ANALYSIS OF WOOD DENSITY AND SPRIAL GRAIN AT SEVEN CONTRASTING SITES

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Report No . 79 November 2001

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FOREST & FARM PLANTATION MANAGEMENT COOPERATIVE

EXECUTIVE SUMMARY

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In this study, a sub-sample of the families represented in the '850'-Diallel experiment was selected to evaluate their performance for a range of wood properties including wood density and spiral grain. Ten trees from each of the 10 unrelated full-sib families and a control were sampled at all seven locations. The seven locations selected for this study are Woodhill, Kaingaroa, Awahohonu, Golden Downs, Mawhera, Eyrewell and Taringatura. For wood density and spiral grain determination, two 5mm pith-to-bark increment cores were collected from each of 10 individuals in each chosen family. The main objective of this study was to evaluate the stability of family performance for both wood density and spiral grain over a wide range of sites.

At each site, the correlation (at individual-tree and family level) between early ring (rings 4 and 8) and late measurements (rings 15 and 20) was high for both spiral grain and wood density. These results suggest that selection at early age for these traits will be efficient. The broad national wood density patterns (north - south decrease) were confirmed. All families showed the expected pith-to-bark trend of increasing wood density. Family ranking of wood density across sites was relatively stable, suggesting that genotype x site interaction for this trait is small. Spiral grain values showed significant regional variation and a suggestion of a decreasing north-south trend. All families showed the expected pith-to-bark trend of decreasing spiral grain. Family ranking of spiral grain across sites was relatively variable, suggesting that genotype x site interaction for this trait is large.

INTRODUCTION

Wood density is considered to be one of the most important wood properties because of its strong influence on the quality of a wide range of end-products including solid wood and fiber products (Cown *et al.*, 1991a). It is well accepted that as a wood property it is under strong environmental control (Harris, 1965a; Cown et al. 1991a). Spiral grain is also regarded as an important wood property trait in radiata pine because it contributes significantly to the instability of the timber (Harris 1965; Cown et al. 1991b; Sorensson et al. 1998a). With end-products like, lumber and poles, excessive spirality (> 5^0) tends to cause the material to twist significantly with repeated wet-dry cycles. Excessive spirality also reduces board strength (Cown et al. 1995). Wood density and spiral grain are now being measured routinely in the New Zealand Radiata Pine Breeding Cooperative (NZRPBC) trails. Various aspects of spiral grain, i.e., tree-to-tree variation, inheritance pattern and site interaction have been studied by various authors (Cown et al. 1991; Burdon and Low 1992; Sorensson et al. 1998b). All of these studies were confined to a maximum of either 2 or 3 sites (within the North Island) and have reported various degrees of site interaction, so the environmental influence on spiral grain is largely unknown. A range of contrasting sites will be required to study the stability of the performance of the genetic material. This particular analysis was undertaken with main objective of evaluating the stability of family performance for both wood density and spiral grain over a wide range of sites.

MATERIALS AND METHODS

The genetic material used in this study was a sub-sample of the families represented in the '850'-Diallel experiment across 11 sites. Details of the experimental design and the mating structure can be found in Carson (1991). The seven locations selected for this study are Woodhill, Kaingaroa, Awahohonu, Golden Downs, Mawhera, Eyrewell and Taringatura. The locations of these sites are shown in Appendix 1. These sites represented a wide range of rainfall and temperature conditions (Table 1). The 10 unrelated full-sib families and a control (documented in Table 2) were selected to evaluate their performance for a range of wood properties including wood density and spiral grain.

Across the seven sites, 10 individuals were chosen from each of the full-sib families for sample collection. For wood density determination, 5 mm pith-to-bark increment cores were collected from each of 10 individuals in each chosen family, avoiding compression wood. These cores were resin-extracted and machined to 1.5 mm tangentially before assessment in an x-ray densitometer (Cown and Clement, 1983). Of all the variables assessed, only growth ring mean density will be discussed here. Information on the average ring density for each individual was grouped into two categories: juvenile wood density (JWD - representing ≤ 10 rings) and mature wood density (MWD - representing > 10 rings). Area weighted juvenile wood density (JWD) and mature wood density (MWD) were used for across site analyses. Patterns of variation in mean ring density, at the individual and family levels, were studied by examining correlations among various ring measurements.

For spiral grain assessment, two increment cores from opposite directions were taken at breast height of each tree. Two bark windows were also cut in order to obtain reference angles for spiral gain. Spiral grain measurements were adjusted based on the reference angle information. After this adjustment, spiral grain measurements (from the opposite directions) were averaged and then used in the analysis. Preliminary analysis of the information used in this study was reported by Barker et al. (2001).

Spiral grain measurements for the latewood of individual rings, taken from machined increment cores, are subjected to high sampling errors. Thus the averages (over several rings), as opposed to the individual ring measurements, should be used for genetical and/or statistical analysis (personal communication with Rowland Burdon and Garry Hodge). Thus, for the analyses of spiral grain data, ring measurements were grouped into two categories: juvenile wood zone (within 10 rings from the pith) and mature wood zone (outside the inner 10 rings). Averages of spiral grain data from rings 2, 4, 6 and 8 were thus used to represent the juvenile wood spiral gain information. Similarly, averages of ring 10, 15 and 20 was used to represent the mature wood spiral grain. The notations for these two spiral grain measurements will be ring2_8 and ring10_20, respectively. The across-site statistical analysis for ring2_8 and ring10_20 spiral grain will be presented in this report.

Past research has shown that significant spirality of radiata pine is mostly limited to the innermost 10 rings in the juvenile wood zone. Spirality in the mature wood zone is generally below the acceptability threshold ($<5^0$). Pattern of spirality from pith to bark might be quite different for different individuals. It would mean that an individual (or family) with relatively high spiral grain in first few rings might not be the same in later rings. Stability of the relative spirality of an individual (or family) across various rings was evaluated by obtaining correlation among various ring measurements.

Across-sites analyses of wood density and spiral grain data were undertaken to study the extent of the interaction of the genotypes across sites. For across-sites analysis, the following model can be fitted:

$$Phenotype = mean + site + family + family \times site + error$$

For wood density, to study the potential effect of variation in wood density on structural lumber performance, the proportion of good stems, (defined by ring mean juvenile wood density > $350 kg/m^3$), was analysed. The model fitted (a binomial generalised linear model with logit link) was

$$\log(p/(1-p)) = mean + site + family,$$

where p is the proportion of `good' stems, in a family at a site, assumed to follow a binomial distribution with proportion, p, of successes, possibly with overdispersion. This model was used to assess the importance of any GxE interaction on the proportion of good stems, by comparing residual variation to the binomial. For spiral grain, a similar model was fitted to the proportion of stems with spiral grain $< 5^o$.

RESULTS AND DISCUSSION

Wood Density

Surveys of wood density in New Zealand have shown that there is a broad north-south trend in decreasing wood density (Harris, 1965a; Cown *et al.* 1991). However, the only relatively strong correlations have been with mean annual temperature. Interactions with genotype have not been thoroughly studied. For the current study, pith-to-bark trends of ring mean density are shown in Fig 1. In accordance with past results, there was a gradual increase in average ring density from pith-to-bark. The range of mean ring density at Woodhill, Kaingaroa, Awahohonu, Golden Downs, Mawhera, Eyrewell and Taringatura was 331 - 541, 318 - 437, 330 - 445, 331 - 396, 329 - 391, 346 - 437 and 331 - 368 kg/m^3, respectively (Fig 1).

The average JWD and MWD at each of the seven sites are shown in Fig 2 and Table 3. The JWD at sites Woodhill, Kaingaroa, Awahohonu, Golden Downs, Mawhera, Eyrewell and Taringatura was 400, 342, 355, 349, 345, 358 and 338 kg/m^3, respectively. Similarly, the MWD at these sites was 494, 396, 403, 371, 385, 412 and 351 kg/m^3, respectively. Deviations from the model are also shown in Table 3. Overall the density has decreased with average deviations of -19, -42 for JWD, MWD respectively. Eyrewell had densities close to the model, while Kaingaroa, Awahohonu, and Mawhera had the greatest deviations (around -30 for JWD, -44 to -69 for MWD).

The patterns of variation in the average ring density of each family were studied and the results are shown in Fig 3. It can be seen that there is, in general, a gradual increase in the ring density from pith-to-bark. In general, the family with high ring density in the juvenile wood zone (< 10 rings) also has high ring density in the mature wood zone. It reflects little change in the family rankings in the juvenile wood and mature wood zones. This provides support to the current practice of selecting families at the age of 6 to 10 years.

Stability of the ranking was also studied by estimating the correlation between successive ring measurements at each site separately, and by examining the rankings of family means directly. Correlations at the individual-tree level and the family level are shown in Table 4. In general, adjacent ring groups have high correlations compared to distant ring measurements. For example, the correlation between rings 4 and 8 measurements is higher than that between rings 4 and 20. As expected, the family-mean correlation between successive ring measurements are higher that observed at the individual-tree level. Almost similar magnitude of correlation between various ring measurements was obtained at each site except at Eyrewell where a poor correlation was observed between rings 4 and 20. Family means for each site are shown in Table 5 and the corresponding family rankings in Table 6. For juvenile wood density the range in rankings (highest minus lowest ranking for a family) averaged 3.6 for juvenile wood density and 4.7 for mature wood density. Rank changes were generally within 2 of the mean rank for each family. The ranges in rankings were fairly consistent i.e. no families had very large ranges.

The generalised linear model fit for the proportion of trees that had ring density $\geq$ 350 kg/m^3 is shown in Appendix 2. The estimated dispersion factor was close to 1 indicating a good fit for the additive model, i.e. no evidence of a GxE effect. The results shown in Fig 4 reflect the fact that the within-family average ring density can vary significantly at different sites. The average (over families) proportion of trees with ring density $\geq$ 350 kg/m^3 is also shown in Fig 4. Woodhill had the highest proportion of trees meeting the threshold of 350 kg/ m^3. On the other hand, Kaingaroa and Taringatua sites had only about 35% of the trees meeting the threshold level.

Such within-family variation across sites would affect the overall ranking of families across sites if there are different pattern of variation within different families. The estimates of correlation between family means across sites are shown in Table 7. High family-mean correlation across sites showed that there is little genotype x environment interaction for this trait. This result is in agreement with previous findings (Burdon and Low 1992). Across-site analysis of variance (ANOVA) shown in Table 8 shows that family x site interaction is significant only at a P-value of 0.03, and had a substantially smaller mean squares than the site or family term.

Spiral Grain (SG)
For each site, pith-to-bark trends of spiral grain are shown in Fig 5. As shown previously for central North Island sites, there was a gradual decrease in the average SG from pith-to-bark at all locations. The range of average ring spirality at Woodhill, Kaingaroa, Awahohonu, Golden Downs, Mawhera, Eyrewell and Taringatura was 2.8 - 7.3, 1.8 - 6.2, 2.0 - 6.2, 2.3 - 4.2, 2.2 - 5.7, 1.9 - 7.0 and 2.0 - 4.3, respectively (Fig 5). Overall, a broad geographic trend emerged similar to that for wood density, i.e. an average decrease north to south. Woodhill consistently registered the highest averages and the southern sites tended to have lower values.

Average SG values for the juvenile wood zone (< ring 10 assumed for this trait in this study) and mature wood zone (≥ ring 10) at each of the seven sites are shown in Fig 6, where a loose geographic trend is apparent for the juvenile zone. The average SG in juvenile wood zone at sites Woodhill, Kaingaroa, Awahohonu, Golden Downs, Mawhera, Eyrewell and Taringatura was 6.2, 5.2, 5.1, 3.4, 4.6, 5.2 and 3.6, respectively. Similarly, the mature wood SG at these sites was 3.3, 2.6, 2.9, 2.5, 2.9, 2.4 and 2.5, respectively. It shows that the average SG in the mature wood zone at all seven sites is well within the acceptable level (5^0).

The pattern of variation in the ring spirality of each family is shown in Fig 7. It can be seen that there is, in general, gradual decrease in the average ring spirality from pith-to-bark in each family. In general, the families with high SG in the juvenile wood zone (< 10 rings) also have relatively high ring spirality values in the mature wood zone. However, some families did not follow the general trend. For example, family 11 had low SG in the juvenile wood zone but comparatively high SG in the mature wood zone. On the other hand, family 4 had comparatively high SG in the juvenile wood zone and comparatively low SG in the mature wood zone.

Stability of the ranking was also studied using the correlations between ring groups at each site separately. These correlations at the individual-tree level and the family level are shown in Table 9. Just as in case of WD, the closer ring SG measurements have higher correlations than distant ring measurements. For example, the correlation between rings 4 and 8 measurements is higher than that between rings 4 and 20. As expected, the family-mean correlations between successive ring measurements are higher than those observed at the individual-tree level. The correlation suggests that the selection of families at age 6 to 8 years would be quite efficient. The magnitude of correlation at all sites was reasonably high except in the case of Kaingaroa and Eyrewell where poor correlation was observed between rings 4 and 20 measurements.

The proportion of trees with < 5^0 SG in a given family might varies considerably between sites. Within-family variation in SG at each site was studied by calculating the proportion of trees that had ring spirality < 5^0 in the juvenile wood zone. The average proportion (over all families) of trees with SG < 5^0 is also shown in Fig 8. Golden Downs and Taringatura sites had the highest proportion (about 80 %) of trees meeting the threshold of < 5^0. On the other hand, Woodhill and

Kaingaroa had only about 40% of the trees meeting the threshold level. There appears to be a broad pattern of variation from north to south. The generalised linear model fit for the proportion of trees with absolute value of spiral grain < 5^{o} is shown in Appendix 3. The estimated dispersion factor was 1.33, somewhat greater than 1. A chi-squared test gave $P<0.05$ (just) indicating possible departure from the additive model, i.e. weak evidence of a GxE effect on the proportion of acceptable stems.

Family means (absolute values) for spiral grain for each site are shown in Table 10. The estimates of correlation between family means across sites are shown in Table 11 where it can be seen that there is poor consistency in relative family performance. This suggests strong genotype x environment interaction for ring spirality. Family rankings for absolute value of average spiral grain are shown in Table 12. Rankings were substantially more variable than was the case for wood density, with an average range in rankings of 7.3, 7.9 out of 11, indicating considerable mixing. While studying the SG in progeny trials across three North Island sites (Kaingaroa, Kairara and Pauto), Sorensson et al. (1998b) reported that the families were generally stable in ranking across sites. Burdon and Low (1992) reported the existence of genotype x site interaction at two sites in Kaingaroa forest. Some of the pair-wise correlations found in this Diallel study were even negative which reflects that there may be significant change in the family ranks across sites.

The initial analysis of variance (using original signs of the observed data) for spiral grain showed a very large mean square for site, and relatively small mean squares (only about 1/60th the magnitude) for family and family by site respectively. It was suspected that the site variation has been inflated by differences between assessors (different staff assessed the spiral grain at the various sites). Thus, the across sites ANOVA was undertaken using the absolutes values of spiral grain measured on each individual tree. The analyses of variance for SG in the juvenile wood zone (ring2_8) shows a highly significant ($p = 0.01$) component of genotype x environment (Table 13). As there were only 10 families considered in this study and thus no definite conclusion can be drawn regarding the interaction of genotype with environment.

CONCLUSIONS

The Diallel trial offered an opportunity to study some family and regional effects on wood properties. In this report, wood density and spiral grain data from 10 families across seven sites gave the following information.

- The broad national wood density patterns (north - south decrease) were confirmed. The actual levels assessed suggested that these "850" families had slightly lower density than the material surveyed in the 1970's (on average 19kg/m^3 for juvenile wood and 42 kg/m^3 lower for mature wood).
- All families showed the expected pith-to-bark trend of increasing wood density.
- Family ranking of wood density across sites was relatively stable, suggesting that genotype x site interaction for this trait is small.
- Spiral grain values showed significant regional variation and a suggestion of a decreasing north-south trend.
- All families showed the expected pith-to-bark trend of decreasing spiral grain.
- Family ranking of spiral grain across sites was relatively variable, suggesting that genotype x site interaction for this trait is large.
- Systems for assessing the genetic value of traits (e.g. indices) need to take account of the strong environmental effects on wood properties.

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Table 1. Latitude, altitude, mean annual temperature (MAT) and mean annual rainfall (MAR) data from the sample sites.

Site	**Latitude (^{0}S)**	**Altitude (m)**	**MAT (^{0}C)**	**MAR (mm)**
Woodhill	$35^0 00'$	20	14.6	1300
Kaingaroa	$38^0 30'$	560	10.7	1490
Awahohonu	$39^0 10'$	500	11.9	1750
Golden Downs	$41^0 43'$	670	10.5	1300
Mawhera	$42^0 27'$	100	11.3	1890
Eyrewell	$43^0 25'$	180	11.0	850
Taringatura	$45^0 59'$	350	10.1	840

Table 2. Family codes and the parents involved.

Family code	Parents
4	97 x 7
8	121 x 55
11	99 x 96
19	88 x 37
24	91 x 82
26	98 x 90
32	87 x 93
40	119 x 117
43	100 x 120
45	191 x 81
Control	UKB (R69 854)

Table 3. Site means for wood density. Figure in parenthesis is the deviation from the predicted using national model.

	Whl	**Kai**	**Awa**	**Gld**	**Maw**	**Eyr**	**Tar**	**Av**
JWD	400 (-9)	343 (-32)	355 (-30)	349 (-10)	346 (-34)	358 (-1)	339 (-19)	356 (-19)
MWD	495 (-13)	397 (-51)	403 (-44)	371 (-48)	385 (-69)	412 (-6)	351 (-63)	402 (-42)

Table 4. Phenotypic correlation (at individual-tree level and family-mean level) between different ring WD measurements at different sites.

Individual tree correlations					**Family mean correlations**		
Awahonu							
	ring8	**ring15**	**ring20**		**ring8**	**ring15**	**ring20**
ring4	0.62	0.45	0.35		0.89	0.80	0.69
ring8		0.62	0.45			0.93	0.81
ring15			0.52				0.94
Eyerwell							
ring4	0.45	0.17	0.13		0.66	0.38	0.57
ring8		0.60	0.36			0.83	0.41
ring15			0.31				0.38
Golden							
ring4	0.63	0.52	0.39		0.77	0.70	0.38
ring8		0.65	0.41			0.77	1.00
ring15			0.68				0.79
Kaingaroa							
ring4	0.50	0.38	0.29		0.82	0.66	0.43
ring8		0.44	0.36			0.70	0.33
ring15			0.66				0.72
Mawhera							
ring4	0.31	0.45	0.32		0.55	0.73	0.68
ring8		0.48	0.29			0.37	0.05
ring15			0.74				0.74
Taringatura							
ring4	0.41	0.37	0.37		0.68	0.52	0.40
ring8		0.65	0.60			0.84	0.71
ring15			0.81				0.92
Woodhill							
ring4	0.46	0.40	0.30		0.60	0.63	0.35
ring8		0.68	0.65			0.92	0.83
ring15			0.73				0.84

Table 5. Site by family means for wood density, with national model predicted densities. Values are average wood densities (kg/m^3) for each site for juvenile wood (rings 1-10), and mature wood (rings 11-20). Values higher than the national model are shown in bold.

	Family											
JWD	**4**	**8**	**11**	**19**	**24**	**26**	**32**	**40**	**43**	**45**	**61**	**National model**
Whl	407	370	409	**418**	**381**	383	403	**411**	394	395	**431**	40
Kai	344	324	342	**378**	323	328	349	348	344	329	360	37
Awa	362	345	354	**377**	327	328	356	383	369	341	363	37
Gld	**360**	318	348	**373**	343	345	356	**364**	351	330	358	35
Maw	352	316	350	361	350	336	361	352	349	329	357	37
Eyr	361	331	367	369	348	347	353	382	361	349	**372**	35
Tar	338	322	327	**376**	323	331	342	356	343	316	348	35
Average	36	332	357	**379**	342	34	360	371	35	341	370	37
MWD												
Whl	**515**	462	**544**	**521**	465	445	**478**	**493**	**478**	**505**	**538**	47
Kai	**414**	385	402	**429**	356	361	388	**414**	**421**	377	**418**	40
Awa	399	388	390	**433**	386	362	**413**	**456**	**414**	378	**412**	40
Gld	**389**	345	369	**400**	357	354	364	**392**	**381**	348	**387**	38
Maw	407	352	404	406	390	359	390	373	393	377	394	40
Eyr	**427**	**382**	**423**	**438**	**401**	**399**	**414**	**438**	**403**	**383**	**429**	37
Tar	359	352	328	**382**	332	323	357	**392**	356	318	364	37
Average	**41**	381	**408**	**430**	384	37	400	**422**	**40**	384	**420**	403

Table 6. Variation in family ranks for juvenile wood density (JWD) and mature wood density (MWD).

JWD	**4**	**8**	**11**	**19**	**24**	**26**	**32**	**40**	**43**	**45**	**61**
Whl	7	1	8	10	2	3	6	9	4	5	11
Kai	7	2	5	11	1	3	9	8	6	4	10
Awa	7	4	5	10	1	2	6	11	9	3	8
Gld	9	1	5	11	3	4	7	10	6	2	8
Maw	7	1	5	11	6	3	10	8	4	2	9
Eyr	7	1	8	9	3	2	5	11	6	4	10
Tar	6	2	4	11	3	5	7	10	8	1	9
SD	0.9	1.11	1.6	0.79	1.7	1.07	1.77	1.27	1.86	1.41	1.11
range	3	3	4	2	5	3	5	3	5	4	3
average range = 3.64											
MWD	**4**	**8**	**11**	**19**	**24**	**26**	**32**	**40**	**43**	**45**	**61**
Whl	8	2	11	9	3	1	4	6	5	7	10
Kai	8	4	6	11	1	2	5	7	10	3	9
Awa	6	4	5	10	3	1	8	11	9	2	7
Gld	9	1	6	11	4	3	5	10	7	2	8
Maw	11	1	9	10	6	2	5	3	7	4	8
Eyr	8	1	7	10	4	3	6	11	5	2	9
Tar	8	5	3	10	4	2	7	11	6	1	9
SD	1.5	1.72	2.63	0.69	1.51	0.82	1.38	3.15	1.91	2	0.98
range	5	4	8	2	5	2	4	8	5	6	3
average range = 4.73											

Table 7. Across sites family-mean correlation for wood density.

	Awa	Eyr	Gld	Kain	Maw	Tar
Eyr	0.79					
Gld	0.79	0.94				
Kain	0.83	0.76	0.85			
Maw	0.43	0.75	0.74	0.65		
Tar	0.92	0.75	0.84	0.82	0.41	
Whl	0.50	0.73	0.64	0.72	0.75	0.41

Table 8. Across-sites analysis of variance (ANOVA) for juvenile wood density (JWD).

For Juvenile Wood Density				
Source	**DF**	**MSS**	**F value**	**Pr (F)**
Site	6	47147.5	104.9	<.0001
Family	10	14621.3	32.6	<.0001
Site x Family	60	630.1	1.4	.03
Error	673	449.0		

Table 9. Phenotypic correlation (at individual-tree level and family-mean level) between different ring SG measurements at different sites.

Individual tree correlations					**Family mean correlations**		
Awahonu							
	ring8	**ring15**	**ring20**		**ring8**	**ring15**	**ring20**
ring4	0.87	0.78	0.78		0.95	0.94	0.9
ring8		0.83	0.83			0.97	0.89
ring15			0.79				0.92
Eyerwell							
ring4	0.5	0.3	0.22		0.67	0.36	0.15
ring8		0.47	0.34			0.46	0.27
ring15			0.8				0.87
Golden							
ring4	0.71	0.73	0.71		0.86	0.86	0.86
ring8		0.74	0.71			0.87	0.73
ring15			0.76				0.81
Kaingaroa							
ring4	0.71	0.52	0.35		0.93	0.74	0.58
ring8		0.64	0.44			0.82	0.71
ring15			0.69				0.83
Mawhera							
ring4	0.79	0.73	0.7		0.89	0.94	0.85
ring8		0.76	0.69			0.85	0.77
ring15			0.71				0.92
Taringatura							
ring4	0.64	0.6	0.55		0.8	0.7	0.74
ring8		0.78	0.66			0.75	0.81
ring15			0.69				0.64
Woodhill							
ring4	0.79	0.71	0.68		0.9	0.84	0.62
ring8		0.81	0.7			0.87	0.65
ring15			0.88				0.67

Table 10. Site by family means (absolute values) for spiral grain. Means are averages for each site for juvenile wood (rings 2-8), and mature wood (rings 10-20).

	Family										
JWD	**4**	**8**	**11**	**19**	**24**	**26**	**32**	**40**	**43**	**45**	**61**
Awa	3.76	4.73	4.03	6.31	8.11	6.49	6.81	4.18	4.41	3.06	3.86
Eyre	4.44	5.65	4.58	5.06	4.43	6.96	5.51	5.33	6.28	4.01	4.64
Gold	5.12	2.66	2.68	2.32	4.33	5.45	4.32	2.32	2.53	2.41	2.84
Kain	3.95	5.72	3.90	4.54	5.20	6.42	4.33	5.38	6.63	5.09	5.69
Maw	3.03	3.93	3.83	5.29	3.21	5.18	7.82	5.69	4.70	4.00	4.13
Tar	3.22	3.43	3.01	2.78	2.38	4.84	4.06	3.48	4.10	4.13	4.46
Wood	5.78	5.94	3.99	7.26	4.53	6.70	7.83	5.45	9.17	5.64	NA
MWD											
Awa	2.28	3.13	1.73	3.68	3.65	2.84	3.50	2.68	2.34	3.22	2.65
Eyre	1.98	2.48	2.22	2.10	2.65	3.81	1.42	2.02	2.95	2.48	2.89
Gold	2.41	2.96	2.82	2.59	2.68	2.55	2.44	2.04	2.57	2.02	2.45
Kain	1.67	2.16	2.53	2.01	2.17	2.53	2.02	2.41	4.31	3.15	3.11
Maw	2.22	2.88	3.61	2.13	1.99	2.78	4.45	3.45	3.03	2.63	2.36
Tar	2.39	2.25	2.08	2.11	1.83	3.38	2.60	2.09	2.65	2.54	3.10
Wood	2.03	2.67	3.41	5.13	2.26	2.42	3.12	4.28	4.24	3.58	NA

Table 11. Across sites family-mean correlation for juvenile wood spiral grain.

	Awa	Eyr	Gld	Kain	Maw	Tar
Eyer	0.30					
Gold	0.47	0.24				
Kain	0.05	0.65	-0.07			
Mawh	0.32	0.47	0.00	0.02		
Tari	-0.27	0.50	0.15	0.55	0.36	
Wood	0.11	0.62	-0.02	0.45	0.55	0.52

Table 12. Variation in family ranks for spiral grain. Ranks are rankings of the families for each site families are ranked in order absolute value of average spiral grain.

	Family									
JWD	**4**	**8**	**11**	**19**	**24**	**26**	**32**	**40**	**43**	**45**	**61**
Awa	2	7	4	8	11	9	10	5	6	1	3
Eyre	3	9	4	6	2	11	8	7	10	1	5
Gold	10	5	6	1	9	11	8	1	4	3	7
Kain	2	9	1	4	6	10	3	7	11	5	8
Maw	1	4	3	9	2	8	11	10	7	5	6
Tar	4	5	3	2	1	11	7	6	8	9	10
Wood	5	6	1	8	2	7	9	3	10	4	NA
SD	3.0	2.0	1.8	3.2	4.0	1.6	2.6	2.9	2.5	2.8	2.4
Range	9	5	5	8	10	4	8	9	7	8	7
Average range = 7.3											
MWD											
Awa	2	7	1	11	10	6	9	5	3	8	4
Eyre	2	6	5	4	8	11	1	3	10	6	9
Gold	3	11	10	8	9	6	4	2	7	1	5
Kain	1	4	7	2	5	7	3	6	11	10	9
Maw	3	7	10	2	1	6	11	9	8	5	4
Tar	6	5	2	4	1	11	8	3	9	7	10
Wood	1	4	6	10	2	3	5	9	8	7	NA
SD	1.7	2.4	3.5	3.8	3.9	2.9	3.6	2.9	2.6	2.8	2.8
Range	5	7	9	9	9	8	10	7	8	9	6
Average range = 7.9											

Table 13. Across-sites analysis of variance (ANOVA) for spiral grain in juvenile wood (SG2_8).

For Spiral Grain in juvenile wood (SG2_8)				
Source	**DF**	**MSS**	**F value**	**Pr (F)**
Site	6	98.67	13.8	<.0001
Family	10	35.17	4.9	<.0001
Site x Family	60	10.67	1.5	0.01
Error	658	7.15		

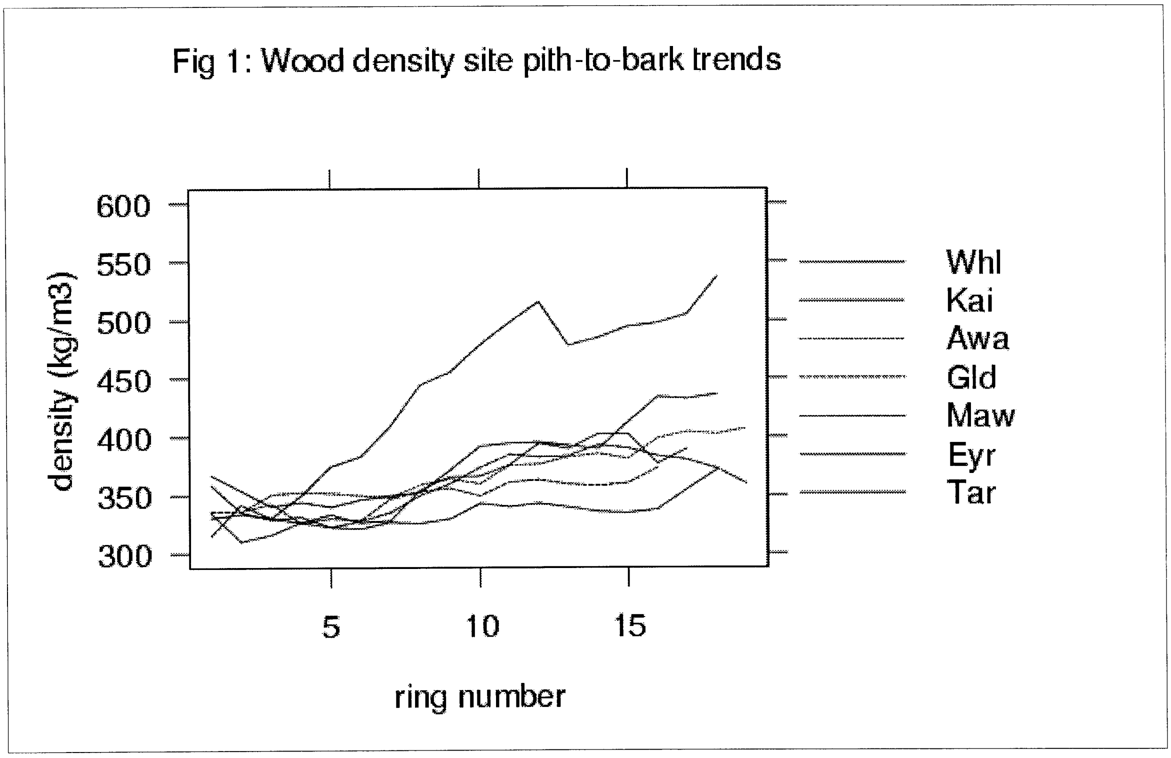


Fig 1: Wood density site pith-to-bark trends
density (kg/m3)
600
550
500
450
400
350
300
5
10
15
ring number
Whl
Kai
Awa
Gld
Maw
Eyr
Tar

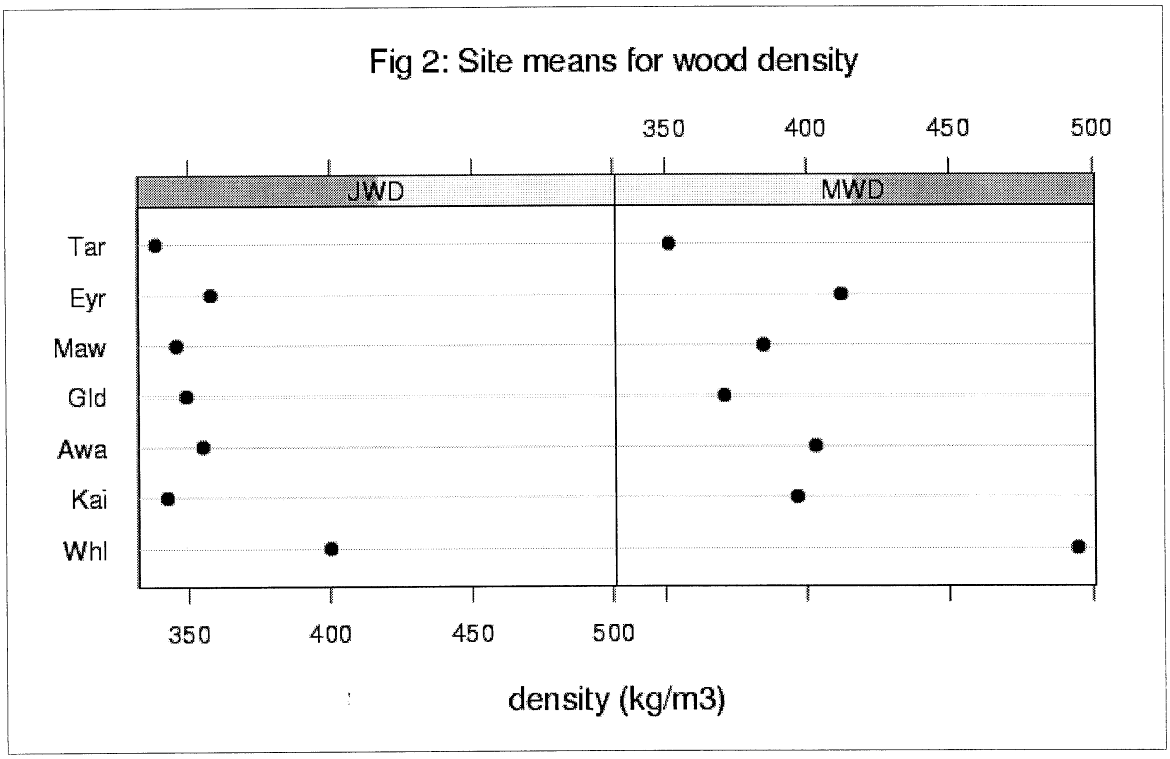


Fig 2: Site means for wood density
JWD
MWD
Tar
Eyr
Maw
Gld
Awa
Kai
Whl
350
400
450
500
density (kg/m3)

Fig 3: Wood density pith to bark trends by family

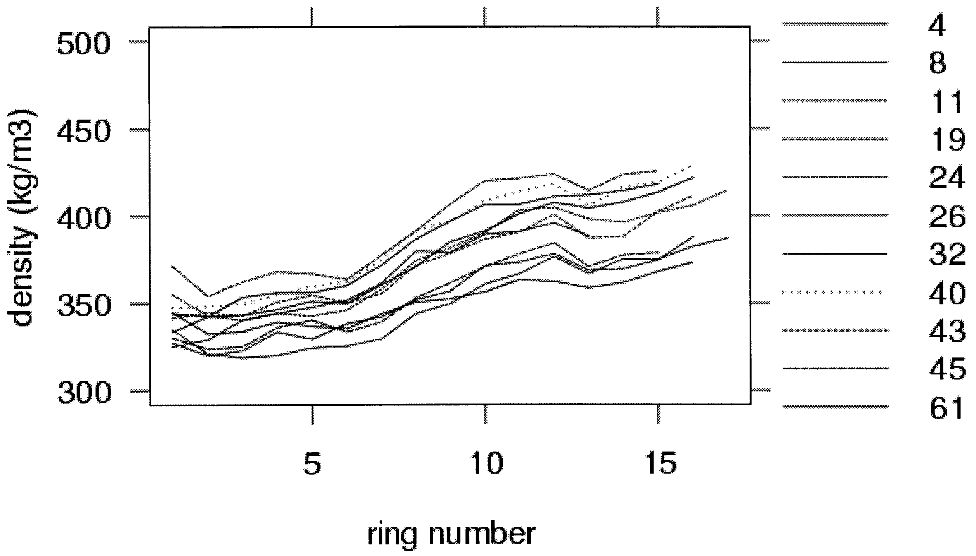
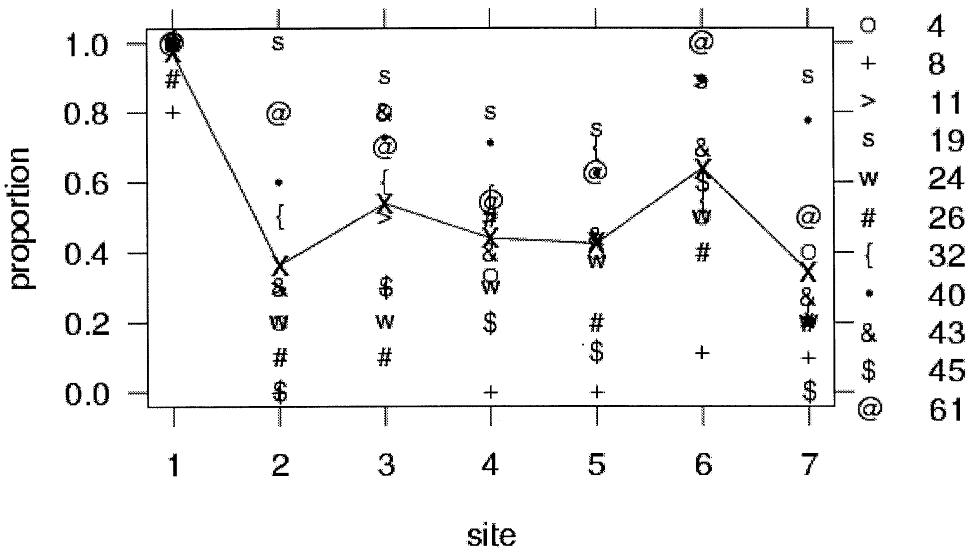


Fig 4: Proportion of trees with density >= 350



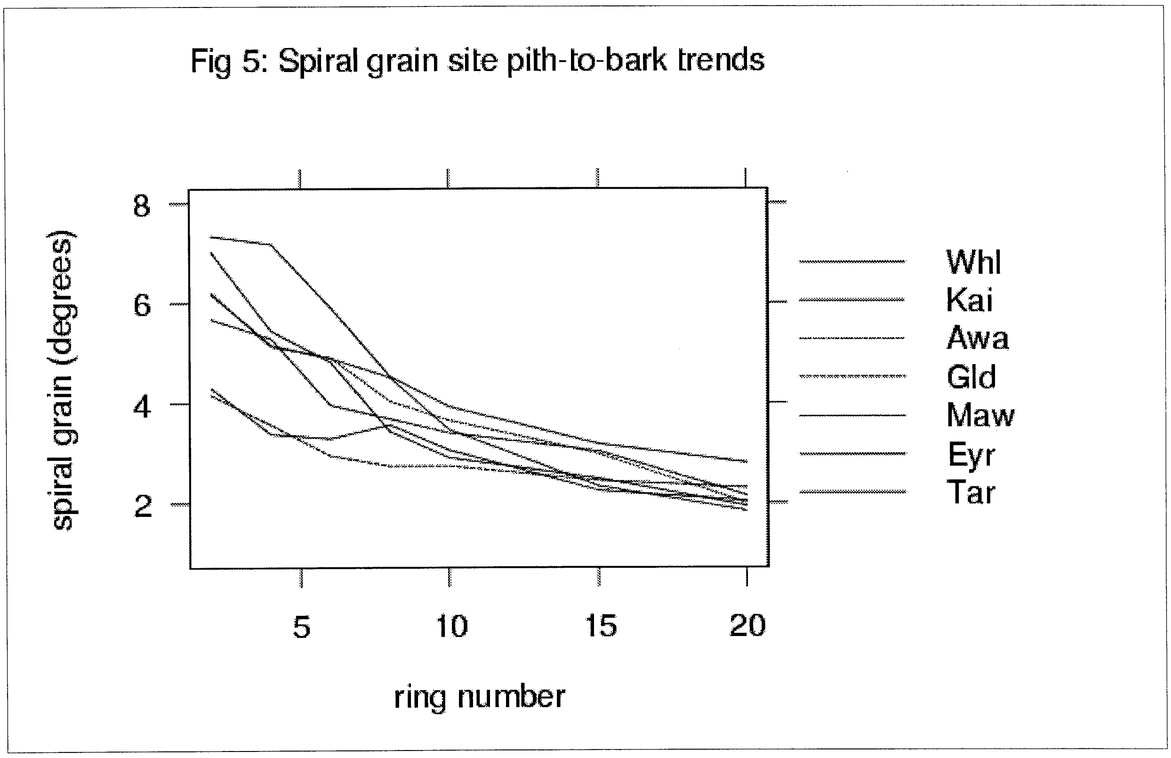


Fig 5: Spiral grain site pith-to-bark trends
spiral grain (degrees)
8
6
4
2
5
10
15
20
ring number
Whl
Kai
Awa
Gld
Maw
Eyr
Tar

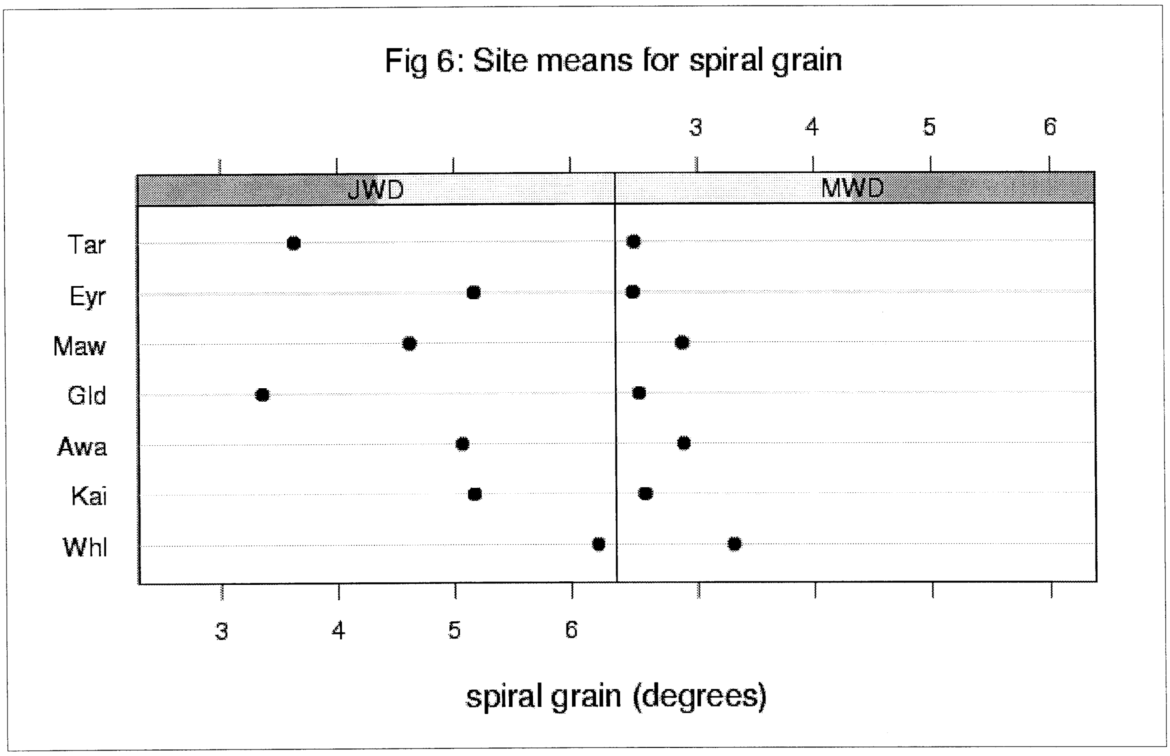


Fig 6: Site means for spiral grain
JWD
MWD
Tar
Eyr
Maw
Gld
Awa
Kai
Whl
3
4
5
6
spiral grain (degrees)

Fig 7: Spiral grain family pith-to-bark trends

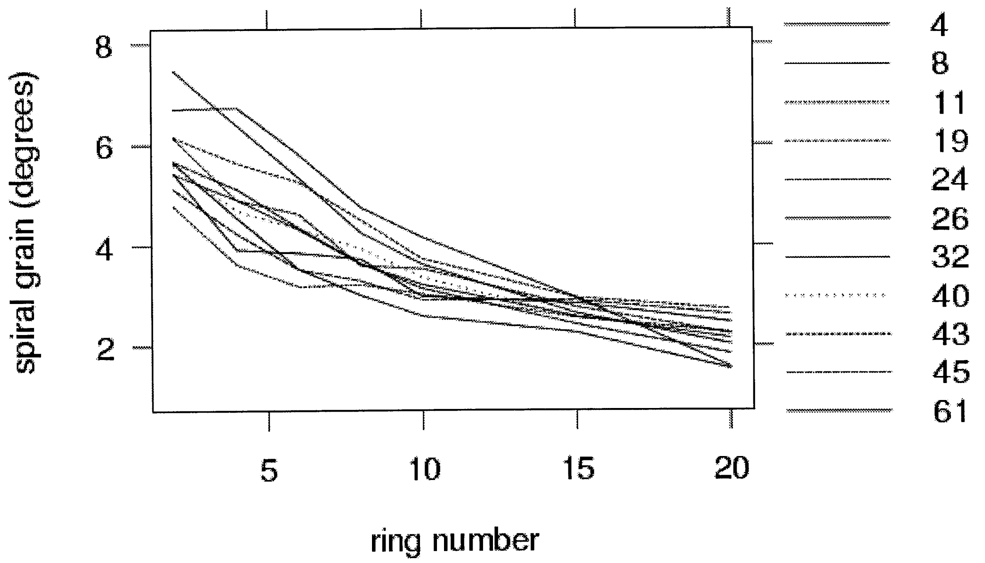
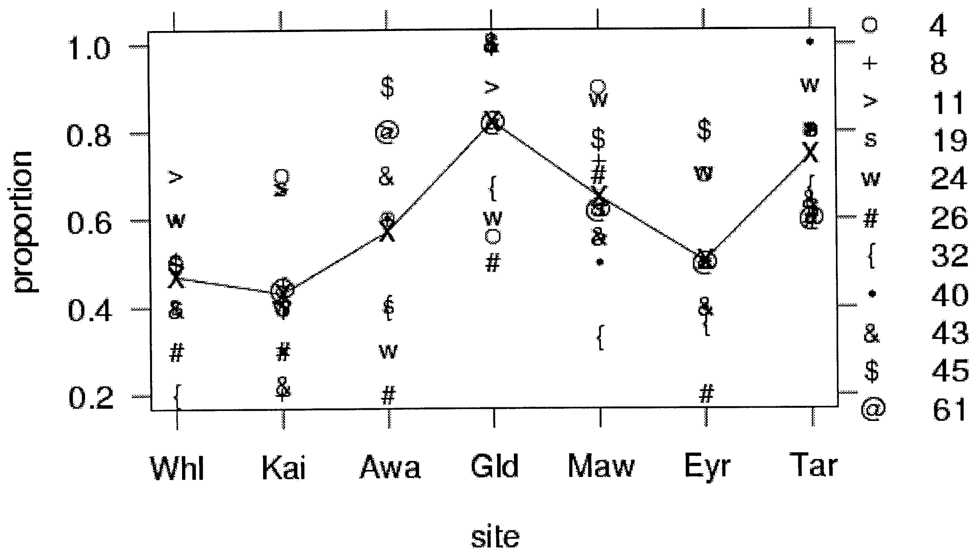
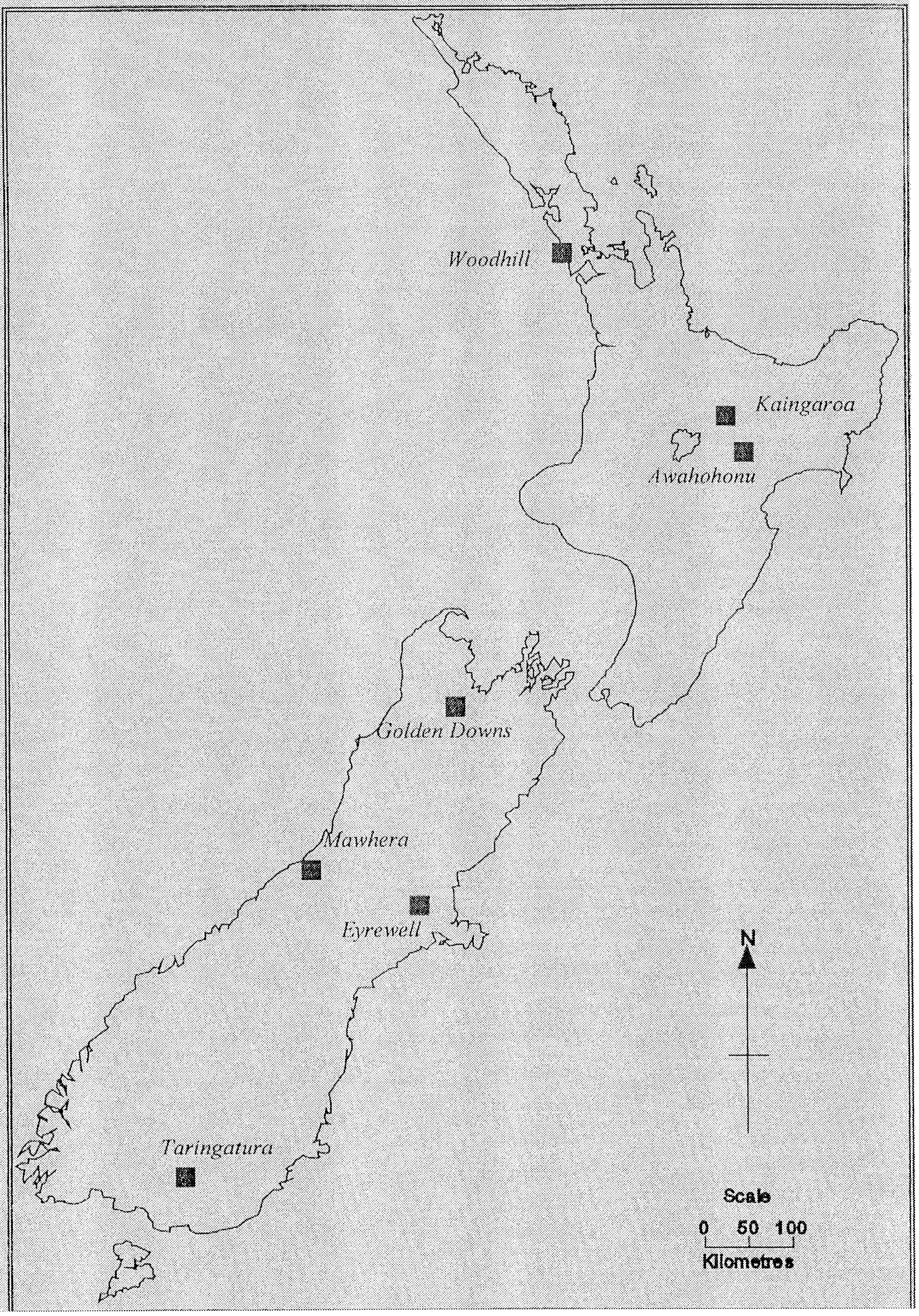


Fig 8: Proportion of trees with SG < 5



Appendix 1: Location of the seven diallel sites



Appendix 2: Binomial generalised linear model fit for the proportion of stems with juvenile wood density > 350kg/m^3.

```
Binomial model
Response: num.poor/num.trees
Terms added sequentially (first to last)
        Df Deviance Resid. Df Resid. Dev
   NULL                    76      374.1
   site  6    154.1        70      220.0
ffamily 10    161.5        60       58.5

> summary(wd.poor.fit1)
Call: glm(formula = num.poor/num.trees ~ site + ffamily, family =
binomial(link =
     logit), data = family.df, weights = num.trees)
Deviance Residuals:
   Min     1Q Median    3Q  Max
 -2.01 -0.531 0.0247 0.565 1.68

Coefficients:
             Value Std. Error t value
(Intercept) -0.402     0.2831  -1.421
      site1  2.499     0.3364   7.429
      site2  0.524     0.1323   3.965
      site3  0.390     0.0813   4.796
      site4  0.248     0.0592   4.184
      site5 -0.019     0.0457  -0.416
      site6  0.209     0.0386   5.426
   ffamily2  2.399     0.5380   4.458
   ffamily3 -0.122     0.3827  -0.319
   ffamily4 -2.320     0.4911  -4.723
   ffamily5  0.679     0.3994   1.700
   ffamily6  0.988     0.4093   2.415
   ffamily7 -0.335     0.3813  -0.879
   ffamily8 -1.266     0.4122  -3.071
   ffamily9 -0.191     0.3795  -0.505
  ffamily10  1.142     0.4223   2.704
  ffamily11 -1.111     0.3978  -2.792

(Dispersion Parameter for Binomial family taken to be 1 )
    Null Deviance: 374 on 76 degrees of freedom
Residual Deviance: 58.5 on 60 degrees of freedom
Number of Fisher Scoring Iterations: 6
```

Appendix 3: Binomial generalised linear model fit for the proportion of stems with juvenile wood spiral grain < 5°.

```
Analysis of Deviance Table
Binomial model
Response: sg.prop.poor
Terms added sequentially (first to last)
        Df Deviance Resid. Df Resid. Dev
   NULL                    75        170
   site  6     59.1        69        111
ffamily 10     32.3        59         78
> summary(sg.poor.fit1,disp=78.3/59)

Call: glm(formula = sg.prop.poor ~ site + ffamily, family = binomial(link =
logit),
     data = family.df[!is.na(family.df$sg.prop.poor),  ], weights =
     num.trees)
Deviance Residuals:
   Min      1Q  Median     3Q  Max
 -2.15 -0.758 -0.0217 0.676 2.36

Coefficients:
              Value Std. Error t value
(Intercept) -0.8547     0.3099  -2.758
      site1  0.0833     0.1647   0.506
      site2 -0.1716     0.0933  -1.838
      site3 -0.4051     0.0820  -4.943
      site4 -0.0621     0.0556  -1.117
      site5  0.0666     0.0423   1.573
      site6 -0.1114     0.0401  -2.777
   ffamily2  0.3208     0.4285   0.749
   ffamily3 -0.1249     0.4437  -0.282
   ffamily4  0.2639     0.4333   0.609
   ffamily5  0.3141     0.4305   0.730
   ffamily6  1.2915     0.4285   3.014
   ffamily7  1.1174     0.4267   2.619
   ffamily8  0.2908     0.4334   0.671
   ffamily9  0.5811     0.4242   1.370
  ffamily10 -0.1860     0.4466  -0.416
  ffamily11  0.3586     0.4537   0.791

 (Dispersion Parameter for Binomial family taken to be 1.33 )
    Null Deviance: 170 on 75 degrees of freedom
Residual Deviance: 78.3 on 59 degrees of freedom
Number of Fisher Scoring Iterations: 4
```