Breeding for Wood Quality and Profit in Radiata Pine: A Review of Genetic Parameters

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ABSTRACT

The history of genetics and breeding studies for wood quality traits in radiata pine were reviewed. We have surveyed published radiata pine genetic studies involving 11 growth, form and wood quality traits in a total of 54 publications from 1960 to 2007. The traits included: diameter at breast height (DBH), stem straightness (STS), branch size (BRS), branch angle (BRA), branch cluster frequency (BRC), wood density (DEN), microfibril angle (MfA), stiffness (static MoE-modulus of elasticity or stiffness measured by acoustic instruments), spiral grain (SPG), shrinkage (SHR), and fiber (tracheid) length (FBL).

Genetic parameters varied with different populations, environments and ages. In radiata pine heritability for wood quality traits (except for shrinkage) was always larger than for growth and form traits. Wood density had the highest heritability among the six wood quality traits, followed by MFA, FBL, SPG, STF and SHR. This indicates that selective breeding for these wood quality traits (except for SHR) would be very effective, more effective than growth and form traits. Among the five growth and form traits, BRC had the highest heritability, followed by BRS, BRA, DBH and STS. It was found that growth rate was unfavourably correlated with all wood quality traits. This indicates that breeding for overcoming the unfavourable genetic correlations is the most challenging issue in the advanced generations.

One solution in dealing with unfavourable genetic correlation in radiata pine is developing economic breeding objectives. But a better and long term solution in dealing with the unfavourable genetic relationship between wood quantity and quality traits in radiata pine is to overcome or breed out the unfavourable genetic correlation by dissecting its genetic base of and developing optimal breeding strategies.

INTRODUCTION

The importance of wood quality in radiata pine (*Pinus radiata)* was recognized a long time ago in Australia. Jacobs (1938) recorded the occurrence and importance of spiral grain in radiata pine in the Australian Capital Territory in 1938. Genetic variation in wood quality traits such as density, spiral grain and tracheid length was reported in 1953 by Fielding (1953), and heritability for wood density in Australian radiata pine was estimated as early as 1960 (Fielding and Brown 1960, Dadswell et al. 1961). Around that time, in 1957, the first radiata pine 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 and Harris 1973). These early genetic studies on radiata pine wood quality were reviewed by Nicholls (1978).

Although the significance of wood quality traits in radiata pine breeding was recognized at the same time as radiata pine breeding programs started more than 50 years ago, it is only in the last few years that effective breeding for wood quality has been applied. The first assessments of wood qualities for radiata pine breeding started before 1960 (Nicholls and Dadswell 1965), and the initial concern about a possible unfavourable relationship between growth and wood density was raised in 1958 (Fielding 1958). Wood density was often used 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 (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 were included in an index selection for the second breeding population (White et al. 1992). 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 et al. 2006a). 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 a couple of 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 and 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 programs, such as:

1. There was no requirement or market push for improving wood density in the initial selection and breeding program. The connection between wood quality and 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.
2. Measuring large numbers of trees for wood density was too slow and expensive using hand operated increment corers and, later, ancillary equipment such as torsiometer and Pilodyn penetrometer.
3. Large breeding populations were not established until the 1980s and breeding objectives were not well defined for the first two generations.

Breeding for wood density and quality was more seriously recognized in recent years because of shorter rotations. This is due to a significant boost of growth rate through the first generation of genetic improvement and optimal silvicultural regimes applied to the new plantations. In Australia, realized genetic gain 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 gain trials measured at 10-15 years produced an average of 20-25% volume gain (Eldridge 1982, Johnson 1992). In New Zealand, growth rate increased from 3% to 35% in volume with majority of gains around 20% (Shelbourne et al. 1986) from the first generation of selection. With such increase in growth rate, plantation rotations have become shorter. In New Zealand rotation length has been shortened from of 37-40 years to 27 years in 1999 (Jayawickrama 2001) and to 20 years for some stands (Macalister 1997); while in Australia, plantation rotation have been shortened from about 45 years to 30 years (Ivković et al. 2006a). With such shortened rotation, the proportion of juvenile wood, also called core wood (Burdon et al. 2004) with unfavourable characteristics (Cown 1980) increased greatly. This in turn affects grade outturn in sawmills (Ivković et al. 2006a).

To breed for wood quality traits alone would be effective because heritability for wood quality traits such as wood density, microfibril angle and modulus of elasticity were usually high and there were sizable genetic variation (Wu et al. 2006, Baltunis et al. 2007). The decline of wood density from faster growing trees was contributed partly by negative genetic correlations and partly by negative environmental correlations (Zobel and Buijtenen 1989; Downes et al. 2002). Our biggest challenge is breeding against the negative genetic correlation (unfavourable relationship between wood quantity and quality). This challenge has been raised by radiata pine breeders (Dean 1986) several times but has never been implemented in breeding programs. To overcome the negative genetic correlation, we have adopted two approaches for Australian radiata pine breeding programs:

1. In a short-term, developing breeding objectives for structural timber products, and
2. In a long-term developing optimal breeding strategies to overcome or breed out the unfavourable relationship by dissecting the genetic base of unfavourable relationship between quantity and quality traits.

The economic breeding objectives were developed for Australian radiata pine structural timber production, by estimating optimal economic weights for breeding objective traits (Ivković et al. 2006a, b).To estimate the economic weights precisely, five general steps were undertaken for structural wood production in radiata pine: 1) Specification of the breeding, production and marketing system; 2) identification of sources of income and expense in the specified production and marketing system; 3) Determination of biological traits influencing income and expense 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 radiata pine companies. These were mean annual increment ,branch size or BIX index, 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 breeding objective traits. Economic weights for the four breeding objective traits reflect how the improvement in those traits impact 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 an unit increase in a given breeding objective trait. A selection index was developed that combines those economic weights and genetic parameters (heritabilities and correlations) (Ivković et al. 2006a). Although, an economic index is optimal for the current population, it does not necessarily diminish unfavourable correlation between traits (Sanchez et al. 2007).

For a long-term solution to overcome the unfavourable genetic correlation between quantity and quality of radiata pine wood production, understanding of the genetic basis is critical. To understand the genetics basis of the unfavourable genetic correlation and to improve juvenile wood of radiata pine, a juvenile wood initiative was launched with four objectives: (1) develop optimal methods to measuring juvenile wood; (2) understanding the quantitative genetics of juvenile wood traits; (3) understanding the molecular genetics of juvenile wood traits; (4) develop strategies to improve juvenile wood. Our current focuses are integrating molecular information into quantitative genetics and breeding programs, and developing strategies to deal with unfavourable genetic correlations between wood quantity and quality.

Both the developing breeding objective and overcoming the unfavourable genetic correlation require understanding of the pattern and inheritance of wood traits. In developing breeding objectives for tree species, selection is usually conducted long before rotation age due to the long generation interval. Breeding objective traits are usually defined at harvest (rotation) age, around 30 years, while selection of genotypes for breeding purposes is usually done at an earlier age based on the measurements at 6 or 7 years. To link selection criteria to breeding objective traits for breeding purposes, genetic and phenotypic covariances between traits at selection (early age) and rotation ages are necessary.

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

In this paper, genetic parameters for 11 radiata pine 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). The review is only based on published genetic parameters.

MATERIALS AND METHODS

There were several studies to examine tree-to-tree variation for wood characteristics before the 1960s, but none of them estimated ratio of genetic to environmental variation in radiata pine. Beginning in the 1960s with the first paper by Fielding and Brown (1960), experiments were set up to study inheritance of wood density and other wood quality traits. Since then, numerous inheritance and genetic correlations among growth, morphology, form and wood quality traits in radiata pine were estimated. We have surveyed published radiata pine genetic studies involving 11 traits in a total of 54 publications from 1960 to 2007 (Appendix 1). These publications represent the most important inheritance estimates in radiata pine, and heritabilities and genetic correlations are summarized in the results and discussion section.

The sample size varied widely among the publications and estimates, from a minimum of 9 clones to a maximum of 580 families. Pedigrees used varied from clone (Cl) to half- (Hs) or full-sib (Fs) families or mixture 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 (BS), repeatability of clone (BS) to narrow-sense heritability (NS). 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 average estimate was calculated for each publication, and a grand mean was computed based on the average of each publication.

RESULTS AND DISCUSSION

Growth Rate

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

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. In general, narrow-sense heritability estimates were lower than estimates of broad-sense heritability.

Among the 37 studies, sample sizes varied from only ten clones up to 580 half-sib and 216 full-sib families. Tree age varied from one to 30 years at breast height. There were a total of 228 heritability estimates with a mean of 0.26 and a median of 0.21. The normal distribution fitted well with the data, showing a small skewness of 1.13 (Figure 1). The average heritability based on each publication varied from 0.03 to 0.88 among the 37 studies with a grand mean of 0.23 for all studies (Table 1).

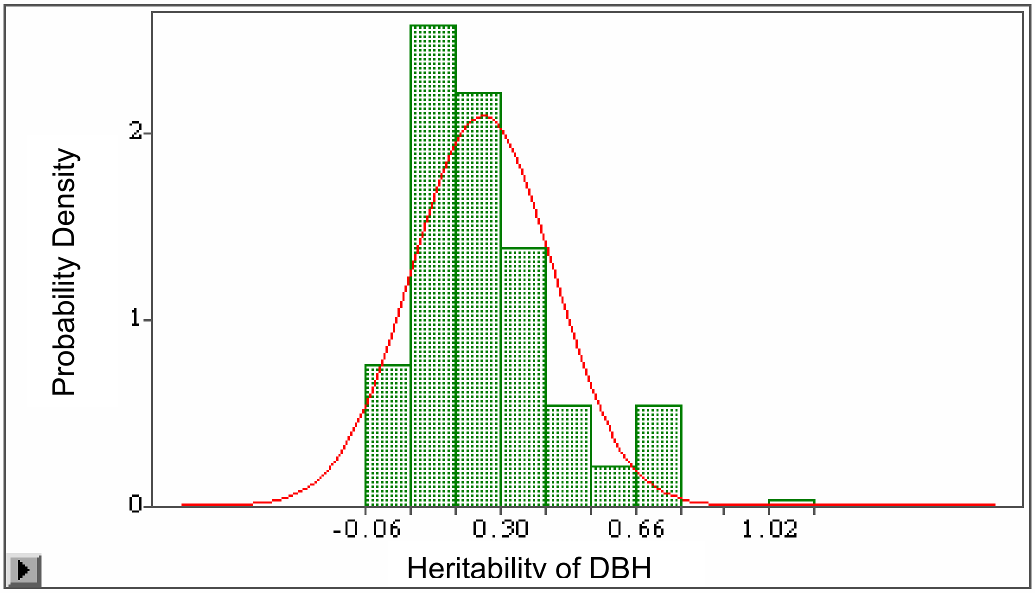


Figure 1: Probability density distribution of heritability of diameter at breast height (DBH)

Genetic correlations were also estimated between DBH and other traits in these publications. The estimated genetic correlation between DBH and STS averaged 0.22 (favourable , ranged from -0.02 to 0.48). There were four positive and two negative correlation estimates between DBH and BRA, with an average of 0.05. Genetic correlations between DBH and BRS ranged from -0.89 to 0.37 with a mean of -0.21 (unfavourable). Genetic correlations between DBH and BRC were all positive except for one small negative estimate of -0.01 and the average was 0.29 (favourable). There were only one estimate each between DBH and MfA (0.26, unfavourable) and between DBH and SPG (0.34, unfavourable). All three genetic correlations between DBH and MoE were negative, ranging from -0.30 to -0.65 with an average of -0.48 (unfavourable).

Table 1: Summary of radiata pine genetic parameters for growth rate (DBH)

Sample size	Age	Heritability (average)		Genetic correlation							Ref. No.
		Value	No. of estimates	STS	BRA	BRS	BRC	MfA	MoE	SPG	
22(Cl), 29(Hs))	Ring 2-8	0.18	2 (BS)								2
33(Hs)	Ring 5 and 7	0.03	2 (NS)								3
11(Cl) -18(Cl)	Year 12	0.42	4 (4 BS)								7
19-39(Hs)	Year 5-8	0.18	4 (NS)	0.48	-0.28	-0.28	0.43				11
17(Fs)	Ring 3 and 4	0.10	4 (NS)								12
302(Hs)	Year 7	0.19	5 (NS)	0.19	0.37	0.37					13
30(Hs)	Year 4.5 and 6	0.23	1 (NS)	0.35	-0.24	-0.24					14
25-30(Hs)	Year 8-11	0.16	11 (NS)								15
15-100(Hs)	Year 19 and 20	0.18	2 (NS)								16
150 (Fs)	Year 4	0.10	2 (NS)								17
28 (Hs)	Year 4.5, 6.5 and 10.5	0.10	3 (NS)								18
16-18 (Hs)	Year 12-15	0.21	7 (NS)								19
170(Hs)	Year 4.5	0.19	4 (NS)								20
410(Hs)	Year 5, 10,17	0.29	3 (NS)								21
16(Hs)	Year 8	0.23	3 (NS)								22
50(Fs)	Year 9	0.10	1 (NS)								23
30(Hs)	Ring 1-20	0.13	1 (NS)								24
50(Hs)*6 [b]	Year 8 and 11.5	0.21	8 (NS)								25
60(Cl)*6	Year 8 and 9	0.33	9 (NS)								26
50(Hs)*6, 60(Cl)*6	Year 8 and 9		2 (GC)[a]	0.22	0.15	0.19	0.42				27
73 (Hs)	Year 12		Family herit. only								29
16(Fs)	Year 6-7	0.14	2 (NS)								30
11(Cl)	Ring 1,5,10,15	0.50	4 (BS)								31
10(Cl)	Year 16	0.51	2 (BS)								32
25(Hs)	Year 13, 25	0.88	2 (NS)								33
73-467(Hs)	Year 8 and 10	0.22	4 (NS)				0.28				35
28 (Hs)	Year 7	0.22	1 (NS)		0.13	-0.89					36
154(Fs)	Year 7	0.14	4 (NS)								37
11(Fs)	Year 10,12,14,16,18	0.25	5 (NS)								38
11(Fs)	Year 23	0.16	1 (NS)								39
125-580(Hs)	Year 6-11	0.20	26 (NS)	0.04			0.34			0.34	40
224(Hs)	Year 12	0.10	1 (NS)	0.26					-0.65		42
29-72 (Hs)	Year 7,8 10,11,13,14, 15	0.18	4(NS)						-0.3		44
100-216(Fs)	Year 9-10	0.15	10 (NS)	-0.02	0.17	-0.42	-0.01				45
30 (Hs)	Year 1-26	0.29	26(NS)								47
30(Hs)	Year 1-28 (30)	0.34	58 (NS)								49
110-250(Fs and Hs)	Ring 1-6	0.15	2 (NS)					0.26	-0.5		52
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	

[a] Only GCA were estimated; [b] six population with each of 50 families.

Wood Density (DEN)

Considerable research on inheritance of wood density has been done in the last three decades for radiata pine. Wood density is the second most studied trait in radiata pine with 24 published reports listed in Table 2. Heritability estimated using Pilodyn was not included. Heritability estimates for wood density were based on whole increment core in some studies, or based on individual rings or accumulated area (e.g. area-weighted) in other studies. Heritability based on individual rings was usually lower than based on whole core or disk (area-weighted). In general, if heritability was estimated based on individual rings and area-weighted cross-section, then heritability estimates based on area-weighted were used for compilation.

A total of 238 estimates of heritability are summarized in Table 2 with estimates ranging from 0.16 to 1.02 based on average of each publication and a grand mean of 0.63. The arithmetic mean of all 238 estimates was 0.59 with a median of 0.64. Therefore the distribution was slightly negatively skewed (Figure 2).

Table 2: Summary of radiata pine genetic parameters for wood density (DEN)

Sample size	Age	Heritability		Genetic correlation								Ref. No.
		Value	No. of estimates	DBH	STS	BRA	BRS	BRC	MfA	MoE	SHR	
14(Hs),9(Cl), 9(Cl),10(Cl)	Year 6,13,19,20	0.53	4 (1 NS and 3 BS)									1
22(Cl), 29(Hs))	Ring 2-8	0.66	2 (BS)	-0.66								2
33(Hs)	Ring 5 and 7	0.16	1 (NS)									3
19(Cl)	Ring 2-19, 2-21	0.51	19 (BS)									4
11(Cl) - 18(Cl)	Ring 1-10	0.79	12 (BS)	-0.30								8
Unknown	Ring 3-5	0.72	1 (BS)									10
17(Fs)	Ring 3 and 4	0.49	4 (NS)	-0.41								12
30(Hs)	Year 4.5 and 6	0.33	1 (NS)	-0.45	-0.03	0.01	0.01					14
16(Hs)	Year 8	0.74	3 (NS)	-0.56								22
30(Hs)	Ring 1-20	1.02	4 (NS)	-0.61								24
50(Hs)*6	Year 8	0.87	7 (NS)	-0.08								28
10(Cl)	Year 16	0.92	2 (BS)									32
25(Hs)	Year 13 and 25	0.77	2 (NS)	-0.41								33
11(Fs)	Year 25	0.93	1 (NS)							1.04	-0.82	34
11(Fs)	Year 10,12,14,16,18	0.34	5 (NS)									38
125-580(Hs)	Year 6-11	0.73	3 (NS)	-0.16	-0.26							40
50(Hs)	Year 2-30	0.73	10 (NS)									41
72(Hs)	Year 12	0.7	1(NS)	-0.97	-0.21			-0.4		0.61		42
50(Hs)	Ring 5, 10, 30	0.6	6 (NS)									43
29-72 (Hs)	Year 7,8 10,11,13,14, 15	0.57	4(NS)	-0.33						0.54		44
30 (Hs)	Year 1-26	0.30	26(NS)	-0.73								47
50(Hs), 20(FS)	Year 3-25 (28)	0.49	49(NS)									48
30(Hs)	Year 1-28 (30)	0.73	58(NS)									49
110-250(Fs and Hs)	Ring 1-6	0.53	13 (NS)	-0.6					-0.1	0.43		52
Min		0.16		-0.97	-0.26	0.01	0.01	-0.4	-0.1	0.43	-0.82	
Max		1.02		-0.08	-0.03	0.01	0.01	-0.4	-0.1	1.04	-0.82	
Grand Mean		0.63		-0.48	-0.17	0.01	0.01	-0.36	-0.14	0.66	-0.82	

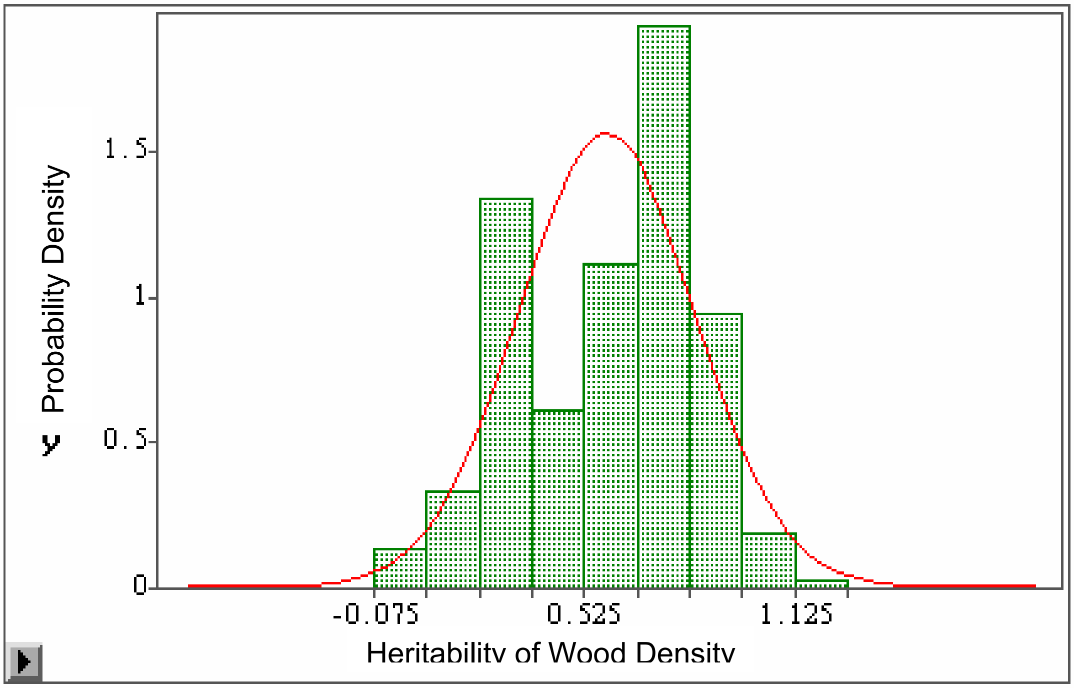


Figure 2: Probability density distribution of heritability for wood density.

There were a total of 64 genetic correlations between DEN and DBH (or ring width) estimated from 13 publications, ranging from -1.08 to 0.60 with a mean of -0.51 and a median of -0.62 (Figure 3). The genetic correlations based on average of each publication were all negative ranging from -0.97 to -0.08 with a grand mean of -0.48.

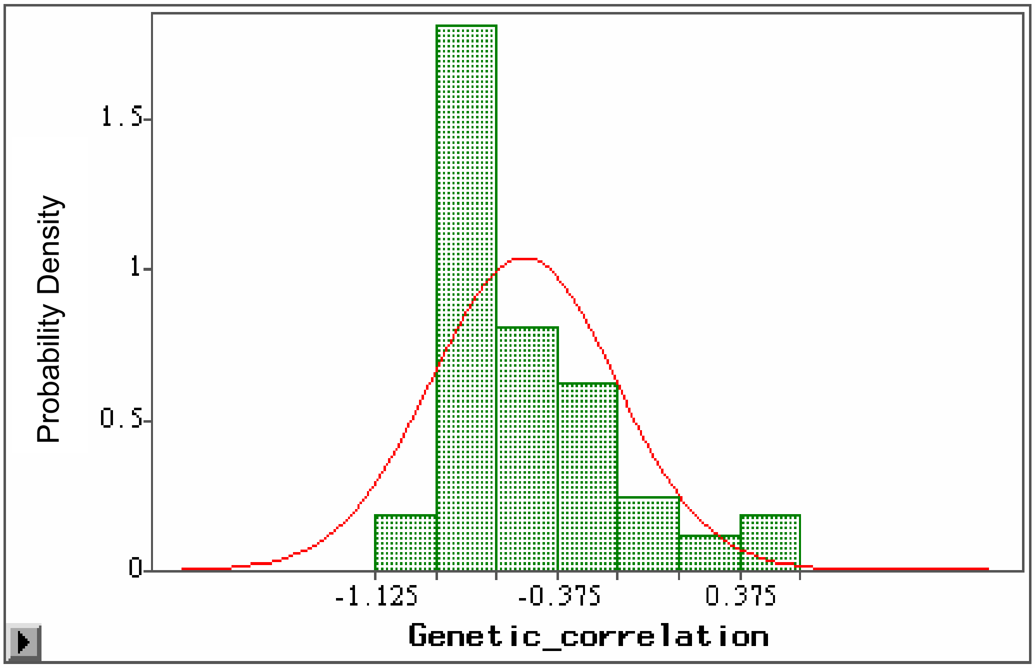


Figure 3: Probability density of genetic correlation between wood density and DBH (or Ring width).

Three negative genetic correlations were estimated between DEN and STS with an average of -0.17. There was only one correlation estimate between DEN and branch quality (BRA and BRS), the correlations were near zero (0.01). Similarly, only one genetic correlation was estimated between DEN and BRC, MfA, and SHR, and they were all negative (-0.36, -0.14, -0.82, respectively). Genetic correlation between DEN and MoE were all positive among 4 publications with a mean of 0.66.

Stem Straightness (STS)

Stem straightness is sometimes referred to as stem form or as antonym sweep. In Australia, a 6 point system was usually used to measure STS with 1 referring to the least straight 5% of trees and 6 is the best with 5% straightest stems in the trial. In New Zealand, a 9 point system was usually used with 1=crooked and 9=very straight tree (Carson 1986). There were a total of 20 studies which estimated a total of 93 heritabilities for STS. All estimates were made at young ages between age 4 and 12 years. Average heritability based on each publication varied between 0.02 and 0.57 with a grand mean of 0.23 (Table 3).

Table 3: Summary of radiata pine genetic parameters for stem straightness (or sweep) (STS)

Sample size	Age	Heritability		Genetic correlation					Ref. No.
		Value	No. of estimates	BRA	BRS	BRC	MoE	SPG	
11(Cl) -18(Cl)	Year 12	0.57	4 (BS)						7
19-39(Hs)	Year 5-8	0.21	4 (NS)	0.11	0.11	0.41			11
302(Hs)	Year 7	0.17	5 (NS)	0.41	0.41				13
30(Hs)	Year 4.5 and 6	0.33	1 (NS)	0.59	0.59				14
25-30(Hs)	Year 8-11	0.40	4 (NS)						15
150 (Fs)	Year 4	0.16	2 (NS)						17
16-18 (Hs)	Year 12-15	0.34	7 (NS)						19
170(Hs)	Year 4.5	0.15	3 (NS)						20
50(Fs)	Year 9	0.11	1 (NS)						23
50*6(Hs)	Year 8 and 11.5	0.22	8 (NS)						25
60(Cl)*6	Year 8 and 9	0.28	9 (NS)						26
50(Hs)*6, 60(Cl)*6	Year 8 and 9		2 (GC)	0.14	0.61	0.42			27
73 (Hs)	Year 12		Family herit. only						29
50 (Fs)	Year 9	0.11	1 (NS)						23
73-467(Hs)	Year 8 and 10	0.25	4 (NS)			0.39			35
28 (Hs)	Year 7	0.02	1 (NS)						36
154(Fs)	Year 7	0.17	2 (NS)						37
125-580(Hs)	Year 6-11	0.22	26 (NS)			0.38		-0.38	40
224(Hs)	Year 12	0.17	1 (NS)				-0.06		42
100-216(Fs)	Year 9-10	0.22	10 (NS)	-0.06	0.38	0.47			46
Min		0.02		-0.06	0.11	0.38	-0.06	-0.38	
Max		0.57		0.59	0.61	0.47	-0.06	-0.38	
Grand Mean		0.23		0.24	0.42	0.41	-0.06	-0.38	

There were five estimates for the genetic correlation between STS and three other form traits (BRA, BRS and BRC), and they were all positive except for one small negative genetic correlation (-0.06) between STS and BRA. The mean correlations were 0.24, 0.42 and 0.41 between STS and BRA, and BRS, and BRC, respectively. Only one correlation between STS and MoE, and between STS and SPG was estimated and they were negative.

Branch Angle (BRA)

Branch angle was measured using a score system from 1 to 6 in Australia, with 6 as the best score representing 5% of trees with the flattest branches and 1 as the worst score representing 5% of trees with the steepest branch angles in the trial. Some earlier studies used branch quality

(BRQ) score with score 6 for the best 5% of trees with the finest and flattest branches in the trial and score 1 for the worst 5% largest and steepest branches. In New Zealand, breeders often used branch habit quality (BR QU) to describe branching quality. BR QU was measure using a score from 1 to 9 with 9 as the best score for multinodal, flat angle and light branches, and 1 as the worst score for uninodal, steep angle and heavy branches. The heritability estimated for BRQ and BR QU traits was regarded as for both BRS and BRA in this report.

A total of 38 heritabilities for BRA was reported in 11 publications for trees between 5 and 10 years old. Heritability varied among the 11 studies with a minimum of 0.15 and a maximum of 0.45. The average heritability of these studies was 0.25, similar to STS.

All estimated genetic correlations between BRA and BRS, and between BRA and BRC were positive with an average of 0.33 and 0.46, respectively.

Table 4: Summary of radiata pine genetic parameters for branch angle (BRA)

Sample size	Age	Heritability		Genetic correlation		Ref. No.
		Value	No. of estimates	BRS	BRC	
19-39(Hs)	Year 5-8	0.23	2 (NS)		0.49	11
302(Hs)	Year 7	0.28	5 (NS)			13
25-30(Hs)	Year 8-11	0.45	4 (NS)			15
50*6(Hs)	Year 8	0.20	4 (NS)			25
60(Cl)*6	Year 8 and 9	0.28	9 (NS)			26
50(Hs)*6, 60(Cl)*6	Year 8 and 9		2 (GC)	0.62	0.51	27
73 (Hs)	Year 12		Family herit. only			29
50 (Fs)	Year 9	0.21	1 (NS)			23
28 (Hs)	Year 7	0.15	1 (NS)	0.07		36
154(Fs)	Year 7	0.23	2 (NS)			37
100-216(Fs)	Year 9-10	0.24	10 (NS)	0.30	0.38	46
Min		0.15		0.07	0.38	
Max		0.45		0.62	0.51	
Grand Mean		0.25		0.33	0.46	

Branch Size (BRS)

Branch size was frequently measured in the Australian radiata pine breeding program. In New Zealand, branch index (BIX) was more frequently used in describing radiata pine branch size in utilization studies. BIX 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. In this report, BRS was used inter-changeably with BIX. Although BRS was defined differently from BIX, there is a close correlation. Genetic parameters for BRS are summarized for 13 publications in Table 5. There were 49 estimates from these studies, with considerable variation of the estimated heritability. Similar to BRA, genetic parameters were estimated at relatively early ages between ages 5 to 16 years. Average heritability for each publication varied from 0.14 to 0.54, with a grand mean of 0.27. Genetic correlations were only estimated between BRS and BRC in three publications with a range from 0.49 to 0.70 and a mean of 0.56.

Table 5: Summary of radiata pine genetic parameters for branch size (BRS)

Sample size	Age	Heritability		Genetic correlation	Ref. No.
		Value	No. of estimates	BRC	
19-39(Hs)	Year 5-8	0.20	2 estimates (NS)	0.49	11
302(Hs)	Year 7	0.28	5 estimates (NS)		13
25-30(Hs)	Year 8-11	0.45	4 (NS)		15
16-18 (Hs)	Year 12-15	0.40	7 (NS)		19

50*6(Hs)	Year 8 and 11.5	0.17	8 (NS)		25
60(Cl)*6	Year 8 and 9	0.23	9 (NS)		26
50(Hs)*6, 60(Cl)*6	Year 8 and 9		2 (GC)	0.70	27
73 (Hs)	Year 12		Family herit. only		29
50 (Fs)	Year 9	0.21	1 (NS)		23
10(Cl)	Year 16	0.54	2 (BS)		32
28 (Hs)	Year 7	0.14	1 (NS)		36
154(Fs)	Year 7	0.23	2 (NS)		37
100-216(Fs)	Year 9-10	0.17	10 (NS)	0.50	46
Min		0.14		0.49	
Max		0.54		0.70	
Grand Mean		0.27		0.56	

Branch Cluster (BRC)

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

Only 12 studies estimated genetic parameters for branch cluster with a total of 63 estimates of heritability. Three were based on clonal studies and others were based on family studies. Average heritability for each publication ranged from 0.06 to 0.56 with a grand mean of 0.34 (Table 6). The genetic correlation between BRC and MoE was estimated at -0.74.

Table 6: Summary of radiata pine genetic parameters for number of branch clusters (BRC)

Sample size	Age	Heritability		Genetic Correlation	Ref. No.
		Value	No. of estimates	MoE	
26(Hs)	Year 5 and 7	0.41	2 (NS)		6
11(Cl) -18(Cl)	Year 12	0.56	4 (BS)		7
19-39(Hs)	Year 5-8	0.50	2 (NS)		11
170(Hs)	Year 4.5	0.21	3 (NS)		20
50(Fs)	Year 9	0.21	1 (NS)		23
50*6(Hs)	Year 8 and 11.5	0.43	8 (NS)		25
60(Cl)*6	Year 8 and 9	0.37	9 (NS)		26
10(Cl)	Year 16	0.39	1 (BS)		32
73-467(Hs)	Year 8 and 10	0.30	4 (NS)		35
125-580(Hs)	Year 6-11	0.37	24 (NS)		40
224(Hs)	Year 12	0.06	1 (NS)	-0.74	42
100-216(Fs)	Year 9-10	0.21	10 (NS)		46
Min		0.06		-0.74	
Max		0.56		-0.74	
Grand Mean		0.34		-0.74	

Microfibril Angle (MfA)

Among five genetic studies that reported heritability for microfibril angle, two were based on clonal trials in the mid 1990s with three estimates of heritability only. Detailed genetic studies of MfA were conducted in more recently in radiata pine using SilviScan techniques (Evans 1999). A total of 123 heritabilities for MfA was estimated, ranging from 0.00 and 1.05 with a mean of 0.61 and median of 0.62, and perfectly fitting with a normal distribution (Figure 4). Based on the average for each publication, heritability for MfA ranged from 0.44 to 0.79 with a grand mean of 0.61 (Table 7). The genetic correlation between MfA and MoE was -0.92 based on a recent study on juvenile wood.

Figure 4: Frequency density of heritability distribution for stiffness in radiata pine

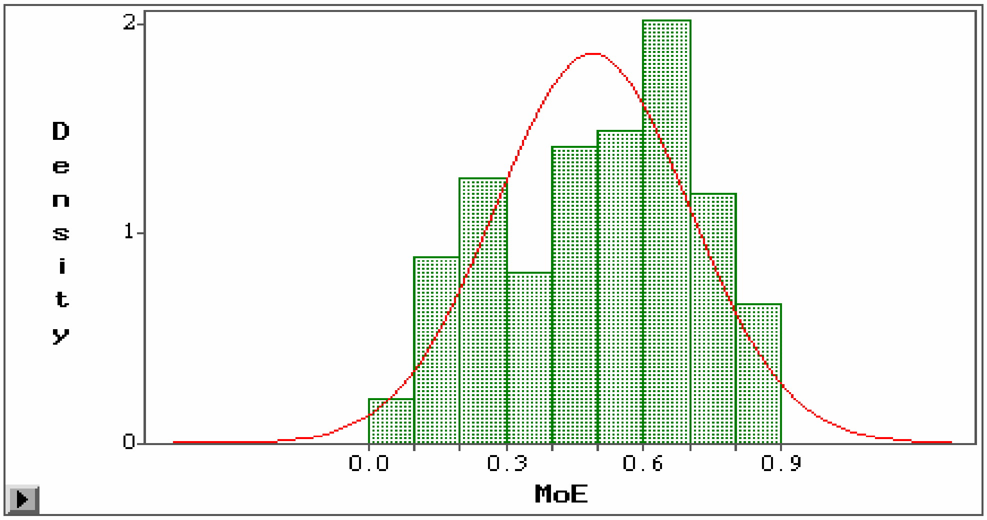


Table 7: Summary of radiata pine genetic parameters for microfibril angle

Sample size	Age	Heritability		Genetic correlation	Ref. No.
		Value	No. of estimates	MoE	
11(Cl)	Ring 1,5,10,15	0.69	1 (BS)		31
10(Cl)	Year 16, 28	0.60	2 (BS)		32
50(Hs), 20(Fs)	Year 3-25 (28)	0.44	23+26(NS)		48
30(Hs)	Year 1-28 (30)	0.79	58 (NS)		49
110-250(Fs and Hs)	Ring 1-6	0.52	13 (NS)	-0.92	52
Min		0.44		-0.92	
Max		0.79		-0.92	
Grand Mean		0.61		-0.92	

Wood Stiffness

Similarly to MFA, most genetic studies of timber stiffness, either through static, dynamic or acoustic measurement of Modulus of Elasticity (MoE) were conducted only recently, especially with the development of acoustic tools for standing trees. Eight studies were reviewed in this report. A total of 134 heritabilities was estimated in these reports, from a minimum of 0.04 to a maximum of 0.85 with a mean of 0.49 and a median of 0.52 (Figure 4). The average of each publication varied from 0.29 and 0.75 with a grand mean of 0.50 (Table 8).

Table 8: Summary of radiata pine genetic parameters for stiffness (MoE)

Sample size	Age	Heritability		Ref. No.
		Value	No. of estimates	
10(Cl)	Year 16	0.75	2 (BS)	32
11(Fs)	Year 25	0.42	1 (NS)	34
72(Hs)	Year 12	0.49	3 (NS)	42
29-72 (Hs)	Year 7,8 10,11,13,14, 15	0.29	6 (NS)	44

50(Hs), 20(Fs)	Year 3-25 (28)	0.47	23+26(NS)	48
30(Hs)	Year 1-28 (30)	0.52	58 (NS)	49
110-250(Fs)	Ring 1-6	0.5	13 (NS)	52
110-250(Fs and Hs)	Year 8-9	0.56	2 (NS)	53
Min		0.29		
Max		0.75		
Grand Mean		0.50		

Spiral Grain (SPG)

Spiral grain is one of the earliest wood quality traits that were studied genetically in radiata pine (Fielding 1953). There were 9 reports with a total of 35 estimates of heritability. Heritability varied from 0.29 to 0.83 with a grand mean of 0.51, based on average of each publication.

Table 9: Summary of radiata pine genetic parameters for spiral grain (SPG)

Sample size	Age	Heritability		Ref. No.
		Value	No. of estimates	
22(Cl), 29(Hs))	Ring 2-8	0.66	1 (BS)	2
33(Hs)	Ring 5 and 7	0.34	2 (NS)	3
19(Cl)	Ring 2-9,11,14,17,21	0.29	12 (BS)	4
14(Hs)	Year 9	0.55	1 (NS)	5
Unknown	Ring 4	0.4	1 (NS)	10
50(Hs)*6	Ring 2 and 5	0.83	6 (NS)	28
10(Cl)	Year 16	0.75	2 (BS)	32
125-580(Hs)	Year 6-11	0.35	8 (NS)	40
110-250(Fs and Hs)	Year 8-9	0.45	2 (NS)	51
Min		0.29		
Max		0.83		
Grand Mean		0.51		

Shrinkage (SHR)

Estimating heritability for shrinkage is challenging. This is because samples used usually contain several rings of different ages. Therefore, age effect was usually confounded with genetic effect, increasing error variances. In young trees it is also often not easy to distinguish between radial and tangential surface because of high ring curvature. Nevertheless, four publications estimated heritability for 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).

Table 10: Summary of radiata pine genetic parameters for shrinkage

Sample size	Age	Heritability		Ref. No.
		Value	No. of estimates	
22(Cl), 29(Hs))	Ring 2-8	0.54	1 (BS)	2
33(Hs)	Ring 5 and 7	0.00	1 (NS)	3
11(Fs)	Year 25	0.08	2 (NS)	34
110-250(Fs and Hs)	Year 8-9	0.17	12 (NS)	54
Min		0.00		
Max		0.54		
Grand Mean		0.20		

Fiber (Tracheid) Length (FBL)

Genetic parameters for fiber length in radiata pine were studied in four publications with a total of 14 heritability estimates. Most of these studies were based on clonal material with small number of samples and were conducted in the 1960s except for one publication. The heritability estimates varied from 0.28 to 0.78 with a grand mean of 0.54 (Table 11).

Table 11: Summary of radiata pine genetic parameters for fiber (tracheid) length

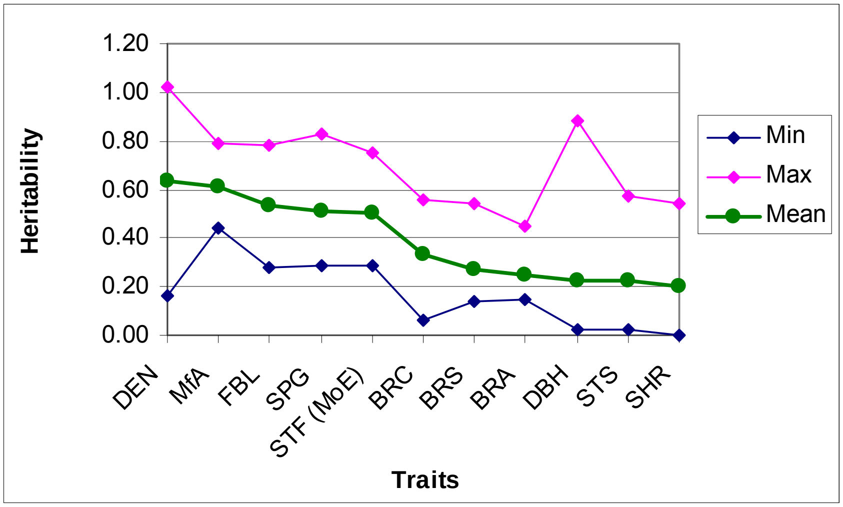
Sample size	Age	Heritability		Ref. No.
		Value	No. of estimates	
22(Cl), 29(Hs))	Ring 2-8	0.78	2 (BS)	2
33(Hs)	Ring 5 and 7	0.28	1 (NS)	3
19(Cl)	Ring 2,3,5,7,9,11,14,17,21	0.32	9 (BS)	4
10(Cl)	Year 16	0.76	2 (BS)	32
Min		0.28		
Max		0.78		
Grand Mean		0.54		

CONCLUSION

It is generally true that genetic parameters varied with different populations and environments and ages. In radiata pine, we observed heritability for wood quality traits were always larger than growth and form traits except for shrinkage. The lower heritability in shrinkage may be due to sampling confounding of age effects with genetic effects, not the lack of genetic control. Figure 6 indicated that density had the highest heritability among the six wood quality traits, followed by MfA, FBL, SPG, STF and SHR. The high heritability estimates for wood traits in general indicate that selective breeding for these traits individually would be very effective, more effective than growth and form traits. Among the five growth and form traits, BRC had the highest heritability, followed by BRS, BRA, DBH and STS. The variation among the estimates was the largest for DBH and wood density, partially reflecting the large number of estimates or highly influenced by environment, particularly for the DBH.

The critical information from this review is that growth (DBH) was unfavourably related with all four wood quality traits (DEN, MfA, MoE, and SPG) that had estimates of genetic correlations. This confirms that breeding for overcoming the unfavourable genetic correlations is our first priority in the advanced generations in order to lift genetic and financial gain for radiata pine industries.

Figure 6: Decreasing order of mean heritability for 11 growth, form and wood traits in radiata pine (minimum and maximum averages based on publications were also shown)



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Appendix 1: Radiata pine publications surveyed for heritability and genetic correlation estimates for 11 wood quality, growth, and form traits

Ref. No.	Author	Publication	Year/pages	Title
1	Fielding, J.M.and Brown, A.G.	Forestry and Timber Bureau, leaflet 77	1960:1-28	Variations in the density of the wood of Monterey pine from tree to tree
2	Dadswell, H.E., Fielding, J.M., Nicholls, J.W.P.,and Brown, A.G.	Tappi	1961:44:174-179	Tree-to-tree variations and the gross heritability of wood characteristics of *Pinus radiata*
3	Nicholls, J.W.P., Dadswell, H.E., and Fielding, J.M	Silvae Genet.	1964:13:68-71	The heritability of wood characteristics of *Pinus radiata*
4	Nicholls, J.W.P.	Silvae Genet.	1967:16:18-20	Preliminary observations on the change with age of the heritability of certain wood characters in *Pinus radiata* clones
5	Fielding, J.M.	Forestry and Timber Bureau, leaflet 103	1967	Spiral grain in *Pinus radiata* plantations in the Australian Capital Territory
6	Bannister, M.H.	N. Z. J. Bot.	1969:7:316-335	An early progeny trial in *Pinus radiata* 1. juvenile characters
7	Burdon,R.D.	Silvae Genet.	1971:20:33-39	Clonal repeatabilities and clone-site interactions in *Pinus radiata*
8	Burdon, R.D. and Harris, J.M.	N. Z. J. For. Sci.	1973:3:286-303	Wood density in radiata pine clones on four different sites
9	Wilcox, M.D., Shelbourne, C.J.A. and Firth, A.	N. Z. J. For. Sci.	1975:219-225	General and specific combining ability in eight selected clones of radiata pine
10	Nicholls, J.W.P.	Proc.RWG1, Coffs Harbour	1978:57-71	A review of the genetic parameters of some wood characteristics
11	Cotterill P.P. and Zed, P.G.	Aus. For. Res.	1980:10:155-167	Estimates of genetic parameters for growth and form traits in four *Pinus radiata* progeny tests in South Australia
12	Nicholls, J.W.P., Morris, J.D. and Pederick, L.A.	Silvae Genet.	1980:29:54-61	Heritability estimates of density characteristics in juvenile *Pinus radiata* wood
13	Shelbourne, C.J.A. and Low, C.B.	N. Z. J. For. Sci.	1980:10:307-324	Multi-trait index selection and associated genetic gains of *Pinus radiata* progenies at five sites
14	Dean, C.A., Cotterill, P.P. and Cameron, J.N.	Aus. For. Res.	1983:13:271-278	Genetic parameters and gains expected from multiple trait selection of radiata pine in eastern Victoria
15	Matheson, A.C. and Raymond, C.A.	Aus. For. Res.	1984:14:11-25	The impact of genotype x environment interactions on Australian *Pinus radiata* breeding programs
16	Matheson, A.C. and Raymond, C.A.	Silvae Genet.	1984:33:125-128	Effects of thinning in progeny tests on estimates of genetic parameters in *Pinus radiata*

17	Carson, M.J.	Plant breeding Symposium	1986:5:144-149	Control-pollinated seed orchards of best general combiners-a new strategy for radiata pine improvement
18	Cotterill, P.P. and Dean, C.A.	Silvae Genet.	1988:37:138-146	Changes in the genetic control of growth of radiata pine to 16 years and efficiencies of early selection
19	Pederick, L.A,	Silvae Genet.	1990:39:134-40)	Family X Site interactions in *Pinus radiata* in Victoria, Australia, and Implications for breeding strategy
20	Johnson, G.R.and Burdon, R.D.	Silvae Genet.	1990:39:55-62	Family-site interaction in *Pinus radiata*: implications for progeny testing strategy and regionalised breeding in New Zealand
21	King, J.N.and Burdon, R.D.	Can. J.For.Res.	1991:21:1200-1207	Time trends in inheratance and projected efficiencies of early selection in a large 17-year-old progeny test of *Pinus radiata*
22	Johnson, G.R.and Colley, R.	Proc. of 11th RWG1 meeting	1991:144-149	Diameter-wood density relationships in radiata pine at three sites
23	Carson, S.D.	N. Z. J. For. Sci.	1991:21:32-49	Genotype x environment interaction and optimal number of progeny test sites for improving *Pinus radiata* in New Zealand
24	Cown, D.J., Young, G.D. and Burdon, R.D.	N. Z. J. For. Sci.	1992:22:63-76	Variation in wood characteristics of 20-year-old half-sib families of *Pinus radiata*
25	Burdon, R.D., Bannister, M.H. and Low, C.B.	N. Z. J. For. Sci.	1992:22:160-186	Genetic survey of *Pinus radiata*. 3: variance structures and narrow-sense heritabilities for growth variables and morphological traits in seedlings
26	Burdon, R.D., Bannister, M.H. and Low, C.B.	N. Z. J. For. Sci.	1992:22:187-210	Genetic survey of *Pinus radiata*. 4: variance structures and heritabilities in juvenile clones
27	Burdon, R.D., Bannister, M.H. and Low, C.B.	N. Z. J. For. Sci.	1992:22:211-227	Genetic survey of *Pinus radiata*. 5: Between-trait and age-age correlations for growth rate, morphology, and disease resistance
28	Burdon, R.D., Bannister, M.H. and Low, C.B.	N. Z. J. For. Sci.	1992:22:228-245	Genetic survey of *Pinus radiata*. 6: Wood properties: variation, heritabilities, and interrelationship with other traits
29	Johnson, I.G.	Silvae Genet.	1992:41:55-62	Family-site interactions in radiata pine families in New South Wales Australia
30	Matheson, A.C., Spencer, D.J. and Magnussen, D.	Silvae Genet.	1994:43:352-357	Optimum age for selection in *Pinus radiata* using basal area under bark for age:age correlations
31	Donaldson, L.A.and Burdon, R.D.	N. Z. J. For. Sci.	1995:25:164-174	Clonal variationand repeatability of microfibril angle in *Pinus radiata*

32	Shelbourne, C.J.A.	IUFRO '97 Genetics of radiata pine, FRI bulletin no.203	1997:129-141	Genetics of adding value to the end-products of radiata pine
33	Shelbourne, C.J.A., Evans, R., Kibblewhite P. and Low C.B.	Appita	1997:50:47-67	Inheritance of tracheid transverse dimensions and wood density in radiata pine
34	Matheson, A.C., Yang, J.L. and Spencer, D.J.	CTIA/IUFRO Wood Quality Workshop	1997:IV:19-26	Breeding radiata pine for improvement of sawn product value
35	Jayawickrama, K.J.S., Shelbourne, C.J.A., Carson, M.J.	N. Z. J. For. Sci.	1997:126-141	New Zealand' long internode breed of Pinus radiata
36	Espinel, S. and Aragones, A.	N. Z. J. For. Sci.	1997:272-279	Genetic parameter estimates for *Pinus radiata* in Basque country, Northern Spain
37	King, J.H. Carson, M.J., and Johnson, G.R.	Silvae Genet.	1998:47:80-87	Analysis of disconnected diallel mating designs. II Results from a third generation progeny test of the New Zealand radiata pine improvement programme
38	Nyakuengama, J.G., Matheson, A.C., Evans, R., Spencer, D., and Vinden, P.	Appita	2000:53:103-107	Effect of age on genetic control of *Pinus radiata* earlywood and latewood properties
39	Nyakuengama, J.G., Matheson, A.C., Evans, R., Spencer, D., and Vinden, P.	Appita	2000:53:30-35	Genetics of heartwood formation and moisture status in Pinus radiata
40	Jayawickrama, K.J.S.	Silvae Genet.	2001:50:45-53	Genetic parameter estimates for radiata pine in New Zealand and New South Wales: A synthesis of results
41	Kumar, S. & Lee, L.	Forest Genetics	2002:323-330	Age-Age correlations and early selection for end-of-rotation wood density in radiata pine
42	Kumar, S, Jayawickrama, K.J.S., Lee, J and Lausberg, M.	Silvae Genetica	2002: 51, 256-261	Direct and indirect measure of stiffness and strength show high heritability in a wind-pollinated radiata pine progeny test in New Zealand
43	Kumar, S	Silvae Genetica	2002: 51, 241-246	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
44	Kumar, S.	Can. J.For.Res.	2004:2601-2610	Genetic parameter estimates for wood stiffness, strength, internal checking and resin bleeding for radiata pine.

45	Wu, H.X., and Matheson, A.C.	Theor and Appl. Genet.	2004:108:1503-1512	General and specific combining ability for partial diallels of radiata pine: Implications for utility of SCA in breeding and deployment populations
46	Wu, H.X., and Matheson, A.C.	Forest Science	2005:51:29-40	Genotype by environment interaction in an Australia-wide radiata pine diallel mating experiment: Implications for regionalized breeding.
47	Li L. and Wu, X. H	Can. J.For.Res.	2005:2019-2029	Efficiency of early selection for rotation-aged growth and wood density traits in *Pinus radiata*
48	Dungey, H.S., Matheson, A.C., Kain, D. and Evans, R	Can. J.For.Res.	2006:36:1165-1178	Genetics of wood stiffness and its component traits in *Pinus radiata*.
49	Wu, H.X., Powell, M.B. Yang, J.L., Ivković, M., and McRae, T.A.	Ann. For. Sci.	2007:64:1-9	Efficiency of early selection for rotation-aged wood quality traits in radiata pine
50	Gapare, W. J., Wu, H.X., and Abarquez, A	Ann. For. Sci.	2006:63: 871-878	Genetic control of the time of transition from juvenile to mature wood in *Pinus radiata* D. Don
51	Gapare, W., Hathorn, A., Kain, D., Matheson, A.C. and Wu, H.X	Can. J.For.Res.	2007:37: 116-127	Inheritance of spiral grain in the juvenile core of *Pinus radiata* D. Don
52	Baltunis, B.S. Wu, H.X, and Powell, M.B.	Can. J.For.Res.	2007 in press	Inheritance of juvenile wood properties (density, microfibril angle and modulus of elasticity) in radiata pine
53	Matheson, A.C., Gapare, W.J. Ilic, U., and Wu, H.X.	Silvae Genet.	2007 in press	Inheritance and genetic gain in wood stiffness in radiata pine measured acoustically in young standing trees.
54	Gapare, W.J., Ivković, M. and Wu, H.X.	Silvae Genet.	2007 in press	Genetics of shrinkage in juvenile trees of radiata pine from two test sites in Australia