 26(N)     | -0.73                |       |      |      |      |       |       |           |       | 47 |
| 50(Hs), 20(FS)         | Year 3–25 (28)              | 0.49         | 49(N)     |                      |       |      |      |      |       |       |           |       | 48 |
| 30(Hs)                 | Year 1–28 (30)              | 0.73         | 58(N)     |                      |       |      |      |      |       |       |           |       | 49 |
| 110–250<br>(Fs and Hs) | Ring 1–6                    | 0.53         | 13(N)     | -0.6                 |       |      |      |      | -0.1  |       |           | 0.43  | 52 |
| Min                    | 0.16                        |              | -0.97     | -0.26                | 0.01  | 0.01 | 0.01 | 0.01 | -0.4  | -0.1  | 0.43      | -0.82 |    |
| Max                    | 1.02                        |              | -0.08     | -0.03                | 0.01  | 0.01 | 0.01 | 0.01 | -0.4  | -0.1  | 1.04      | -0.82 |    |
| Grand Mean             | 0.63                        |              | -0.48     | -0.17                | 0.01  | 0.01 | 0.01 | 0.01 | -0.36 | -0.14 | 0.66      | -0.82 |    |

† Clone (CL), Half-sib (HS), Full-sib (Fs)

‡ Genetic correlations: dbh diameter at breast height; STS stem straightness; BRA branch angle; BRS branch size; BRC branch cluster frequency; MfA microfibril angle; MoE modulus of elasticity; SHR shrinkage

§ References listed in Appendix 1

¶ Narrow-sense (N), Broad-sense (B); .

on whole increment cores in some studies, or on individual rings or cumulative cross-sectional data (e.g., area-weighted) in other studies. Heritability based on individual rings was usually lower than that based on the whole core or disc (area-weighted). In general, if heritability was estimated based on both individual rings and area-weighted cross-section, then heritability estimates on an area-weighted basis were used for compilation.

A total of 244 estimates of heritability are summarised in Table 2 with an arithmetic mean of 0.59 and a median of 0.64. Therefore the distribution had slightly negative skewness (Fig. 2). Heritability estimates ranged from 0.16 to 1.02 based on the average of each publication, with a grand mean of 0.63. Two studies had unusually high estimates for wood density. Cown *et al.* (1992) presented an average estimate of 1.02 from four estimates based on the top 30 families selected for growth and form. A study with only 11 families had a heritability estimate of 0.93 (Matheson *et al.* 1997). In an earlier study by Nicholls *et al.* (1964), a low heritability estimate (0.16) was based on a study of 33 open-pollinated families. In contrast to diameter at breast height, the difference in heritability between broad-sense (0.71) and narrow-sense (0.61) was smaller, and genotype  $\times$  environment interaction for wood density was smaller and insignificant in most studies. As for age trend, heritability estimates for wood density rise more quickly from early ages to a relative stable value at ages around 3 and 5 years.

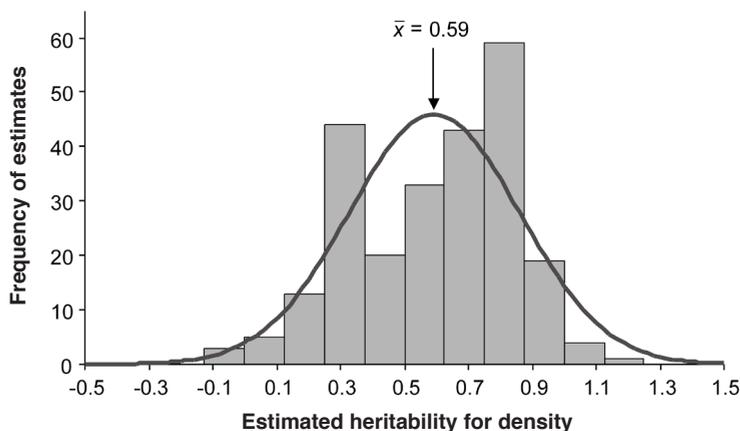


FIG. 2—Frequency distribution of heritability estimates for wood density

There was a total of 64 estimates of genetic correlations between wood density and diameter at breast height (or ring width) from 13 publications, ranging from  $-1.08$  to  $0.60$  with a mean of  $-0.51$  and a median of  $-0.62$  (Fig. 3). The genetic correlations based on average values for each individual publication were all negative, ranging from  $-0.97$  to  $-0.08$  with a grand mean of  $-0.48$ .

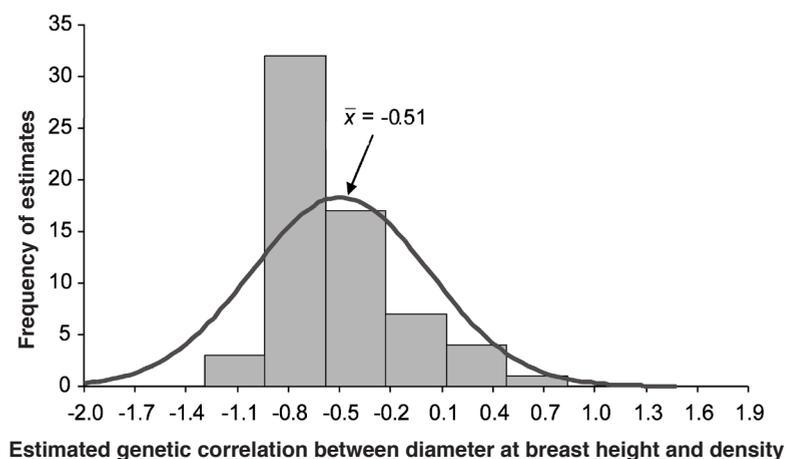


FIG. 3—Frequency distribution of genetic correlation estimates between wood density and diameter at breast height (or ring width).

Three negative genetic correlations were estimated between wood density and stem straightness, with an average of  $-0.17$ . There was only one correlation estimate between density and each of branch quality (branch angle and branch size), the value being near zero ( $0.01$ ). Similarly, only one genetic correlation was estimated between density and each of branch cluster frequency, microfibril angle, and shrinkage, and they were all negative ( $-0.36$ ,  $-0.14$ ,  $-0.82$ , respectively). Genetic correlations between density and modulus of elasticity were all positive among four publications, with a mean of  $0.66$ .

### Stem Straightness

Stem straightness is sometimes referred to as stem form or as antonym sweep and sinuosity. In Australia, a 6-point scale was usually used to measure stem straightness with 1 referring to the least straight 5% of trees and 6 the best 5% with the straightest stems in the trial. In New Zealand, a 9-point scale was usually used with 1=crooked and 9=very straight (Carson 1986). Altogether there were 20 studies which estimated a total of 111 heritabilities for stem straightness. All estimates were made at young ages between age 4 and 15 years. Average heritability based on each published report varied between  $0.02$  and  $0.57$ , with a grand mean of  $0.23$  (Table 3). One study had very low heritability estimates for all three form-traits ( $0.02$ ,  $0.15$ , and  $0.14$  for stem straightness, branch angle, and branch size, respectively) based on 28 half-sib families (Espinel & Aragónés 1997).

There were five estimates for the genetic correlation between stem straightness and three other form traits (branch angle, branch size, and branch cluster frequency), and they were all positive except for one small negative  $r_g$  ( $-0.06$ ) between stem straightness and branch angle. The mean  $r_g$  values were  $0.24$ ,  $0.42$ , and  $0.41$  between

TABLE 3—Summary of genetic parameter estimates for stem straightness (or sweep) (STS)

| Sample size†      | Age(s)               | Heritability |            | Genetic correlation‡ |             |             |              | Ref. No.§    |
|-------------------|----------------------|--------------|------------|----------------------|-------------|-------------|--------------|--------------|
|                   |                      | Aver. value  | No. est.§  | BRA                  | BRS         | BRC         | MoE          |              |
| 11(Cl)—18(Cl)     | Year 12              | 0.57         | 4 (B)      |                      |             |             |              | 7            |
| 19–39(Hs)         | Year 5-8             | 0.21         | 4 (N)      | 0.11                 | 0.11        | 0.41        |              | 11           |
| 302(Hs)           | Year 7               | 0.17         | 5 (N)      | 0.41                 | 0.41        |             |              | 13           |
| 30(Hs)            | Year 4, 5 and 6      | 0.33         | 1 (N)      | 0.59                 | 0.59        |             |              | 14           |
| 25–30(Hs)         | Year 8-11            | 0.40         | 4 (N)      |                      |             |             |              | 15           |
| 150 (Fs)          | Year 4               | 0.16         | 2 (N)      |                      |             |             |              | 17           |
| 16–18 (Hs)        | Year 12-15           | 0.34         | 7 (N)      |                      |             |             |              | 19           |
| 170(Hs)           | Year 4,5             | 0.15         | 3 (N)      |                      |             |             |              | 20           |
| 50(Fs)            | Year 9               | 0.11         | 1 (N)      |                      |             |             |              | 23           |
| 50*6(Hs)          | Year 8 and 11.5      | 0.22         | 8 (N)      |                      |             |             |              | 25           |
| 60(Cl)*6          | Year 8 and 9         | 0.28         | 9 (N)      |                      |             |             |              | 26           |
| 50(Hs)*6          |                      |              |            |                      |             |             |              |              |
| 60(Cl)*6          | Year 8 and 9         |              | 2 (G)¶     | 0.14                 | 0.61        | 0.42        |              | 27           |
| 73–467(Hs)        | Year 8 and 10        | 0.25         | 4 (N)      |                      |             | 0.39        |              | 34           |
| 28 (Hs)           | Year 7               | 0.02         | 1 (N)      |                      |             |             |              | 35           |
| 154(Fs)           | Year 7               | 0.17         | 2 (N)      |                      |             |             |              | 36           |
| 15–36(Fs)         | Year 5.5, 8.5 and 15 | 0.15         | 3(N), 6(B) |                      |             |             |              | 39           |
| 125–580(Hs)       | Year 6-11            | 0.22         | 26 (N)     |                      |             | 0.38        | –0.38        | 40           |
| 224(Hs)           | Year 12              | 0.17         | 1 (N)      |                      |             |             | –0.06        | 42           |
| 100–216(Fs)       | Year 9-10            | 0.22         | 10 (N)     | –0.06                | 0.38        | 0.47        |              | 46           |
| 19(Fs), 70(Hs)    | Year 7 and 10        | 0.31         | 6(N), 4(B) |                      |             |             |              | 50           |
| <b>Min</b>        |                      | <b>0.02</b>  |            | <b>–0.06</b>         | <b>0.11</b> | <b>0.38</b> | <b>–0.06</b> | <b>–0.38</b> |
| <b>Max</b>        |                      | <b>0.57</b>  |            | <b>0.59</b>          | <b>0.61</b> | <b>0.47</b> | <b>–0.06</b> | <b>–0.38</b> |
| <b>Grand Mean</b> |                      | <b>0.23</b>  |            | <b>0.24</b>          | <b>0.42</b> | <b>0.41</b> | <b>–0.06</b> | <b>–0.38</b> |

† Clone (CL), Half-sib (HS), Full-sib (Fs);

‡ Genetic correlations: BRA branch angle; BRS branch size; BRC branch cluster frequency; MoE modulus of elasticity, SPG spiral grain

§ References listed in Appendix 1; ¶ Narrow-sense (N), Broad-sense (B); ¶ Only general combining ability (GCA) were estimated.

stem straightness and branch angle, and branch size, and branch cluster frequency, respectively. Only one correlation estimate was obtained between stem straightness and each of modulus of elasticity and spiral grain, and each was negative.

### Branch Angle

Branch angle was measured using a score system from 1 to 6 in Australia, with 6 the best score representing the 5% of trees with the flattest branches and 1 the worst score representing the 5% of trees with the steepest branch angles in the trial. Some earlier studies scored branch quality with 6 for the best 5% of trees with the finest and flattest branches in the trial and 1 for the worst 5% with the largest and steepest branches. In New Zealand, breeders often used branch habit quality to describe branching quality. Branch habit quality was scored from 1 to 9 with 9 the best score for multinodal, flat angled, light branches, and 1 the worst score for uninodal, steep angled, heavy branches. The heritability estimated for branch quality and branch habit quality traits was regarded as for both branch size and branch angle in this report, and entered in both Tables.

A total of 38 heritabilities for branch angle were reported in 11 publications for trees between 5 and 10 years old (Table 4). Heritability varied among the 11 studies with a minimum of 0.15 and a maximum of 0.45. The average heritability of these

TABLE 4—Summary of genetic parameter estimates for branch angle (BRA)

| Sample size†          | Age(s)       | Heritability   |                      | Genetic correlation‡ |             | Ref.§<br>No. |
|-----------------------|--------------|----------------|----------------------|----------------------|-------------|--------------|
|                       |              | Aver.<br>value | No. of<br>estimates¶ | BRS                  | BRC         |              |
| 19–39(Hs)             | Year 5–8     | 0.23           | 2(N)                 |                      | 0.49        | 11           |
| 302(Hs)               | Year 7       | 0.28           | 5(N)                 |                      |             | 13           |
| 25–30(Hs)             | Year 8–11    | 0.45           | 4(N)                 |                      |             | 15           |
| 50 (Fs)               | Year 9       | 0.21           | 1(N)                 |                      |             | 23           |
| 50*6(Hs)              | Year 8       | 0.20           | 4(N)                 |                      |             | 25           |
| 60(CI)*6              | Year 8 and 9 | 0.28           | 9(N)                 |                      |             | 26           |
| 50(Hs)*6,<br>60(CI)*6 | Year 8 and 9 |                | 2(G)                 | 0.62                 | 0.51        | 27           |
| 28 (Hs)               | Year 7       | 0.15           | 1(N)                 | 0.07                 |             | 35           |
| 154(Fs)               | Year 7       | 0.23           | 2(N)                 |                      |             | 36           |
| 100–216(Fs)           | Year 9–10    | 0.24           | 10(N)                | 0.30                 | 0.38        | 46           |
| <b>Min</b>            |              | <b>0.15</b>    |                      | <b>0.07</b>          | <b>0.38</b> |              |
| <b>Max</b>            |              | <b>0.45</b>    |                      | <b>0.62</b>          | <b>0.51</b> |              |
| <b>Grand mean</b>     |              | <b>0.25</b>    |                      | <b>0.33</b>          | <b>0.46</b> |              |

† Clone (CL), Half-sib (HS), Full-sib (Fs);

‡ Genetic correlations: BRS branch size; BRC branch cluster frequency;

§ References listed in Appendix 1;

¶ Narrow-sense (N), Broad-sense (B);

|| Only general combining ability (GCA) were estimated.

studies was 0.25, similar to stem straightness. All estimated genetic correlations between branch angle and branch size, and between branch angle and branch cluster frequency were positive with an average of 0.33 and 0.46, respectively.

### Branch Size

Branch size was frequently measured in the Australian *P. radiata* breeding programme. In New Zealand, branch index was more frequently used in describing branch size in utilisation studies (Inglis & Cleland 1982). Branch index is defined as the diameter of the largest branch in each quadrant of a log (stem). The average diameter of these four branches is the branch index, usually specific to a particular zone (log) of the stem. In this report, branch size was used interchangeably with branch index. Although branch size was defined differently from branch index, there is a close correlation (Whiteside *et al.* 1987). Genetic parameter estimates for branch size are summarised for 13 publications in Table 5. There were 49 estimates from these studies, with considerable variation of the estimated heritability. Similar to branch angle, genetic parameters were estimated at relatively early ages between ages 5 and 16 years. Average heritability in each publication varied from 0.14 to 0.54, with a grand mean of 0.27. Genetic correlations between branch size and branch cluster frequency were estimated only in three publications, with a range from 0.49 to 0.70 and a mean of 0.56.

TABLE 5—Summary of genetic parameter estimates for branch size (BRS)

| Sample size†       | Age(s)          | Heritability  |                   | Genetic correlation‡<br>BRC | Ref§<br>No. |
|--------------------|-----------------|---------------|-------------------|-----------------------------|-------------|
|                    |                 | Average value | No. of estimates¶ |                             |             |
| 19–39(Hs)          | Year 5–8        | 0.20          | 2(N)              | 0.49                        | 11          |
| 302(Hs)            | Year 7          | 0.28          | 5(N)              |                             | 13          |
| 25–30(Hs)          | Year 8–11       | 0.45          | 4(N)              |                             | 15          |
| 16–18 (Hs)         | Year 12–15      | 0.40          | 7(N)              |                             | 19          |
| 50 (Fs)            | Year 9          | 0.21          | 1(N)              |                             | 23          |
| 50*6(Hs)           | Year 8 and 11.5 | 0.17          | 8(N)              |                             | 25          |
| 60(Cl)*6           | Year 8 and 9    | 0.23          | 9(N)              |                             | 26          |
| 50(Hs)*6, 60(Cl)*6 | Year 8 and 9    |               | 2(G)              | 0.70                        | 27          |
| 10(Cl)             | Year 16         | 0.54          | 2(B)              |                             | 31          |
| 28 (Hs)            | Year 7          | 0.14          | 1(N)              |                             | 35          |
| 154(Fs)            | Year 7          | 0.23          | 2(N)              |                             | 36          |
| 100–216(Fs)        | Year 9–10       | 0.17          | 10(N)             | 0.50                        | 46          |
| <b>Min</b>         |                 | <b>0.14</b>   |                   | <b>0.49</b>                 |             |
| <b>Max</b>         |                 | <b>0.54</b>   |                   | <b>0.70</b>                 |             |
| <b>Grand mean</b>  |                 | <b>0.27</b>   |                   | <b>0.56</b>                 |             |

† Clone (CL), Half-sib (HS), Full-sib (Fs);

¶ Narrow-sense (N), Broad-sense (B);

‡ Genetic correlation: BRC branch cluster frequency

§ References listed in Appendix 1;

|| Only general combining ability (GCA) were estimated.

### Branch Clusters

Branch cluster refers to the number of “whorls” between 1 and 6 m above-ground on the main stem. In New Zealand, a branch habit or branch cluster frequency score on 5- or 9-point systems (1= “uninodal” and top score= extreme “multinodal”) was used in several studies.

Only 14 studies estimated genetic parameters for branch cluster, with a total of 87 estimates of heritability: three were based on clonal studies, two on clone and seedling comparison, and the rest on seedling studies. Average heritability for each publication ranged from 0.06 to 0.64 with a grand mean of 0.35 (Table 6). There was a tendency for heritability to increase with tree age, based on observation of the same experiment at different ages. There was one unusually low heritability estimate (0.06) for branch frequency in a first-generation 72 open-pollinated family trial (Kumar *et al.* 2002), which resulted in a single genetic correlation between branch cluster frequency and modulus of elasticity, albeit imprecisely, at  $-0.74$ .

### Microfibril Angle

Among five genetic studies that reported heritability for microfibril angle, two were based on clonal trials in the mid-1990s with only three estimates of heritability.

TABLE 6—Summary of genetic parameter estimates for number of branch clusters (BRC)

| Sample size†      | Age(s)               | Heritability  |                   | Genetic correlation‡<br>MoE | Ref.§<br>No. |
|-------------------|----------------------|---------------|-------------------|-----------------------------|--------------|
|                   |                      | Average value | No. of estimates¶ |                             |              |
| 26(Hs)            | Year 5 and 7         | 0.41          | 2(N)              |                             | 6            |
| 11(Cl)–18(Cl)     | Year 12              | 0.56          | 4(B)              |                             | 7            |
| 19–39(Hs)         | Year 5–8             | 0.50          | 2(N)              |                             | 11           |
| 170(Hs)           | Year 4.5             | 0.21          | 3(N)              |                             | 20           |
| 50(Fs)            | Year 9               | 0.21          | 1(N)              |                             | 23           |
| 50*6(Hs)          | Year 8 and 11.5      | 0.43          | 8(N)              |                             | 25           |
| 60(Cl)*6          | Year 8 and 9         | 0.37          | 9(N)              |                             | 26           |
| 10(Cl)            | Year 16              | 0.39          | 1(B)              |                             | 31           |
| 73–467(Hs)        | Year 8 and 10        | 0.30          | 4(N)              |                             | 34           |
| 15–36(Fs)         | Year 5.5, 8.5 and 15 | 0.26          | 4(N), 8(B)        |                             | 39           |
| 125–580(Hs)       | Year 6–11            | 0.37          | 24(N)             |                             | 40           |
| 224(Hs)           | Year 12              | 0.06          | 1(N)              | $-0.74$                     | 42           |
| 100–216(Fs)       | Year 9–10            | 0.21          | 10(N)             |                             | 46           |
| 19(Fs), 70(Hs)    | Year 7 and 10        | 0.64          | 6(N), 4(B)        |                             | 50           |
| <b>Min</b>        |                      | <b>0.06</b>   |                   | <b><math>-0.74</math></b>   |              |
| <b>Max</b>        |                      | <b>0.64</b>   |                   | <b><math>-0.74</math></b>   |              |
| <b>Grand Mean</b> |                      | <b>0.35</b>   |                   | <b><math>-0.74</math></b>   |              |

† Clone (CL), Half-sib (HS), Full-sib (Fs);  
§ References listed in Appendix 1;

‡ Genetic correlation; MoE modulus of elasticity;  
¶ Narrow-sense (N), Broad-sense (B)

Detailed genetic studies of microfibril angle were conducted more recently in *P. radiata* using SilviScan techniques (Evans 1999). A total of 122 heritability estimates for microfibril angle, ranging from 0.00 to 1.05 with the same mean and median of 0.62, fitted almost perfectly with a normal distribution (Fig. 4). Based on the average for each publication, heritability for microfibril angle ranged from 0.44 to 0.79 with a grand mean of 0.61 (Table 7). The single genetic correlation estimate between microfibril angle and modulus of elasticity involved juvenile corewood and was  $-0.92$ .

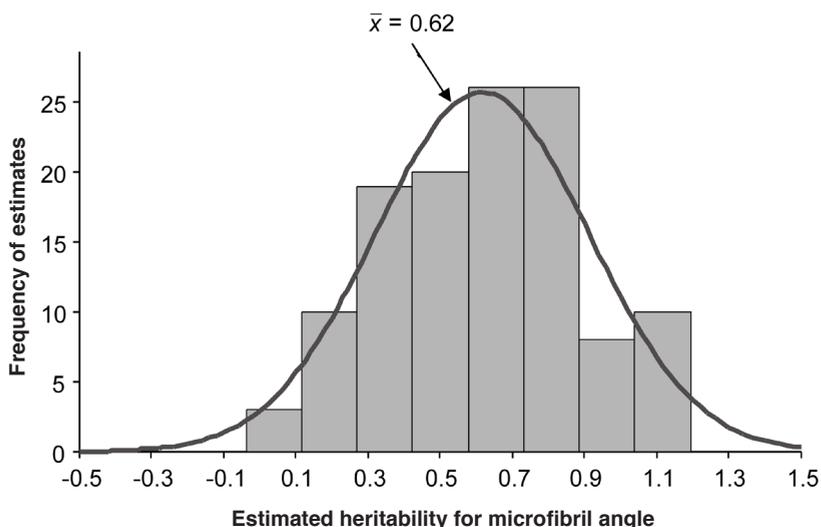


FIG. 4—Frequency distribution of heritability estimates for microfibril angle.

TABLE 7—Summary of genetic parameter estimates for microfibril angle (MfA)

| Sample size†       | Age(s)         | Heritability  |                   | Genetic correlation‡<br>MoE | Ref. No.§ |
|--------------------|----------------|---------------|-------------------|-----------------------------|-----------|
|                    |                | Average value | No. of estimates¶ |                             |           |
| 11(CL)             | Ring 1,5,10,15 | 0.69          | 1(B)              |                             | 30        |
| 10(CL)             | Year 16, 28    | 0.60          | 2(B)              |                             | 31        |
| 50(Hs), 20(Fs)     | Year 3–25 (28) | 0.44          | 49(N)             |                             | 48        |
| 30(Hs)             | Year 1–28 (30) | 0.79          | 58(N)             |                             | 51        |
| 110–250(Fs and Hs) | Ring 1–6       | 0.52          | 13(N)             | -0.92                       | 53        |
| <b>Min</b>         |                | <b>0.44</b>   |                   | <b>-0.92</b>                |           |
| <b>Max</b>         |                | <b>0.79</b>   |                   | <b>-0.92</b>                |           |
| <b>Grand Mean</b>  |                | <b>0.61</b>   |                   | <b>-0.92</b>                |           |

† Clone (CL), Half-sib (HS), Full-sib (Fs);  
§ References listed in Appendix 1;

‡ Genetic correlation: MoE modulus of elasticity;  
¶ Narrow-sense (N), Broad-sense (B).

## Wood Stiffness

As with microfibril angle, most genetic studies of timber stiffness, either through static, dynamic, or acoustic measurement of modulus of elasticity, have been conducted only recently, especially since the development of acoustic tools for standing trees. Eight studies were reviewed in this report. A total of 134 heritability estimates in these reports ranged from a minimum of 0.04 to a maximum of 0.85 with a mean of 0.49 and a median of 0.52 (Fig. 5). The average in each publication varied from 0.29 to 0.75, with a grand mean of 0.50 (Table 8).

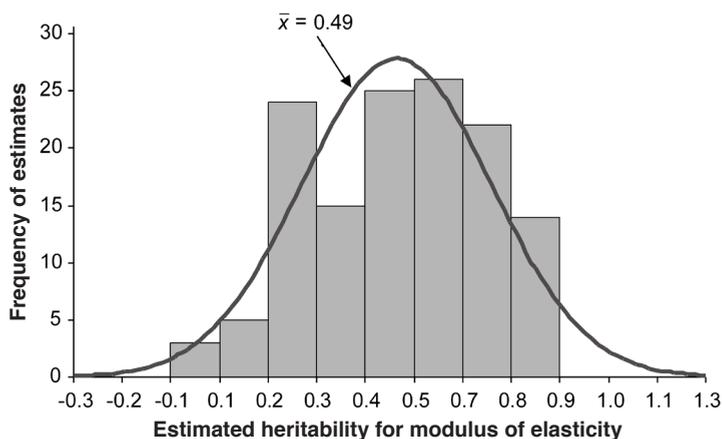


FIG. 5—Frequency distribution of heritability estimates for stiffness (modulus of elasticity).

TABLE 8—Summary of genetic parameter estimates for stiffness (MoE)

| Sample size†       | Age(s)                       | Heritability  |                   | Ref. No.‡ |
|--------------------|------------------------------|---------------|-------------------|-----------|
|                    |                              | Average value | No. of estimates§ |           |
| 10(Cl)             | Year 16                      | 0.75          | 2(B)              | 31        |
| 11(Fs)             | Year 25                      | 0.42          | 1(N)              | 33        |
| 72(Hs)             | Year 12                      | 0.49          | 3(N)              | 42        |
| 29–72 (Hs)         | Year 7,8 10,<br>11,13,14, 15 | 0.29          | 6(N)              | 44        |
| 50(Hs), 20(Fs)     | Year 3–25 (28)               | 0.47          | 49(N)             | 48        |
| 30(Hs)             | Year 1–28 (30)               | 0.52          | 58(N)             | 51        |
| 110–250(Fs)        | Ring 1–6                     | 0.5           | 13(N)             | 53        |
| 110–250(Fs and Hs) | Year 8–9                     | 0.56          | 2(N)              | 54        |
| <b>Min</b>         |                              | <b>0.29</b>   |                   |           |
| <b>Max</b>         |                              | <b>0.75</b>   |                   |           |
| <b>Grand Mean</b>  |                              | <b>0.50</b>   |                   |           |

† Clone (CL), Half-sib (HS), Full-sib (Fs);  
§ Narrow-sense (N), Broad-sense (B).

‡ References listed in Appendix 1;

## Spiral Grain

Spiral grain is one of the earliest wood-quality traits studied genetically in *P. radiata* (Fielding 1953). There were 10 reports with a total of 38 estimates of heritability. Heritability varied from 0.29 to 0.85 with a grand mean of 0.55, based on the average of each publication (Table 9).

TABLE 9—Summary of genetic parameter estimates for spiral grain (SPG)

| Sample size†       | Age (s)              | Heritability  |                   | Ref. No.‡ |
|--------------------|----------------------|---------------|-------------------|-----------|
|                    |                      | Average value | No. of estimates§ |           |
| 22(CL), 29(Hs)     | Ring 2–8             | 0.66          | 1(B)              | 2         |
| 33(Hs)             | Ring 5 and 7         | 0.34          | 2(N)              | 3         |
| 19(CL)             | Ring 2–9,11,14,17,21 | 0.29          | 12(B)             | 4         |
| 14(Hs)             | Year 9               | 0.55          | 1(N)              | 5         |
| Unknown            | Ring 4               | 0.4           | 1(N)              | 10        |
| 50(Hs)*6           | Ring 2 and 5         | 0.83          | 6(N)              | 28        |
| 10(CL)             | Year 16              | 0.75          | 2(B)              | 31        |
| 15(Fs)             | Year 8.5             | 0.85          | 1(N), 2(B)        | 39        |
| 125–580(Hs)        | Year 6–11            | 0.35          | 8(N)              | 40        |
| 110–250(Fs and Hs) | Year 8–9             | 0.45          | 2(N)              | 52        |
| <b>Min</b>         |                      | <b>0.29</b>   |                   |           |
| <b>Max</b>         |                      | <b>0.85</b>   |                   |           |
| <b>Grand Mean</b>  |                      | <b>0.55</b>   |                   |           |

† Clone (CL), Half-sib (HS), Full-sib (Fs);  
§ Narrow-sense (N), Broad-sense (B).

‡ References listed in Appendix 1;

## Shrinkage

Estimating heritability for shrinkage is challenging. This is because samples used usually contain several rings of different ages, making it difficult to ensure a constant set of rings from the pith. Therefore, the age effect was usually partly confounded with any genetic effect, increasing error variances. Also, in young trees it may be difficult to distinguish between radial and tangential surfaces because of high ring curvature. Nevertheless, four publications presented estimates of heritability for both longitudinal and transverse shrinkage, with a total of 15 estimates. Average heritability based on each publication ranged from 0.0 to 0.54 with a grand mean of 0.20 (Table 10).

## Fibre (Tracheid) Length

Genetic parameters for fibre length in *P. radiata* were studied in four publications with a total of 14 heritability estimates. Most of these studies were based on clonal material with a small number of samples, and all except one were conducted in

the 1960s. The heritability estimates varied from 0.28 to 0.78 with a grand mean of 0.54 (Table 11).

TABLE 10—Summary of genetic parameter estimates for shrinkage (SHR)

| Sample size†       | Age          | Heritability |                   | Ref. No.‡ |
|--------------------|--------------|--------------|-------------------|-----------|
|                    |              | Value        | No. of estimates§ |           |
| 22(CL), 29(Hs))    | Ring 2–8     | 0.54         | 1(B)              | 2         |
| 33(Hs)             | Ring 5 and 7 | 0.00         | 1(N)              | 3         |
| 11(Fs)             | Year 25      | 0.08         | 2(N)              | 33        |
| 110–250(Fs and Hs) | Year 8–9     | 0.17         | 12(N)             | 55        |
| <b>Min</b>         |              | <b>0.00</b>  |                   |           |
| <b>Max</b>         |              | <b>0.54</b>  |                   |           |
| <b>Grand Mean</b>  |              | <b>0.20</b>  |                   |           |

† Clone (CL), Half-sib (HS), Full-sib (Fs);‡ References listed in Appendix 1;

§ Narrow-sense (N), Broad-sense (B);

TABLE 11—Summary of genetic parameter estimates for fibre (tracheid) length (FBL)

| Sample size†      | Age                            | Heritability |                   | Ref. No.‡ |
|-------------------|--------------------------------|--------------|-------------------|-----------|
|                   |                                | Value        | No. of estimates§ |           |
| 22(CL), 29(Hs))   | Ring 2–8                       | 0.78         | 2(B)              | 2         |
| 33(Hs)            | Ring 5 and 7                   | 0.28         | 1(N)              | 3         |
| 19(CL)            | Ring 2,3,5,7,<br>9,11,14,17,21 | 0.32         | 9(B)              | 4         |
| 10(CL)            | Year 16                        | 0.76         | 2(B)              | 31        |
| <b>Min</b>        |                                | <b>0.28</b>  |                   |           |
| <b>Max</b>        |                                | <b>0.78</b>  |                   |           |
| <b>Grand Mean</b> |                                | <b>0.54</b>  |                   |           |

† Clone (CL), Half-sib (HS), Full-sib (Fs);

‡ References listed in Appendix 1;

§ Narrow-sense (N), Broad-sense (B).

## CONCLUSION AND DISCUSSION

It is generally true that genetic parameters varied with different populations, environments, ages, and were subject to large sampling errors in small populations. Selection, particularly strong direction selection, can reduce genetic variation and hence heritability of quantitative traits. There was no clear indication that heritabilities estimated from the recent second-generation trials were lower than estimates from the earlier first-generation trials for diameter at breast height and

wood density. This may indicate that selection pressure was not great enough in moving breeding populations forward or that there were large sampling errors in the estimates. In contrast, heritability estimates from native populations seem higher than estimates from local selections in New Zealand and Australian landraces. As coefficients of variation for diameter at breast height were greater in native populations than in New Zealand local populations, breeders might think there was a possible reduction of genetic variation or diversity in diameter at breast height and wood density from native populations to local landraces or from local landraces to breeding selections, in addition to possible causes of non-random mating of native populations.

Some studies included fewer than 30 families, particularly early trials and studies of wood density. However, it is not apparent these small populations produced more extreme values for parameter estimates. Many other factors seem to interfere with the estimates. There are age trends for diameter at breast height, wood density, and other wood properties from more recent publications. For diameter at breast height, estimated heritability is usually low and unstable at early ages, but it increases gradually up to around 11 to 15 years. For wood density and other wood properties, heritability estimates rise more quickly from very early ages and reach a plateau around age 3 to 5 years.

The difference between broad- and narrow-sense heritability estimates is more obvious than other factors such as site, generation, and population for diameter at breast height. For example, the average broad-sense heritability estimate is 0.39 for diameter at breast height compared with the average narrow-sense estimate of 0.21. The difference is smaller for wood density (0.71 *versus* 0.61). There were insufficient estimates of broad-sense heritability for comparison of other traits. Genotype  $\times$  environment was observed in both New Zealand and Australian trials, and is usually larger and less predictable in Australia than in New Zealand.

In *P. radiata*, estimates of heritability for all the wood-quality traits except shrinkage were higher overall than those for growth and form traits. The lower heritability in shrinkage may be due to sampling confounding age effects with genetic effects, not the lack of genotypic effects. Density had the highest heritability (0.63) among the six wood-quality traits (Fig. 6), followed by microfibril angle (0.61), spiral grain (0.55), fibre length (0.54), stiffness (0.50), and shrinkage (0.20). The high heritability estimates for wood traits in general indicate that selective breeding for these traits individually would be very effective. Among the five growth and form traits, branch cluster frequency (0.35) had the highest average  $\hat{h}^2$ , followed by branch size (0.27), branch angle (0.25), diameter at breast height (0.23), and stem straightness (0.23). The variation among the estimates was largest for diameter at breast height and wood density, partly reflecting both the large number of estimates and the large effect of environment, particularly for diameter at breast height.

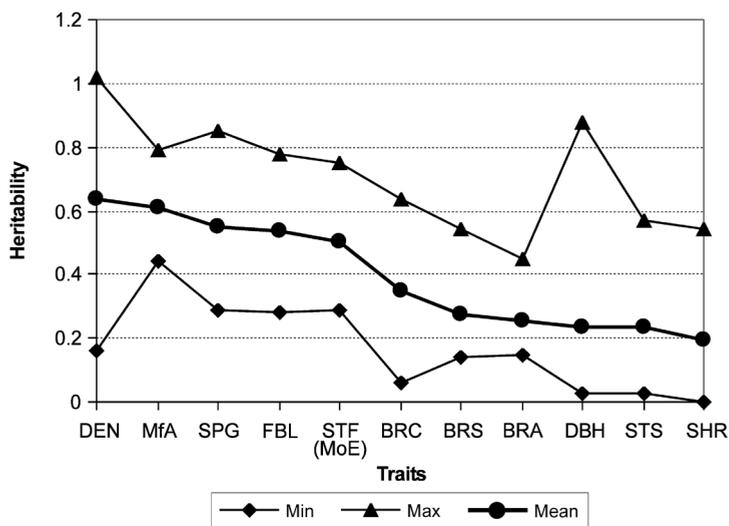


FIG. 6—Decreasing order of overall mean estimated heritability for 11 growth, form, and wood traits (average, minimum, and maximum estimates based on average of each published report).

Effectiveness of selection is influenced not only by heritability, but also by the size of variation of the particular trait. There were only a few publications with estimated coefficient of variation. The coefficient of variation for diameter at breast height was usually larger, between 10% and 20%. For wood density, coefficient of variation was estimated at about 5% to 10%.

Critical information and implications from this review are summarised as:

- (1) Growth (diameter at breast height) was unfavourably related with all four wood-quality traits (with density  $r_g = -0.48$ ; microfibril angle  $r_g = 0.26$ ; modulus of elasticity  $r_g = -0.48$ ; and spiral grain  $r_g = 0.34$ ) that had estimates of genetic correlations. This confirms that breeding for overcoming or otherwise coping with adverse genetic correlations is one of our first priorities in advanced generations in order to lift genetic and financial gain for *P. radiata* industries;
- (2) The large difference between broad- and narrow-sense heritability estimates, and sizable specific combining ability variance estimates, particularly for diameter at breast height, may indicate there is considerable non-additive genetic variance that should be used in breeding and deployment programmes for *P. radiata*.
- (3) Higher heritability and coefficients of variation for diameter at breast height and wood density in native populations than in local landraces and selections may indicate that there is more genetic variation in native populations that should be captured and infused into the breeding populations.

## REFERENCES

- BALTUNIS, B.S.; WU, H.X.; POWELL, M.B. 2007: Inheritance of density, microfibril angle, and modulus of elasticity in juvenile wood of *Pinus radiata* at two locations in Australia. *Canadian Journal of Forest Research* 37: 2164–2174.
- BANNISTER, M.H. 1969: An early progeny trial in *Pinus radiata*. 1. Juvenile characters. *New Zealand Journal of Botany* 7: 316–335.
- BROWN, A.G. 1971: Experience in the management of a radiata pine seed orchard at Tallaganda State Forest, N.S.W. *Australian Forest Research* 5(2): 15–30.
- BURDON, R.D. 1975: Compression wood in *Pinus radiata* clones on four different sites. *New Zealand Journal of Forestry Science* 5: 152–164.
- BURDON, R.D.; HARRIS, J.M. 1973: Wood density in radiata pine clones on four different sites. *New Zealand Journal of Forestry Science* 3: 286–303.
- BURDON, R.D.; LOW, C.B. 1992: Genetic survey of *Pinus radiata*. 6: Wood properties: variation, heritabilities, and interrelationship with other traits. *New Zealand Journal of Forestry Science* 22: 228–245.
- BURDON, R.D.; BANNISTER, M.H.; LOW, C.B. 1992a: Genetic survey of *Pinus radiata*. 3: Variance structures and narrow-sense heritabilities for growth variables and morphological traits in seedlings. *New Zealand Journal of Forestry Science* 22: 160–186.
- 1992b: Genetic survey of *Pinus radiata*. 4: Variance structures and heritabilities in juvenile clones. *New Zealand Journal of Forestry Science* 22: 187–210.
- BURDON, R.D.; KIBBLEWHITE, R.P.; WALKER, J.C.F.; MEGRAW, R.A.; EVANS, R.; COWN, D.J. 2004: Juvenile versus mature wood: a new concept, orthogonal to corewood versus outerwood, with special reference to *Pinus radiata* and *P. taeda*. *Forest Science* 50: 399–415.
- CARSON, M.J. 1986: Control-pollinated seed orchards of best general combiners — a new strategy for radiata pine improvement. Pp. 144–149 in Proceedings of DSIR Plant Breeding Symposium.
- CARSON, S.D.; GARCIA, O.; HAYES, J.D. 1999: Realized gain and prediction of yield with genetically improved *Pinus radiata* in New Zealand. *Forest Science* 45: 186–200.
- COWN, D.J. 1980: Radiata pine: wood age and wood property concepts. *New Zealand Journal of Forestry Science* 10: 504–507.
- COWN, D.J.; YOUNG, G.D.; BURDON, R.D. 1992: Variation in wood characteristics of 20-year-old half-sib families of *Pinus radiata*. *New Zealand Journal of Forestry Science* 22: 63–76.
- DADSWELL, H.E.; FIELDING, J.M.; NICHOLLS, J.W.P.; BROWN, A.G. 1961: Tree-to-tree variations and the gross heritability of wood characteristics of *Pinus radiata*. *Tappi* 44: 174–179.
- DEAN, C.A. 1986: Wood quality vs. quantity: a dilemma facing tree breeders. Pp. 1–6 in Proceedings of Forest Products Conference, Melbourne, Section 5/3, CSIRO.
- DOWNES, G.M.; WIMMER, R.; EVANS, R. 2002: Understanding wood formation: Gains to commercial forestry through tree ring research. *Dendrochronologia* 20(1–2): 37–51.
- ELDRIDGE, K.G. 1962: Improvement of *Pinus radiata* for forestry in Gippsland. *APPITA* 15(5): 111–115.

- 1982: Genetic improvements from a radiata pine seed orchard. *New Zealand Journal of Forestry Science* 12: 404–411.
- EVANS, R. 1999: A variance approach to the X-ray diffractometric estimation of microfibril angle in wood. *Appita Journal* 52: 363–367.
- FIELDING, J.M. 1953: Variation in Monterey pine. *Forestry and Timber Bureau, Australia Bulletin No.31*. 43 p.
- 1958: Problems and trends in pine tree breeding. Paper presented at 33rd ANZAAS Congress, Adelaide, Australia, Section K. 9 p.
- 1967: Spiral grain in *Pinus radiata* plantations in the Australian Capital Territory. *Forestry and Timber Bureau, Leaflet* 103.
- FIELDING, J.M.; BROWN, A.G. 1960: Variations in the density of the wood of Monterey pine from tree to tree. *Forestry and Timber Bureau, Leaflet* 77: 1–28.
- HARRIS, J.M.; JAMES, R.N.; COLLINS, M.J. 1976: Case for improving wood density in radiata pine. *New Zealand Journal of Forestry Science* 5: 347–354.
- INGLIS, C.S.; CLELAND, M.R. 1982: Predicting final branch size in thinned radiata pine stands. *New Zealand Forest Service, FRI Bulletin No. 3*.
- IVKOVIĆ, M.; WU, H.W.; McRAE, T.A.; MATHESON, A.C. 2006: Developing breeding objectives for radiata pine structural wood production. II. Sensitivity analyses. *Canadian Journal of Forest Research* 36: 2932–2942.
- IVKOVIĆ, M.; WU, H.X.; McRAE, T.A.; POWELL, M.B. 2006: Developing breeding objectives for radiata pine structural wood production. I. Bioeconomic model and economic weights. *Canadian Journal of Forest Research* 36: 2920–2931.
- JACOBS, M.R. 1938: The occurrence and importance of spiral grain in *Pinus radiata* in the Federal Capital Territory. Commonwealth Government Printer, Canberra. *Commonwealth Forestry Bureau Leaflet* 50.
- JAYAWICKRAMA, K.J.S. 2001: Genetic parameter estimates for radiata pine in New Zealand and New South Wales: A synthesis of results. *Silvae Genetica* 50: 45–53.
- JAYAWICKRAMA, K.J.S.; CARSON, M.J. 2000: A breeding strategy for the New Zealand radiata pine breeding cooperative. *Silvae Genetica* 49: 82–90.
- JAYAWICKRAMA, K.J.S.; SHELBOURNE, C.J.A.; CARSON, M.J. 1997: New Zealand's long internode breed of *Pinus radiata*. *New Zealand Journal of Forestry Science* 27(2): 126–141.
- JOHNSON, G.R.; ROBINSON, G.; O'HARA, A.J. 1992: Wood production and economic gains from the use of seed orchard stock in radiata pine plantations in New South Wales. *Australian Forestry Journal* 55: 126–134.
- MACALISTER, P. 1997: Cutting forestry's future? *New Zealand Forest Industries* 28(12): 9–10.
- MATHESON, A.C.; YANG, J.L.; SPENCER, D.J. 1997: Breeding radiata pine for improvement of sawn product value. Pp. 19–26 in *Proceedings of CTIA/IUFRO Wood Quality Workshop, Quebec, Canada, IV*.
- MATHESON, A.C.; ELDRIDGE, K.G.; BROWN, A.G.; SPENCER, D.J. 1986: Wood volume gains from first-generation radiata pine seed orchards. Forest Research, CSIRO, Canberra. *DFR User Series, No. 4*.
- NICHOLLS, J.W.P. 1967: Preliminary observations on the change with age of the heritability of certain wood characters in *Pinus radiata* clones. *Silvae Genetica* 16: 18–20.

- 1978: A review of the genetic parameters of some wood characteristics. Pp. 57–71 in Proceedings of RWG1, Coffs Harbour, 1978.
- NICHOLLS, J.W.P.; DADSWELL, H.E. 1965: Assessment of wood qualities for tree breeding. III. In “*Pinus radiata* D. Don”. CSIRO Division of Forest Products, Technological Paper No. 37. 34 p.
- NICHOLLS, J.W.P.; DADSWELL, H.E.; FIELDING, J.M. 1964: The heritability of wood characteristics of *Pinus radiata*. *Silvae Genetica* 13: 68–71.
- SÁNCHEZ, L.; YANCHUK, A.A.; KING J.N.: Gametic models for multitrait selection schemes to study variance of response and drift under adverse correlations. *Tree Genetics & Genomes* (in press).
- SHELBOURNE, C.J.A.; BURDON, R.D.; CARSON, S.D.; FIRTH, A.; VINCENT, T.G. 1986: “Development Plan for Radiata Pine Breeding”. New Zealand Forest Research Institute, Rotorua, New Zealand. 142 p.
- THULIN, I.J. 1957: Applications of tree breeding to forestry in New Zealand. *New Zealand Journal of Forestry* 12: 41–46.
- WALKER, J.C.F.; BUTTERFIELD, B.G. 1996: The importance of microfibril angle for the processing industries. *New Zealand Journal of Forestry* 40(4): 34–40.
- WHITE, T.L.; MATHESON, A.C.; COTTERILL, P.P.; JOHNSON, R.G.; ROUT, A.F.; BOOMSMA, D.B. 1999: A nucleus breeding plan for radiata pine in Australia. *Silvae Genetica* 48: 122–133.
- WHITESIDE, I.D.; MCGREGOR, M.J.; MANLEY, B.R. 1987: Prediction of radiata pine log grades. Pp. 55–69 in Kininmonth, J.A. (Comp.) Proceedings of the Conversion Planning Conference. Rotorua, 8–11 April 1986. *NZ Forest Service, FRI Bulletin No. 128*.
- WU, H.X.; MATHESON, A.C. 2005: Genotype by environment interaction in an Australia-wide radiata pine diallel mating experiment: Implications for regionalized breeding. *Forest Science* 51: 29–40.
- WU, H.X.; POWELL, M.B.; YANG, J.L.; IVKOVIĆ, M.; McRAE, T.A. 2007: Efficiency of early selection for rotation-aged wood-quality traits in radiata pine. *Annals of Forest Science* 64: 1–9.
- XU, P.; WALKER, J.C.F. 2004: Stiffness gradients in radiata pine trees. *Wood Science Technology* 38: 1–9.
- ZOBEL, B.J.; VAN BUIJTENEN, J.P. 1989: “Wood Variation: Its Causes and Control”. Springer-Verlag, Berlin. 363 p.

**APPENDIX 1****PUBLICATIONS SURVEYED FOR HERITABILITY AND GENETIC CORRELATION ESTIMATES FOR 11 WOOD-QUALITY, GROWTH, AND FORM TRAITS IN *PINUS RADIATA***Ref.  
No.

- 1 Fielding, J.M.; Brown, A.G. 1960–61: Variations in the density of the wood of Monterey pine from tree to tree. *Forestry and Timber Bureau, Leaflet 77*: 1–28
- 2 Dadswell, H.E.; Fielding, J.M.; Nicholls, J.W.P.; Brown, A.G. 1961: Tree-to-tree variations and the gross heritability of wood characteristics of *Pinus radiata*. *Tappi 44*: 174–179.
- 3 Nicholls, J.W.P.; Dadswell, H.E.; Fielding, J.M. 1964: The heritability of wood characteristics of *Pinus radiata*. *Silvae Genetica 13*: 68–71.
- 4 Nicholls, J.W.P. 1967: Preliminary observations on the change with age of the heritability of certain wood characters in *Pinus radiata* clones. *Silvae Genetica 16*: 18–20.
- 5 Fielding, J.M. 1967: Spiral grain in *Pinus radiata* plantations in the Australian Capital Territory. *Forestry and Timber Bureau, Leaflet 103*.
- 6 Bannister, M.H. 1969: An early progeny trial in *Pinus radiata*. 1. Juvenile characters. *New Zealand Journal of Botany 7*: 316–335.
- 7 Burdon, R.D. 1971: Clonal repeatabilities and clone-site interactions in *Pinus radiata*. *Silvae Genetica 20*: 33–39.
- 8 Burdon, R.D.; Harris, J.M. 1973: Wood density in radiata pine clones on four different sites. *New Zealand Journal of Forestry Science 3*: 286–303.
- 9 Wilcox, M.D.; Shelbourne, C.J.A.; Firth, A. 1975: General and specific combining ability in eight selected clones of radiata pine. *New Zealand Journal of Forestry Science 5*: 219–225.
- 10 Nicholls, J.W.P. 1978: A review of the genetic parameters of some wood characteristics. Proceedings of 6th RWG1 Meeting: 57–71.
- 11 Cotterill, P.P.; Zed, P.G. 1980: Estimates of genetic parameters for growth and form traits in four *Pinus radiata* progeny tests in South Australia. *Australian Forest Research 10*: 155–167.
- 12 Nicholls, J.W.P.; Morris, J.D.; Pederick, L.A. 1980: Heritability estimates of density characteristics in juvenile *Pinus radiata* wood. *Silvae Genetica 29*: 54–61.
- 13 Shelbourne, C.J.A.; Low, C.B. 1980: Multi-trait index selection and associated genetic gains of *Pinus radiata* progenies at five sites. *New Zealand Journal of Forestry Science 10*: 307–324.

- 14 Dean, C.A.; Cotterill, P.P.; Cameron, J.N. 1983: Genetic parameters and gains expected from multiple trait selection of radiata pine in eastern Victoria. *Australian Forest Research* 13: 271–278.
- 15 Matheson, A.C.; Raymond, C.A. 1984: The impact of genotype  $\times$  environment interactions on Australian *Pinus radiata* breeding programs. *Australian Forest Research* 14: 11–25.
- 16 Matheson, A.C.; Raymond, C.A. 1984: Effects of thinning in progeny tests on estimates of genetic parameters in *Pinus radiata*. *Silvae Genetica* 33: 125–128
- 17 Carson, M.J. 1986: Control-pollinated seed orchards of best general combiners — a new strategy for radiata pine improvement. Proceedings DSIR Plant Breeding Symposium 5: 144–149
- 18 Cotterill, P.P.; Dean, C.A. 1988: Changes in the genetic control of growth of radiata pine to 16 years and efficiencies of early selection. *Silvae Genetica* 37: 138–146.
- 19 Pederick, L.A. 1990: Family  $\times$  site interactions in *Pinus radiata* in Victoria, Australia, and implications for breeding strategy. *Silvae Genetica* 39: 134–40.
- 20 Johnson, G.R.; Burdon, R.D. 1990: Family-site interaction in *Pinus radiata*: implications for progeny testing strategy and regionalised breeding in New Zealand. *Silvae Genetica* 39: 55–62.
- 21 King, J.N.; Burdon, R.D. 1991: Time trends in inheritance and projected efficiencies of early selection in a large 17-year-old progeny test of *Pinus radiata*. *Canadian Journal of Forest Research* 21: 1200–1207.
- 22 Johnson, G.R.; Colley, R. 1991: Diameter-wood density relationships in radiata pine at three sites. Proceedings of 11th RWG1 meeting: 144–149.
- 23 Carson, S.D. 1991: Genotype  $\times$  environment interaction and optimal number of progeny test sites for improving *Pinus radiata* in New Zealand. *New Zealand Journal of Forestry Science* 21: 32–49.
- 24 Cown, D.J.; Young, G.D.; Burdon, R.D. 1992: Variation in wood characteristics of 20-year-old half-sib families of *Pinus radiata*. *New Zealand Journal of Forestry Science* 22: 63–76.
- 25 Burdon, R.D.; Bannister, M.H.; Low, C.B. 1992: Genetic survey of *Pinus radiata*. 3: Variance structures and narrow-sense heritabilities for growth variables and morphological traits in seedlings. *New Zealand Journal of Forestry Science* 22: 160–186.
- 26 Burdon, R.D.; Bannister, M.H.; Low, C.B. 1992: Genetic survey of *Pinus radiata*. 4: Variance structures and heritabilities in juvenile clones. *New Zealand Journal of Forestry Science* 22: 187–210.

- 27 Burdon, R.D.; Bannister, M.H.; Low, C.B. 1992: Genetic survey of *Pinus radiata*. 5: Between-trait and age-age correlations for growth rate, morphology, and disease resistance. *New Zealand Journal of Forestry Science* 22: 211–227.
- 28 Burdon, R.D.; Low, C.B. 1992: Genetic survey of *Pinus radiata*. 6: Wood properties: variation, heritabilities, and interrelationship with other traits. *New Zealand Journal of Forestry Science* 22: 228–245.
- 29 Matheson, A.C.; Spencer, D.J.; Magnussen, D. 1994: Optimum age for selection in *Pinus radiata* using basal area under bark for age:age correlations. *Silvae Genetica* 43: 352–357.
- 30 Donaldson, L.A.; Burdon, R.D. 1995: Clonal variation and repeatability of microfibril angle in *Pinus radiata*. *New Zealand Journal of Forestry Science* 25: 164–174.
- 31 Shelbourne, C.J.A. 1997: Genetics of adding value to the end-products of radiata pine. “IUFRO ‘97 Genetics of radiata pine”, *FRI Bulletin No.203*: 129–141.
- 32 Shelbourne, C.J.A.; Evans, R.; Kibblewhite, P.; Low, C.B. 1997: Inheritance of tracheid transverse dimensions and wood density in radiata pine. *Appita Journal* 50: 47–67.
- 33 Matheson, A.C.; Yang, J.L.; Spencer, D.J. 1997: Breeding radiata pine for improvement of sawn product value. *Proceedings of CTIA/IUFRO Wood Quality Workshop IV*: 19–26.
- 34 Jayawickrama, K.J.S.; Shelbourne, C.J.A.; Carson, M.J. 1997: New Zealand long internode breed of *Pinus radiata*. *New Zealand Journal of Forestry Science* 27: 126–141.
- 35 Espinel, S.; Aragonés, A. 1997: Genetic parameter estimates for *Pinus radiata* in Basque country, Northern Spain. *New Zealand Journal of Forestry Science* 27: 272–279.
- 36 King, J.H.; Carson, M.J.; Johnson, G.R. 1998: Analysis of disconnected diallel mating designs. II Results from a third generation progeny test of the New Zealand radiata pine improvement programme. *Silvae Genetica* 47: 80–87.
- 37 Nyakuengama, J.G.; Matheson, A.C.; Evans, R.; Spencer, D.; Vinden, P. 2000: Effect of age on genetic control of *Pinus radiata* earlywood and latewood properties. *Appita Journal* 53: 103–107.
- 38 Nyakuengama, J.G.; Matheson, A.C.; Evans, R.; Spencer, D.; Vinden, P. 2000: Genetics of heartwood formation and moisture status in *Pinus radiata*. *Appita Journal* 53: 30–35.

- 39 Jayawickrama, K.J.S. 2001: Estimated among-family and within-family variances and heritabilities from three radiata pine clonal trials. *Forest Genetics* 8: 247–257.
- 40 Jayawickrama, K.J.S. 2001: Genetic parameter estimates for radiata pine in New Zealand and New South Wales: A synthesis of results. *Silvae Genetica* 50: 45–53.
- 41 Kumar, S.; Lee, L. 2002: Age-age correlations and early selection for end-of-rotation wood density in radiata pine. *Forest Genetics* 9: 323–330.
- 42 Kumar, S.; Jayawickrama, K.J.S.; Lee, J.; Lausberg, M. 2002: Direct and indirect measures of stiffness and strength show high heritability in a wind-pollinated radiata pine progeny test in New Zealand. *Silvae Genetica* 51: 256–261.
- 43 Kumar, S. 2002: Earlywood-latewood demarcation criteria and their effect on genetic parameters of growth ring density components and efficiency of selection for end-of-rotation density of radiata pine. *Silvae Genetica* 51:241–246.
- 44 Kumar, S. 2004: Genetic parameter estimates for wood stiffness, strength, internal checking and resin bleeding for radiata pine. *Canadian Journal of Forest Research* 34: 2601–2610.
- 45 Wu, H.X.; Matheson, A.C. 2004: General and specific combining ability for partial diallels of radiata pine: Implications for utility of SCA in breeding and deployment populations. *Theoretical and Applied Genetics* 108: 1503–1512.
- 46 Wu, H.X.; Matheson, A.C. 2005: Genotype by environment interaction in an Australia-wide radiata pine diallel mating experiment: Implications for regionalized breeding. *Forest Science* 51: 29–40.
- 47 Li, L.; Wu, X.H. 2005: Efficiency of early selection for rotation-aged growth and wood density traits in *Pinus radiata*. *Canadian Journal of Forest Research* 35: 2019–2029.
- 48 Dungey, H.S.; Matheson, A.C.; Kain, D.; Evans, R. 2006: Genetics of wood stiffness and its component traits in *Pinus radiata*. *Canadian Journal of Forest Research* 36: 1165–1178.
- 49 Gapare, W.J.; Wu, H.X.; Abarquez, A. 2006: Genetic control of the time of transition from juvenile to mature wood in *Pinus radiata* D. Don. *Annals of Forestry Science* 63: 871–878.
- 50 Kumar, S. 2006: Correlation between clonal means and open-pollinated seedling progeny means and its implications for radiata pine breeding strategy. *Canadian Journal of Forest Research* 36: 1968–1975.
- 51 Wu, H.X.; Powell, M.B.; Yang, J.L.; Ivković, M.; McRae, T.A. 2007: Efficiency of early selection for rotation-aged wood quality traits in radiata pine. *Annals of Forestry Science* 64: 1–9.

- 52 Gapare, W.; Hathorn, A.; Kain, D.; Matheson, A.C.; Wu, H.X. 2007: Inheritance of spiral grain in the juvenile core of *Pinus radiata* D. Don. *Canadian Journal of Forest Research* 37: 116–127.
- 53 Baltunis, B.S.; Wu, H.X.; Powell, M.B. 2007: Inheritance of density, microfibril angle, and modulus of elasticity in juvenile wood of *Pinus radiata* at two locations in Australia. *Canadian Journal of Forest Research* 37: 2164–2174.
- 54 Matheson, A.C.; Gapare, W.J.; Ilic, U.; Wu, H.X.: Inheritance and genetic gain in wood stiffness in radiata pine measured acoustically in young standing trees. *Silvae Genetica* (in press)
- 55 Gapare, W.J.; Ivković, M.; Wu, H.X.: Genetics of shrinkage in juvenile trees of radiata pine from two test sites in Australia. *Silvae Genetica* (in press)