Genetic parameters and improvement strategies for the *Pinus elliottii* var. *elliottii* × *Pinus caribaea* var. *hondurensis* hybrid in Queensland, Australia

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Chapter 5 - Age trends in genetic parameters and indirect selection for wood properties and basal area

5.1 Introduction

The length of time taken to evaluate genotypes in genetic tests, and the cost of evaluating wood quality characteristics, are two serious and continuing impediments to improving the profitability of wood growing and processing industries through tree improvement. In hybrid improvement, costly, multi-population breeding strategies with long breeding cycle intervals place even higher priority on reducing the duration and cost of genotype assessment (Paques 1989). In the PEE×PCH hybrid in Queensland, recent utilisation studies have found that stem volume, wood density and spiral grain make a significant contribution to the sawn timber breeding objective (Greaves *et al.* 2000; Harding *et al.* 2000). Therefore, a key priority for research is to develop procedures for assessing these selection criteria efficiently in PEE×PCH and parental species, at the earliest possible age.

The value of early selection for increasing the genetic gain per year from tree improvement has been demonstrated in many taxa and traits (*eg* Lambeth *et al.* 1983; Li *et al.* 1996; Loo *et al.* 1984; Vargas-Hernandez and Adams 1994; Williams and Megraw 1994). The main benefit of early selection is a shorter breeding cycle, through reduction of the time taken to determine the genetic worth of candidate genotypes for further breeding or deployment. Ancillary benefits include the opportunity to increase selection intensity or reduce field test size, and the opportunity to use early measurements to improve the accuracy of selection at a later age (*eg* Apiolaza *et al.* 2000, Wu 1998). Evidence accumulated from a large number of early selection studies over the past 20 years has allowed reduction of the age at which selection takes place, from the broad prescription of half rotation age (Franklin 1979; Zobel and Talbert 1984), down to 4-8 years in most warm temperate and subtropical conifers (*eg* Gwaze *et al.* 1997; King and Burdon 1991; McKeand 1988). Despite these often dramatic reductions, genetic testing remains the activity of longest duration in tree improvement.

The results of early testing studies have not always been consistent among taxa and experiments. For example, in studies of diameter growth in *Pinus radiata*, King and Burdon (1991) found optimum genetic gain per year from selection at 7-8 years for a mature age of 17 years, and Cotterill and Dean (1988) found 6.5 years to be the optimum for a mature age of 16 years, while Matheson *et al.* (1994) found that optimum selection age was not reached until 10 years for a mature age of 14 years. Several studies in *Pinus taeda* have suggested selection as young as age 3 (Foster 1986, mature age of 15 years; Gwaze *et al.* 1997, mature age of 22.5 years). Hence, while all studies suggest that selection should be performed well before maturity, generalised prescriptions for efficient juvenile selection for growth characters cannot be made with much confidence.

Increasing interest in improving wood product value has motivated several recent studies of early selection in wood properties. Fewer estimates of the efficiency of early selection are available for wood properties than for growth characters, due to the difficulty of measuring wood properties in individual annual rings or small ring segments. Most of the published studies have found strong genetic relationships between juvenile and mature measurements of wood density, and high heritability at all ages (*eg* Williams and Megraw 1994, Loo *et al.* 1984, Hannrup and Ekberg 1998; Vargas-Hernandez and Adams 1992). However, the optimum age for selection has varied greatly, and several major studies have found less favourable results. Notably, a large study of 56 open-pollinated families in *Pinus elliottii* (Hodge and Purnell 1993) found r_A of only 0.36^{ns} between juvenile wood density and mature wood density. Additionally, although various studies have examined the genetic relationship between juvenile and mature stem density, very few have assessed the genetic relationship between the density of individual rings and mature stem density. Efficient prediction of mature stem properties based on individual ring measurements at an early age, if possible, could allow important reductions in the size and cost of wood samples, or the use of rapid field testing methods that sample only the outermost wood surface on standing trees.

In exotic pine improvement in Queensland, selection of breeding parents in progeny tests typically takes place at age 6, although selection must be performed earlier (around age 4) in clonal tests, to avoid excessive maturation of the ortets. Though

studies in other taxa have suggested early selection may be efficient, the usefulness of early selection for growth and wood characters at ages 4 and 6 remains to be verified in Queensland PEE×PCH hybrids and parental species.

A second key issue for wood property improvement is the expense of trait assessment. Even in cases where wood properties can be reliably assessed at a juvenile age, the expense of wood sampling and laboratory assessment typically exceeds that of growth trait measurement by at least an order of magnitude (Zobel and Jett 1995). In the PEE×PCH hybrid, given the clear need for improvement of wood density (Chapter 3) and possible mild adverse correlation between wood density and growth (Chapter 4), it is likely that a large sample of the hybrid or pure species breeding populations will need to be screened in order to identify families with excellent values for both traits.

It is well known that the high expense of wood sampling using cores or discs precludes large-scale screening of progeny populations for wood properties using these methods (*eg* Downes *et al.* 1997). While numerous alternatives to wood sampling have been proposed for quickly assessing wood properties indirectly in the field, none have been demonstrated to be both cheap and consistently reliable. Of these methods, the pilodyn penetrometer (Hoffmeyer 1978) and the bubble protractor (Harris 1984) have been found to efficiently predict density and spiral grain, respectively, in a range of studies (*eg* Cown and Andrew 1979; Greaves *et al.* 1995; Sprague *et al.* 1983; Sorensson *et al.* 1997a). The pilodyn provides an indirect measure of wood density based on the depth of penetration of a pin fired with constant force into the outermost-formed wood. The bubble protractor, recently digitally redeveloped as the Spiralite® (Sorensson *et al.* 1997a), provides a direct measure of spiral grain angle on the outermost-formed wood surface. Although pilodyn and bubble protractor measurements are typically only moderately well correlated with mean breast height density and spiral grain, respectively, at the individual-tree level (*eg* Cown 1979; Smith *et al.* 1981), the correlations are much higher when estimated at the group mean level (*eg* Sprague *et al.* 1983; Cown 1979; Yanchuk and Kiss 1993; Greaves *et al.* 1995; Muneri and Raymond 2000; Wang *et al.* 1999). In genetic improvement, these instruments have particular potential for assessing the means of groups of trees such as families or clones for density and spiral grain, at low cost.

The usefulness of these methods has not been consistent in all circumstances, however. Muneri and Raymond (2000) found that while the genetic correlation between pilodyn and density was always high, it varied among sites. In other studies, however, poor results from the pilodyn have been due to poor technique in using the instrument. Cown and Andrew (1979) found that the family mean correlation between pilodyn penetration and density varied from -0.4 to -0.82 in the same *Pinus radiata* progeny test, depending on which of 5 operators performed the assessments. In an adjacent clonal *P. radiata* experiment assessed by an experienced operator, a pilodyn-density clonal mean correlation of -0.96 was obtained (Cown 1979). These findings indicate that the usefulness of the pilodyn may be strongly dependent upon careful operating technique (Villeneuve 1999), and therefore may have been underestimated by some previous studies.

Several studies have found stronger genetic correlations between pilodyn and diameter increment than between wood density and diameter increment (*eg* Costa e Silva *et al.* 2000), suggested to reflect increased pin penetration where growth rings are wider. Such differences could adversely affect the accuracy of selection indices that include pilodyn in place of density (*eg* Park *et al.* 1989), and highlight the need to investigate the correlations of pilodyn with growth traits and other selection criteria.

This chapter seeks to address two critical questions for wood improvement in the Queensland PEE×PCH hybrid:

1. Can wood quality characteristics be usefully assessed in genetic tests at the same age or younger than growth traits, and at an age early enough that excessive physiological maturation has not yet occurred in clonal ortets?
2. Can field testing for wood density and spiral grain improve the efficiency of selection for these traits in PEE, PCH and PEE×PCH hybrids?

5.2 Methods and materials

The genetic material, sites, sampling strategy, and field and measurement methodologies have been detailed in Sections 3.3 and 4.2. As in Chapter 4, because the F2 hybrid progeny in EXP674 do not share common ancestry with the other taxa, only the PEE, PCH and PEE×PCH F_1 hybrid progeny are examined in this chapter. This section will describe specific data analyses associated with early selection and indirect selection using field testing.

5.2.1 Field testing for wood properties

The procedure for field assessment of spiral grain using the bubble protractor (Harris 1984) and calculation of the variable PROT (average bark window spiral grain angle) was described in Section 3.3. The bark windows on the north and south aspect of each stem used to assess spiral grain were also used to assess pilodyn pin penetration using the PROCEQ™ 12-Joule Pilodyn penetrometer, a spring-loaded device that fires a steel pin into the tree and measures the depth of penetration (PROCEQ 2002). Penetration depth may be inversely related to wood density (*eg* Greaves *et al.* 1996). Before taking measurements, a preliminary study was carried out to test the relative effectiveness of 2mm and 2.5mm diameter pilodyn striker pins. In pilodyn assessments of a sample of 50 PEE×PCH trees, 2.5mm pins achieved much poorer differentiation among trees than did 2.0mm pins. All measurements were subsequently carried out using 2.0mm pins. Two pin penetration readings were taken in both the northern and southern bark window of each tree. These readings were assigned the names PILN1, PILN2, PILS1 and PILS2, respectively. Readings in the north and south bark windows were averaged to obtain the variables PILNTH and PILSTH, respectively. The mean of all four pilodyn measurements was assigned the name PILMN. PILMN values were examined to ensure that the population of measurements was normally distributed, and variable enough to ensure reasonable differentiation among trees. Both of these conditions were fulfilled in all three taxa at both sites: the ranges and standard deviations of individual-tree PILMN measurements are presented in Table 5.1.

Table 5.1 Range (lowest, highest) and standard deviation (sd) of individual-tree mean pilodyn pin penetration (PILMN) in each taxon at each site

taxon	site	lowest	highest	sd
PEE	Tuan	11.3	18.9	1.50
	Beerwah	10.5	23.8	1.57
PCH	Tuan	12.3	22.6	1.79
	Beerwah	11.5	22.5	1.85
F_1	Tuan	11.0	22.0	1.78
	Beerwah	11.3	25.5	1.95
F_2	Tuan	11.5	23.5	1.94
	Beerwah	11.1	22.0	1.86

Note: the trait PILMN was calculated as the overall average of two readings on the south and two readings on the north of each tree.

5.2.2 Assignment of annual rings

The motivation for comparing wood properties among trees based on their year of formation was discussed in Section 3.3. This approach was considered particularly important in the current study, which focuses on indirect selection for wood properties based on individual-ring measurements and field assessments, which typically sample only the most recently formed wood of each tree. In all cases in this study, rings will be identified by the age of the tree at their year of formation. Given that trees vary in the age at which they reach breast (sampling) height, it was considered that the comparison of rings among trees based on other criteria, such as cambial age, would be confounded by year-to-year climatic variation. This would result in inflated environmental variance and deflated heritabilities and genetic correlations, particularly in taxa or sites where early height growth was variable.

Many earlier studies have found that genetic parameters for individual-ring wood properties are highly variable from year to year, and need to be either smoothed by fitting a curve to density values (*eg* Hodge and Purnell 1993) or analysed as groups of rings (*eg* Hylen 1999), to obtain sensible results. It is proposed that the practice of comparing trees based on individual growth rings that formed in different calendar years is likely to contribute substantially to this variation, and that comparing growth rings formed in the same calendar year (*ie* based on tree age) will provide a more reliable basis for comparison among genotypes. Comparison based on tree age is also expected to provide a more useful indication of the correlation between single-ring

assessments of wood properties and whole-radius wood properties, because the single-ring assessments will not be confounded by the effects of year-to-year climatic variation on wood formation.

5.2.3 *Estimation of juvenile:mature correlations and selection efficiency*

A pooled-site analysis of variance, as described in Section 4.2 (see Equation 4.4) was applied to standardised data for the traits stem basal area underbark, area-weighted mean wood density at breast height, and individual-ring measurements of wood density and spiral grain, measured at each of years 1-12 from seed. This analysis was also applied to all pilodyn traits: PILN1, PILN2, PILS1, PILS2, PILNTH, PILSTH and PILMN, and to the bubble protractor assessment, PROT. Based on the estimated variance components, correlations between stem basal area at each tree age and tree basal area at maturity (age 12) were estimated using the univariate analysis described in Section 4.2 and Appendix 10 for estimating genetic correlations between traits. The genetic correlation between wood density at each tree age and wood density at age 12 was estimated in the same manner. Although strictly speaking, the assumption of uncorrelated residual variance is inappropriate for repeated measures data, univariate analysis was favoured over multivariate or longitudinal data analysis for calculating genetic correlations between traits measured at different ages, mainly because there were insufficient data for the demanding computations of the latter methods. This and other issues associated with longitudinal data analysis were discussed in Section 2.3. The individual-tree heritability of each trait in PEE and PCH, and family heritability of each trait in PEE, PCH and F_1, were calculated as described in Section 4.2. As in Chapter 4, all analyses were conducted on data which had been scaled by the square root of the residual error variance at each site.

The correlated genetic gain from indirect selection estimates the genetic gain per generation from early selection or other types of indirect selection, and was calculated using the following formula (Falconer and Mackay 1996):

$$\Delta G_{FS_{S:T}}\% = \left(\frac{h_{FS_S} h_{FS_T} r_{A_{S:T}} i_{FS_S} \sigma_{P_{FS_T}}}{E(T)} \right) \times 100 \qquad [5.1]$$

where:

$\Delta G_{FS_{S:T}}\%$ = predicted genetic gain in mature, or target trait (T) based on early or indirect selection on screening trait (S), as a percentage of traits mean value;

h_{FS_S} and h_{FS_T} = square root of the narrow-sense full-sib family heritability of the screening trait and the target trait, respectively;

$r_{A_{S:T}}$ = additive genetic correlation between screening trait and target trait;

i_{FS_S} = selection intensity on full-sib families in the screening trait (=1.755, or 10% of an assumed infinite population);

$\sigma_{P_{FS_T}}$ = phenotypic standard deviation of full-sib family means in the target trait;

E(T) = expected value (mean) of target trait.

For brevity, in this chapter genetic gain ($\Delta G_{FS_{S:T}}\%$) was calculated only based on the narrow-sense full-sib family heritability, effectively estimating the genetic gain from backward selection of, and random mating amongst, the parents of the best 10% of full-sib families. The efficiency of indirect selection (screening) and early selection was calculated in all taxa assuming the same selection intensity (i) in the screening trait or juvenile trait, as in the target, or mature, trait. The efficiency of indirect selection of full-sib families by field screening was calculated as:

$$E_{FS_{S:T}}\% = \left(\frac{h_{FS_S} r_{A_{S:T}}}{h_{FS_T}} \right) \times 100 \qquad [5.2]$$

where:

$E_{FS_{S:T}}\%$ = efficiency of full-sib family selection on the screening trait (S) relative to direct selection on the target trait (T);

h_{FS_S} and h_{FS_T} = square root of the narrow-sense full-sib family heritability of the screening trait and target trait, respectively;

$r_{A_{ST}}$ = additive genetic correlation between screening trait and target trait;

Defined non-mathematically, $E_{FS_{S:T}}\%$ is the predicted genetic gain from indirect selection as a percentage of predicted genetic gain from direct selection. To investigate the possibility of screening large, unreplicated populations to uncover new high density candidate trees using the pilodyn penetrometer (*eg* Hall 1988), the efficiency of indirect selection for pilodyn was also calculated based on individual-tree heritability ($E_{i_{S:T}}\%$). Genetic gain from selection of individual trees cannot be reliably predicted in early generation hybrid populations, except for backward selection of individual trees through the use of observational components of variance estimated directly from clonal trials.

The efficiency of early selection of full-sib families was calculated as the predicted genetic gain per year achieved by selection at each juvenile age, as a percentage of the predicted genetic gain per year achieved by selection at maturity, using the following simplified equation, after McKeand (1988):

$$E_{FS_{J:M}}\% = \left(\frac{h_{FS_J} r_{A_{J:M}}}{h_{FS_M}}\right)\left(\frac{T_M}{T_J}\right)\times 100 \qquad [5.3]$$

where:
$E_{FS_{J:M}}\%$ = efficiency of selection for mature trait based on juvenile trait;
h_{FS_J} and h_{FS_M} = square root of narrow-sense full-sib family heritability of juvenile trait and mature trait, respectively;
$r_{A_{J:M}}$ = additive genetic correlation between juvenile and mature trait;
T_M = time taken from seed until selection for mature trait;
T_J = time taken from seed until selection for juvenile trait;

In all calculations of the efficiency of indirect selection and early selection, the mature trait was that measured on the tree at age 12 from seed, and trait-trait genetic correlation estimates that exceeded 1.0 were set to 1.0 prior to using them in further calculations.

5.3 Results

5.3.1 Ring formation

Description of the age of the material under examination refers in all cases to the tree age from seed, in years. However, it is also useful to know the age of the cambium at the time of ring formation, because this characteristic has a strong effect on the ontogeny of wood properties, and must be considered when sampling at different heights and sites (Zobel and Jett 1995). Table 5.2 lists the number of individuals with valid individual-ring measurements of ring width and wood characteristics for each year of wood formation: the corresponding tree age and approximate cambial age for each year are also listed. The first-formed growth ring was, in almost all taxa and trees, at age 3 from seed, though a small proportion of hybrid trees had already

formed a small ring by age 2 from seed, and a similarly small proportion of trees in all taxa did not form their first ring until age 4 from seed. Data at age 2 from seed could not be analysed because so few trees had formed a ring. In the results and discussion, descriptions of the age of the material refer to the tree age from seed.

Table 5.2 Numbers of individuals with measurements for basal area and wood density in each year of wood formation.

year of formation	tree age from seed (years)	approximate cambial age (years)	PEE	PCH	F_1
1989	3	1	511	558	763
1990	4	2	589	592	796
1991	5	3	589	594	796
1992	6	4	589	594	796
1993	7	5	589	594	796
1994	8	6	589	594	796
1995	9	7	589	594	796
1996	10	8	589	594	796
1997	11	9	588	593	792
1998	12	10	576	592	776

Note: highlighted values indicate the total number of trees sampled for wood density in each taxon.

5.3.2 Genetic parameters and early selection in PEE, PCH and F_1

5.3.2.1 Tree basal area

Variance components for all traits examined in this chapter are listed in Appendix 16. The individual-tree heritability of basal area underbark at all ages (3-12 years, from seed) was moderate in PEE, and low in PCH (see Table 5.3). Individual-tree, half-sib family and full-sib family heritabilities of tree basal area underbark increased steadily with tree age in PEE and PCH. Variance due to SCA effects was negligible in both PEE and PCH, except in the early years of growth.

Juvenile-mature (age 12) genetic correlations of basal area in PEE and PCH were consistently significantly different from zero ($p<0.05$), and exceeded 0.9, after age 4. Optimum efficiency of early selection of full-sib families in terms of genetic gain per year in age 12 tree basal area was achieved by selection for age 4 tree basal area in both PEE and PCH; this option resulted in a 2.74-fold increase in genetic gain per year in PEE, and a 2.21-fold increase in PCH, relative to selection at age 12. Little

extra genetic gain per generation could be achieved by waiting any longer to select (see Table 5.3).

In the F_1 hybrid, the half-sib and full-sib family heritability of basal area was low to moderate at all ages, peaking at ages 4-7 (see Table 5.4). SCA variance in basal area increased strongly through ages 3-12, contrary to the opposite trend found in PEE and PCH. In the F_1 hybrid, SCA variance in basal area exceeded overall GCA variance from ages 8-12, and at most ages the SCA variance, as a proportion of GCA variance, was much higher than it was in either PEE or PCH.

The juvenile-mature genetic correlation for basal area in the F_1 hybrid approximated 1 and was highly significantly different from zero ($p<0.001$), after age 6. A strong genetic correlation (0.91) was also found between age 3 basal area and age 12 basal area, although this correlation was considered unreliable as it was only marginally significantly different from zero at the $p<0.05$ level, and further analysis indicated that the family mean correlation between the same pair of traits, considered useful as a conservative estimate of the genetic correlation, was very low. The strong genetic correlation is likely to be an artefact of the high error incurred when trying to identify and measure the width of early growth rings in the hard pines. Ignoring age 3, maximum genetic gain per year was achieved by selecting at age 6, which is expected to achieve 2.14 times the amount possible from selection at age 12 (see Table 5.4).

Table 5.3 Age trends in genetic parameters, juvenile-mature correlations and efficiency of early selection for stem basal area in PEE and PCH.

age	heritabilities				genetic correlation	genetic gain	
	h_i^2 (se)	h_{HS}^2 (se)	h_{FS}^2 (se)	$\frac{\sigma_{SCA}^2}{\sigma_{GCA}^2}$ (se)	$r_{G_{J:M}}$	$\Delta G_{FS_{J:M}}$ %	$E_{FS_{J:M}}$ %
PEE							
3	0.18 (0.10)	0.71 (0.15)	0.47 (0.18)	0.47 (0.66)	0.71*	12.7	222
4	0.25 (0.13)	0.84 (0.10)	0.66 (0.15)	0.08 (0.27)	0.99***	21.0	274
5	0.31 (0.15)	0.87 (0.08)	0.71 (0.12)	0.00 (0.00)	1.04***	21.9	229
6	0.36 (0.16)	0.88 (0.07)	0.74 (0.11)	0.00 (0.00)	1.02***	22.3	195
7	0.43 (0.18)	0.91 (0.05)	0.78 (0.10)	0.00 (0.00)	1.01***	22.9	171
8	0.46 (0.18)	0.92 (0.04)	0.79 (0.09)	0.00 (0.00)	1.02***	23.1	151
9	0.49 (0.18)	0.93 (0.04)	0.81 (0.09)	0.00 (0.08)	1.02***	23.3	135
10	0.51 (0.19)	0.92 (0.04)	0.81 (0.09)	0.02 (0.09)	1.02***	23.3	122
11	0.53 (0.19)	0.92 (0.04)	0.80 (0.09)	0.04 (0.09)	1.00***	23.2	110
12	0.53 (0.19)	0.91 (0.05)	0.78 (0.10)	0.08 (0.09)	1.00***	23.0	100
PCH							
3	0.08 (0.06)	0.55 (0.25)	0.31 (0.20)	0.89 (1.49)	0.31ns	2.4	99
4	0.08 (0.07)	0.55 (0.23)	0.29 (0.20)	1.77 (2.07)	0.93*	7.2	221
5	0.11 (0.09)	0.62 (0.23)	0.37 (0.21)	0.92 (1.30)	0.92*	8.0	196
6	0.14 (0.11)	0.67 (0.22)	0.45 (0.23)	0.16 (0.75)	0.92*	8.9	181
7	0.15 (0.13)	0.61 (0.27)	0.43 (0.25)	0.00 (0.00)	0.91*	8.6	150
8	0.15 (0.15)	0.57 (0.31)	0.41 (0.28)	0.00 (0.00)	0.98***	9.1	138
9	0.15 (0.15)	0.57 (0.31)	0.41 (0.27)	0.00 (0.00)	1.00***	9.2	124
10	0.15 (0.15)	0.55 (0.32)	0.40 (0.29)	0.00 (0.00)	1.03***	9.1	111
11	0.18 (0.16)	0.60 (0.29)	0.45 (0.27)	0.10 (0.61)	0.99***	9.6	106
12	0.19 (0.16)	0.62 (0.28)	0.47 (0.26)	0.11 (0.60)	1.00***	9.8	100

Note: all genetic parameters are for stem basal area estimated based on growth ring widths measured on a single breast height increment core radius from each tree; $r_{G_{J:M}}$ denotes the genetic correlation of basal area measured at each juvenile age with tree basal area at age 12; $\Delta G_{FS_{J:M}}$ % denotes the predicted genetic gain resulting from selection and recombination amongst the best 10% of full-sib families; $E_{FS_{J:M}}$ % denotes the percentage efficiency (genetic gain per year) resulting from selection of full-sib family basal area at any juvenile age, relative to that from selection at age 12. All abbreviations of genetic parameters are explained in sections 4.2 and 5.2. *, ** and *** denote genetic correlations that differ significantly from zero at the 0.05, 0.01 and 0.0005 levels, respectively.

Table 5.4 Age trends in genetic parameters, juvenile-mature correlations and efficiency of early selection for basal area in the F_1 hybrid

age	heritabilities				genetic correlation	genetic gain	
	$h^2_{HS_f}$ (se)	$h^2_{HS_m}$ (se)	h^2_{FS} (se)	$\frac{\sigma^2_{SCA}}{\sigma^2_{GCA}}$ (se)	$r_{G_{J:M}}$	$\Delta G_{FS_{J:M}}$ %	$E_{FS_{J:M}}$ %
3	0.40 (0.34)	0.35 (0.36)	0.30 (0.22)	0 (0)	0.91^{*}	12.8	356
4	0.49 (0.28)	0.52 (0.20)	0.39 (0.16)	0 (0)	0.41^{ns}	6.6	138
5	0.38 (0.37)	0.64 (0.17)	0.43 (0.18)	0.09 (0.93)	0.67^{ns}	11.4	190
6	0.33 (0.36)	0.58 (0.19)	0.37 (0.18)	0.72 (1.05)	0.98^{***}	15.4	214
7	0.38 (0.33)	0.58 (0.19)	0.39 (0.18)	0.81 (1.04)	0.99^{***}	16.0	190
8	0.32 (0.35)	0.51 (0.22)	0.33 (0.19)	1.33 (1.58)	1.05^{***}	14.8	154
9	0.29 (0.36)	0.48 (0.23)	0.30 (0.20)	1.61 (1.95)	1.11^{***}	14.2	131
10	0.31 (0.37)	0.45 (0.24)	0.30 (0.20)	1.55 (2.19)	1.13^{***}	14.1	117
11	0.33 (0.36)	0.41 (0.26)	0.28 (0.21)	1.71 (2.50)	1.10^{***}	13.7	104
12	0.35 (0.35)	0.43 (0.24)	0.31 (0.20)	1.33 (1.95)	1.00^{***}	14.4	100

Note: all genetic parameters are for stem basal area estimated based on growth ring widths measured on a single breast height increment core radius from each tree; $r_{G_{J:M}}$ denotes the genetic correlation of basal area measured at each juvenile age with tree basal area at age 12; $\Delta G_{FS_{J:M}}$ % denotes the predicted genetic gain, in the narrow sense, resulting from selection of the best 10% of full-sib families; $E_{FS_{J:M}}$ % denotes the percentage efficiency (genetic gain per year), base on narrow-sense heritabilities, resulting from selection of full-sib family basal area at any juvenile age, relative to that from selection at age 12. All abbreviations of genetic parameters are explained in sections 4.2 and 5.2; *, ** and *** denote genetic correlations that differ significantly from zero at the 0.05, 0.01 and 0.0005 levels, respectively.

5.3.2.2 Wood density

The individual-tree heritability of area-weighted mean stem wood density at breast height (herein referred to as density) was high and consistent at all ages (ranging between 0.74-0.80) in PEE, but much lower in PCH, gradually increasing from 0.19 at an early age to 0.34 at age 12 (see Table 5.5). Half-sib and full-sib family heritability showed similar trends to individual-tree heritability, in both PEE and PCH. Variance due to SCA effects was basically absent from PEE at all ages; in PCH, SCA variance approximated 0.3 as a proportion of GCA variance at ages 3-5, but was negligible at later ages.

Juvenile-mature genetic correlations for density in PEE and PCH were consistently statistically significant, and exceeded 0.9, after age 4. Optimum predicted genetic gain per year in density at age 12 was achieved by selection on age 4 density in both

PEE and PCH; this option resulted in a 2.7-fold increase in genetic gain per year in PEE, and a 1.96-fold increase in PCH, relative to direct selection.

In the F_1 hybrid, the half-sib and full-sib family heritability of density were high and very consistent from age 3 through age 12 (see Table 5.6). Unlike in basal area, SCA variance in density was negligible at all ages in the F_1 hybrid.

In the F_1, measurements of density from age 4 onwards were strongly and significantly genetically correlated with density at age 12. Selection for density at age 4 achieved 2.83 times the genetic gain per year possible from selection at age 12.

In all taxa, genetic parameter estimates for wood density in individual rings were very similar to those for cumulative density measurements across the stem. Individual-ring genetic parameters are therefore not reported in Table 5.5 and Table 5.6, with the exception of the efficiency of early selection based on individual-ring measurements; other individual-ring parameters are reported in Appendix 16. In all taxa, the expected efficiency of early selection for wood density using individual-ring measurements was approximately equivalent to that from using whole-stem measurements at the same age.

5.3.2.3 Optimum age for early selection

The predicted genetic gain per generation from early selection for age 12 tree basal area and area-weighted stem density in PEE, PCH and F_1 presented in Figure 5.1 indicates that predicted genetic gain per breeding cycle from early selection in all traits except F_1 basal area reaches a plateau at age 4-5, suggesting this as the optimum age for selection of wood and growth traits in progeny tests. Figure 5.2 depicts the genetic gain per year from selection for basal area and density at each age, in each taxon; age 4 is optimal in all taxa and traits except for basal area in the F_1 hybrid. Note that age 4 from seed here equates to age 3 in the field.

In all instances, the efficiency of early selection equalled or exceeded 200% at the optimum age, suggesting strong potential of early selection for both growth and wood density in PEE, PCH and F_1 (Figure 5.2). Optimum predicted efficiency of selection was obtained at age 4 for basal area and density in all taxa, with the exception of basal

area in the F_1 hybrid, where juvenile-mature correlations were variable in the early years. The high efficiency of selection for basal area at age 3 in the hybrid is not considered reliable.

Table 5.5 Age trends in genetic parameters for area-weighted wood density, and efficiency of early selection for area-weighted wood density at age 12 based on area-weighted mean wood density at each juvenile age from 3-11, and based on individual ring wood density at each juvenile age from 3-11, in PEE and PCH.

age	heritabilities					genetic gain (stem mean)		(ind. ring)
	h_i^2 (se)	h_{HS}^2 (se)	h_{FS}^2 (se)	$\frac{\sigma^2_{SCA}}{\sigma^2_{GCA}}$ (se)	$r_{G_{J:M}}$ (DENS)	$\Delta G_{FS_{J:M}}$ %	$E_{FS_{J:M}}$ %	$E_{FS_{J:M}}$ %
PEE								
3	0.35 (0.23)	0.74 (0.19)	0.62 (0.21)	0.06 (0.26)	0.78^{ns}	6.1	262	263
4	0.74 (0.29)	0.94 (0.04)	0.89 (0.07)	0 (0)	0.90^{*}	8.4	270	277
5	0.77 (0.29)	0.94 (0.04)	0.89 (0.06)	0 (0)	0.92^{**}	8.7	223	222
6	0.80 (0.29)	0.95 (0.03)	0.89 (0.06)	0 (0)	0.95^{**}	8.9	192	187
7	0.78 (0.29)	0.94 (0.04)	0.88 (0.07)	0 (0)	0.97^{***}	9.0	166	161
8	0.79 (0.28)	0.95 (0.04)	0.89 (0.06)	0 (0)	0.98^{***}	9.2	148	145
9	0.79 (0.27)	0.95 (0.03)	0.89 (0.06)	0 (0)	0.99^{***}	9.3	133	129
10	0.76 (0.27)	0.94 (0.04)	0.88 (0.07)	0 (0)	1.00^{***}	9.3	120	108
11	0.75 (0.26)	0.94 (0.04)	0.88 (0.06)	0 (0)	1.00^{***}	9.3	109	94
12	0.74 (0.26)	0.94 (0.04)	0.88 (0.06)	0 (0)	1.00^{***}	9.3	100	86
PCH								
3	0.19 (0.14)	0.63 (0.23)	0.46 (0.22)	0.35 (0.74)	0.13^{ns}	0.6	44	53
4	0.19 (0.14)	0.64 (0.22)	0.49 (0.22)	0.25 (0.43)	0.75^{ns}	3.6	196	207
5	0.16 (0.14)	0.58 (0.26)	0.44 (0.24)	0.32 (0.53)	0.83^{ns}	3.7	165	159
6	0.12 (0.15)	0.46 (0.39)	0.36 (0.34)	0.02 (0.48)	1.11^{***}	4.1	150	153
7	0.16 (0.17)	0.50 (0.35)	0.40 (0.32)	0.21 (0.48)	1.12^{***}	4.3	136	149
8	0.26 (0.17)	0.69 (0.22)	0.59 (0.21)	0.02 (0.22)	1.01^{***}	5.2	143	146
9	0.30 (0.17)	0.74 (0.18)	0.63 (0.18)	0 (0)	1.00^{***}	5.4	132	133
10	0.31 (0.18)	0.72 (0.19)	0.62 (0.20)	0.04 (0.19)	1.00^{***}	5.3	118	107
11	0.33 (0.19)	0.74 (0.18)	0.63 (0.19)	0.08 (0.19)	0.99^{***}	5.3	107	107
12	0.34 (0.19)	0.74 (0.18)	0.64 (0.19)	0.06 (0.18)	1.00^{***}	5.4	100	95

Note: $r_{G_{J:M}}$ (DENS) denotes the genetic correlation of area-weighted wood density at each juvenile age with area-weighted wood density at age 12 (DENS); 'stem mean' indicates where early selection is based on the whole-stem mean wood density at each juvenile age; 'ind. ring' indicates where early selection is based on individual ring wood density at each juvenile age; *, ** and *** denote genetic correlations that differ significantly from zero, at the 0.05, 0.01 and 0.0005 levels, respectively.

Table 5.6 Age trends in genetic parameters for area-weighted wood density, and efficiency of early selection for area-weighted wood density at age 12 based on area-weighted mean wood density at each juvenile age from 3-11, and based on individual ring wood density at each juvenile age from 3-11, in the F_1 hybrid.

age	heritabilities				genetic correlation	genetic gain (stem mean)		(ind. ring)
	$h^2_{HS_f}$ (se)	$h^2_{HS_m}$ (se)	h^2_{FS} (se)	$\frac{\sigma^2_{SCA}}{\sigma^2_{GCA}}$ (se)	$r_{G_{J:M}}$ (DENS)	$\Delta G_{FS_{J:M}}$ %	$E_{FS_{J:M}}$ %	$E_{FS_{J:M}}$ %
3	0.84 (0.09)	0.42 (0.32)	0.60 (0.14)	0.11 (0.25)	0.75*	4.9	259	268
4	0.85 (0.09)	0.73 (0.15)	0.74 (0.09)	0 (0)	0.98***	7.1	283	278
5	0.81 (0.11)	0.71 (0.14)	0.71 (0.11)	0.12 (0.18)	1.00***	7.1	225	208
6	0.86 (0.09)	0.77 (0.13)	0.77 (0.09)	0.03 (0.12)	1.01***	7.4	198	190
7	0.85 (0.09)	0.74 (0.14)	0.75 (0.09)	0.09 (0.14)	1.01***	7.3	167	147
8	0.88 (0.07)	0.78 (0.12)	0.79 (0.08)	0.06 (0.12)	0.99***	7.4	147	137
9	0.89 (0.07)	0.81 (0.11)	0.80 (0.07)	0.06 (0.11)	1.00***	7.5	132	131
10	0.89 (0.07)	0.84 (0.09)	0.81 (0.07)	0.07 (0.12)	1.00***	7.5	120	112
11	0.88 (0.07)	0.85 (0.07)	0.80 (0.07)	0.08 (0.13)	1.00***	7.5	109	101
12	0.87 (0.07)	0.85 (0.07)	0.80 (0.07)	0.07 (0.12)	1.00***	7.5	100	87

Note: $r_{G_{J:M}}$ (DENS) denotes the genetic correlation of area-weighted wood density at each juvenile age with area-weighted wood density at age 12 (DENS); 'stem mean' indicates where early selection is based on the whole-stem mean wood density at each juvenile age; 'ind. ring' indicates where early selection is based on individual ring wood density at each juvenile age; *, ** and *** denote genetic correlations that differ significantly from zero at the 0.05, 0.01 and 0.0005 levels, respectively

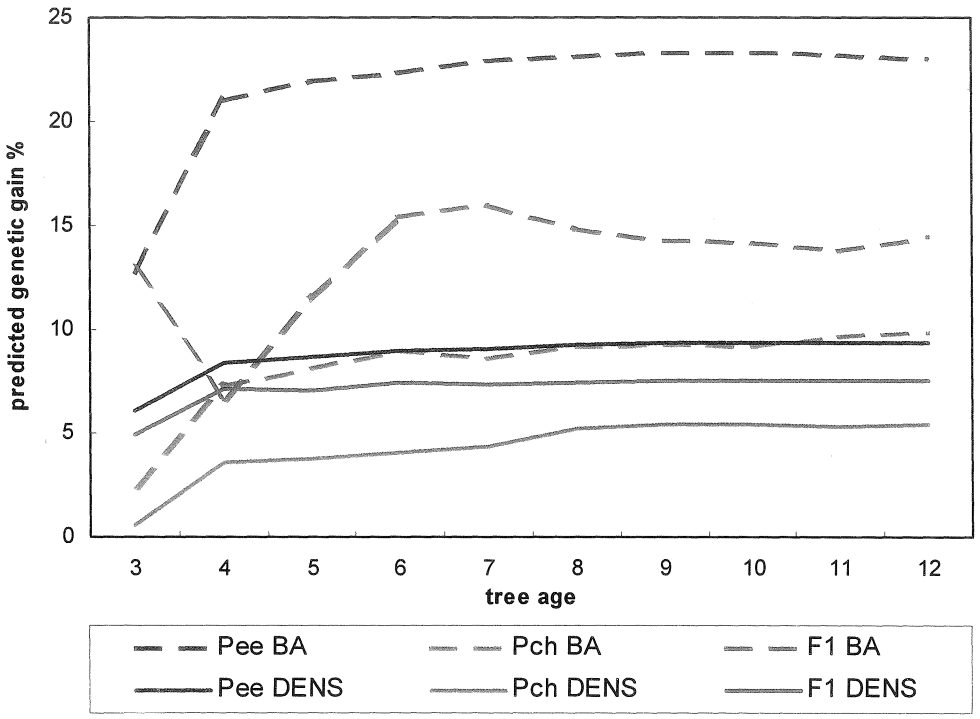

Figure 5.1 Predicted percentage genetic gain per generation from selection for BA (stem basal area) and DENS (area-weighted breast height density) at each juvenile age, relative to direct selection on BA and DENS at age 12, in PEE, PCH and F_1.

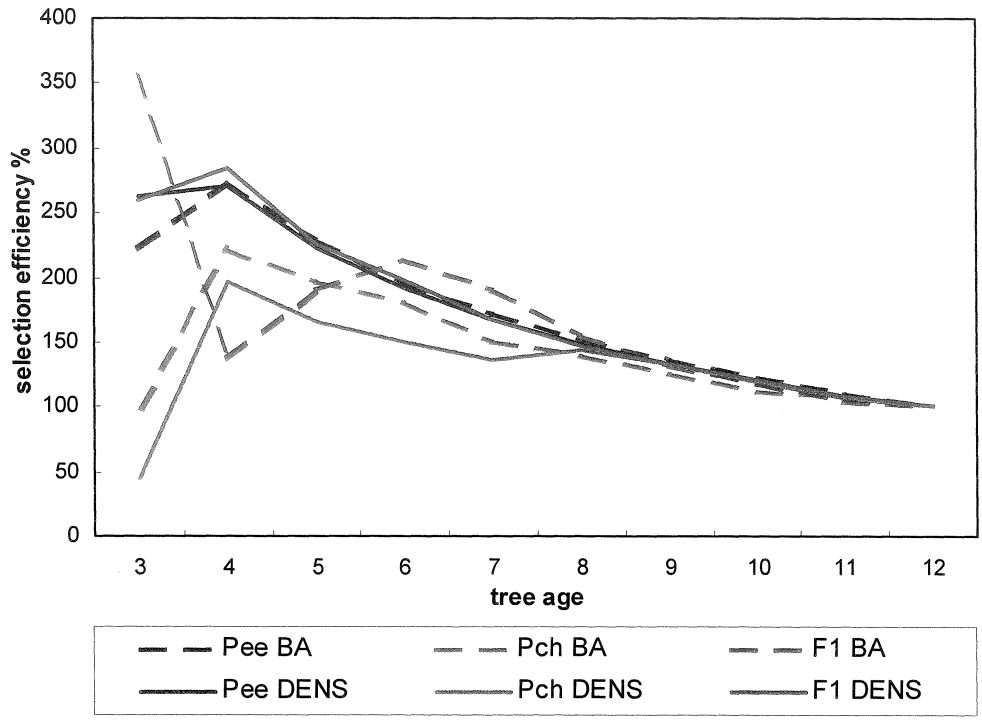

Figure 5.2 Percentage efficiency of early selection for BA (stem basal area) and DENS (area-weighted breast height density) at each juvenile age, relative to direct selection on BA and DENS at age 12, in PEE, PCH and F_1.

5.3.3 Field testing for wood density using the pilodyn

The heritability of pilodyn penetration traits was strong, and similar to or greater than that of wood density, in PEE, PCH and the F_1 hybrid (see Table 5.7, Table 5.8). SCA variance was negligible for pilodyn traits in all taxa, as it was for density; the values are not tabulated here, for the sake of brevity (see Appendix 16). In PEE and F_1, pilodyn penetration and density both had very strong type B genetic correlations; in PCH, however, while density showed only a moderate r_B (0.68), pilodyn traits showed much higher r_B (0.92-0.99), indicating better stability of families across sites for pilodyn penetration than for density. The lower G×E of pilodyn may be responsible for its higher heritability in PCH. In all taxa, the genetic correlation between pilodyn and density was strong and negative, consistently exceeding |0.90| for all pilodyn traits. The number of measurements per tree, and the aspect on which the measurements were taken, appeared to have very little influence on the heritability or G×E of the pilodyn measurements, or on their genetic relationship with density. In PEE, average north and south aspect readings (PILNTH and PILSTH) and the mean reading across both aspects (PILMN) had very slightly higher heritability than single assessments on any aspect. In PCH and F_1 however, the heritabilities of all pilodyn traits were similar, and the marginal genetic gain from taking more than a single measurement on a single aspect was very slight indeed (see Table 5.7 and Table 5.8). In no instance was the genetic gain from sampling two aspects sufficient to justify the increased cost and damage to the tree incurred. The selection efficiency of using the pilodyn in place of direct assessment of density approached or exceeded 100% for any number of pilodyn assessments in any taxon.

The high genetic correlations between pilodyn penetration and area-weighted density were investigated further to determine whether the correlations were in fact due to several outlying families, as is often found in small samples of parents, and whether the correlations varied between sites, as found by Muneri and Raymond (2000). Firstly, least squares means of half-sib families were calculated, and the means for mean south aspect pilodyn penetration (PILSTH) were regressed on the means for area-weighted wood density (DENS), separately for each taxon at each site (see Figure 5.3). In addition to this visual check of the correlations, the family correlation between PILSTH and DENS, on both a half-sib and a broad-sense full-sib family basis, was calculated from the appropriate variance components, at each site separately (see Table 5.9). PILSTH, or average pilodyn assessment on the south side

of the tree, was included as the pilodyn trait due to the practical efficiency of sampling only one side of the tree. The regression of half-sib family means showed a very strong relationship between DENS and PILSTH, with no outliers, in all taxa at both sites (Figure 5.3). This was confirmed by the finding of consistent high family correlations calculated from variance components at both the HS and the broad-sense, FS levels (see Table 5.9). Though not reported in the tables, the phenotypic correlation between density and pilodyn was consistently lower than its genetic counterpart: In PEE, PCH and F_1, the phenotypic correlations were -0.67, -0.70 and -0.68, respectively, on a pooled-site basis.

Furthermore, the ranking of the four taxa was found to be the same for pilodyn and gravimetric density (PCH<F_1<PEE).

Table 5.7 Heritabilities, genetic correlations and efficiency of indirect selection for DENS (area-weighted density) based on some pilodyn traits in PEE and PCH

Trait	h_i^2 (se)	h_{HS}^2 (se)	h_{FS}^2 (se)	r_B (se)	$r_{G_{S:T}}$ (DENS)	$E_{i_{S:T}}$ %	$E_{FS_{S:T}}$ %
PEE							
PILMN	0.76 (0.26)	0.91 (0.06)	0.85 (0.08)	0.90 (0.10)	-0.97***	**97.9**	**95.3**
PILNTH	0.69 (0.24)	0.92 (0.05)	0.85 (0.08)	0.94 (0.08)	-0.96***	**92.5**	**94.2**
PILSTH	0.70 (0.24)	0.93 (0.05)	0.87 (0.07)	0.94 (0.08)	-0.94**	**91.6**	**93.6**
PILN1	0.67 (0.23)	0.94 (0.04)	0.87 (0.07)	0.98 (0.06)	-0.95**	**90.6**	**94.8**
PILN2	0.60 (0.24)	0.90 (0.07)	0.82 (0.09)	0.92 (0.11)	-0.96***	**86.3**	**92.8**
PILS1	0.61 (0.23)	0.91 (0.06)	0.84 (0.09)	0.91 (0.11)	-0.94**	**85.8**	**92.4**
PILS2	0.65 (0.23)	0.94 (0.04)	0.88 (0.06)	0.97 (0.07)	-0.92**	**86.0**	**91.6**
DENS	0.74 (0.26)	0.94 (0.04)	0.88 (0.06)	0.97 (0.06)	1	**100**	**100**
PCH							
PILMN	0.48 (0.19)	0.88 (0.07)	0.76 (0.11)	0.93 (0.10)	-0.95**	**113.0**	**103.5**
PILNTH	0.41 (0.17)	0.89 (0.07)	0.77 (0.11)	0.95 (0.11)	-0.96**	**106.5**	**105.3**
PILSTH	0.44 (0.18)	0.87 (0.08)	0.74 (0.12)	0.94 (0.11)	-0.93*	**106.8**	**99.4**
PILN1	0.35 (0.16)	0.86 (0.09)	0.74 (0.12)	0.92 (0.14)	-0.97**	**99.8**	**103.8**
PILN2	0.40 (0.16)	0.90 (0.06)	0.78 (0.10)	0.99 (0.09)	-0.96**	**104.9**	**105.7**
PILS1	0.40 (0.17)	0.87 (0.08)	0.73 (0.12)	0.96 (0.11)	-0.92*	**100.3**	**97.9**
PILS2	0.40 (0.17)	0.87 (0.08)	0.71 (0.12)	0.94 (0.10)	-0.95**	**103.9**	**100.1**
DENS	0.34 (0.19)	0.74 (0.18)	0.64 (0.19)	0.68 (0.27)	1	**100**	**100**

Note: $r_{G_{S:T}}$ (DENS) denotes the genetic correlation of pilodyn (screening) trait with breast height mean area-weighted density (DENS, the target trait); *, ** and *** denote estimates that differ significantly from zero at the 0.05, 0.01 and 0.0005 levels of probability; Pilodyn traits are: readings 1 and 2 on northern and southern aspects, respectively (PILN1, PILN2, PILS1, PILS2), average reading on northern aspect (PILNTH), average reading on southern aspect (PILSTH), average of all four readings (PILMN).

Table 5.8 Heritabilities, genetic correlations and efficiency of indirect selection for DENS (area-weighted density) based on some pilodyn traits in the F_1 hybrid

Trait	$h_{HS_f}^2$ (se)	$h_{HS_m}^2$ (se)	h_{FS}^2 (se)	r_B (se)	$r_{G_{S:T}}$ (DENS)	$E_{FS_{S:T}}$ %
PILMN	0.87 (0.08)	0.91 (0.05)	0.84 (0.06)	0.98 (0.07)	-0.98**	**99.9**
PILNTH	0.84 (0.09)	0.91 (0.05)	0.83 (0.06)	0.98 (0.07)	-0.98**	**99.4**
PILSTH	0.86 (0.08)	0.90 (0.05)	0.83 (0.06)	0.97 (0.07)	-0.96*	**97.8**
PILN1	0.83 (0.09)	0.89 (0.06)	0.80 (0.07)	0.99 (0.06)	-0.97**	**97.0**
PILN2	0.85 (0.08)	0.90 (0.05)	0.82 (0.07)	1.00 (0.05)	-0.96*	**96.8**
PILS1	0.85 (0.08)	0.88 (0.06)	0.81 (0.07)	0.98 (0.07)	-0.96*	**96.6**
PILS2	0.85 (0.09)	0.85 (0.09)	0.80 (0.08)	0.91 (0.13)	-0.96*	**96.0**
DENS	0.87 (0.07)	0.85 (0.07)	0.80 (0.07)	0.98 (0.06)	1	**100**

Note: $r_{G_{S:T}}$ (DENS) denotes the genetic correlation of a pilodyn (screening) trait with breast height mean area-weighted density (DENS, the target trait); *, ** and *** denote estimates that differ significantly from zero at the 0.05, 0.01 and 0.0005 levels of probability; Pilodyn traits are: readings 1 and 2 on northern and southern aspects, respectively (PILN1, PILN2, PILS1, PILS2), average reading on northern aspect (PILNTH), average reading on southern aspect (PILSTH), average of all four readings (PILMN).

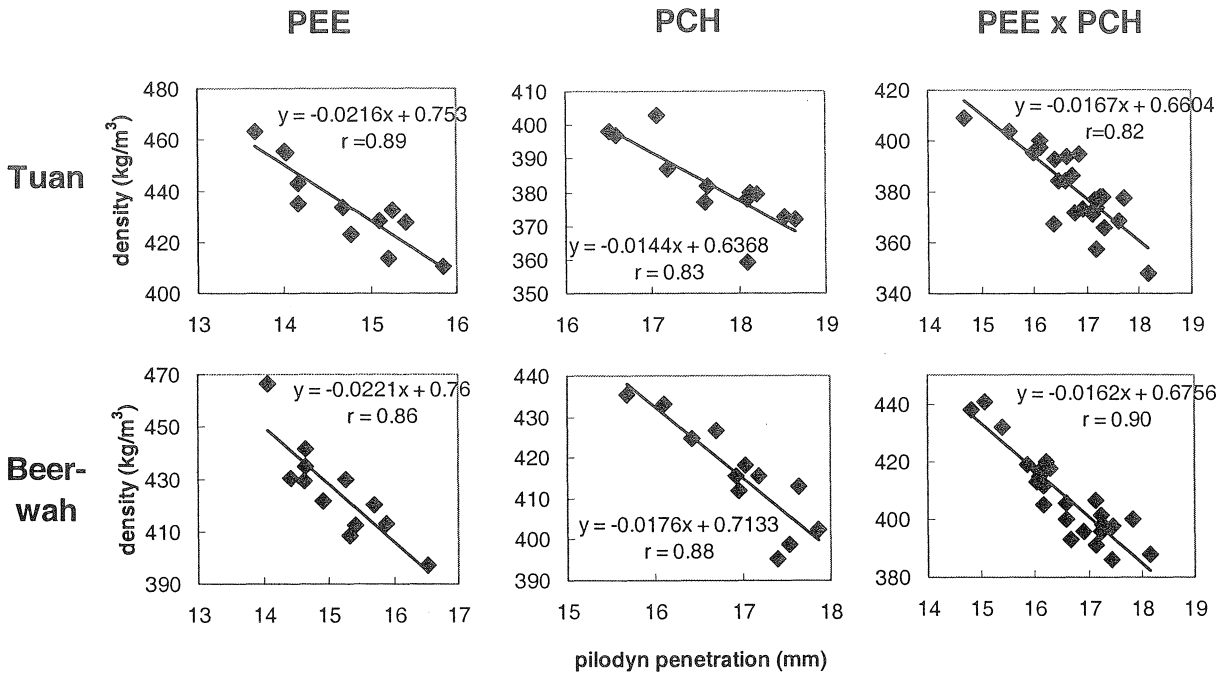

Figure 5.3 Half-sib family mean regressions of PILSTH (mean south aspect pilodyn penetration, age 12) on DENS (area-weighted breast height density, age 12) in PEE, PCH and F_1 at Tuan and Beerwah sites. Each regression shows the regression equation and the product-moment correlation between family means.

Table 5.9 Within-site half-sib and full-sib family correlations (r_{HS} and r_{FS}, respectively) between PILSTH (mean south aspect pilodyn penetration, age 12), for PEE, PCH and F_1 at Tuan and Beerwah sites.

Taxon	Site	r_{HS}	r_{FS}
PEE	Tuan	-0.91^{*}	-0.89^{*}
	Beerwah	-0.92^{*}	-0.92^{*}
PCH	Tuan	-0.89^{*}	-0.89^{*}
	Beerwah	-0.89^{*}	-0.78^{ns}
F1	Tuan	-0.96^{**}	-0.99^{***}
	Beerwah	-1.00^{***}	-1.01^{***}

Note: these are not product-moment correlations of family means; r_{HS} is equivalent to the genetic correlation; *, ** and *** denote genetic correlations that differ significantly from zero at the 0.05, 0.01 and 0.0005 levels, respectively.

Although pilodyn measurements appear to be of high value for predicting density, the relationship between pilodyn and other potential selection criteria needs to be verified. Of particular concern is the correlation between stem growth and pilodyn penetration (*eg* Costa e Silva *et al.* 2000). The genetic correlation of pilodyn penetration with stem diameter overbark (DBHOB), underbark volume (UBVOL), pith-to-bark density gradient (SLOPE) and pooled localised density variation (DEV) is given in Table 5.10. The genetic correlation of DENS with the same traits is repeated from the results of Chapter 4, in the interests of comparing the same correlations involving pilodyn penetration. PILSTH, or average pilodyn assessment on the south side of the tree, was included as the pilodyn trait due to the practical efficiency of sampling only one side of the tree. Correlations were calculated using the inverse of this trait, $PILSTH^{-1}$, to allow easier comparison with correlations involving DENS (see Table 5.10).

The correlations between $PILSTH^{-1}$ and growth traits were of similar magnitude to those between density and growth traits, with two exceptions (see Table 5.10). Firstly, in PCH, although density and underbark volume were strongly and adversely correlated, pilodyn and underbark volume were only weakly and non-significantly correlated. Secondly, in the F_1 hybrid, while density and stem diameter were significantly adversely correlated, pilodyn and stem diameter exhibited an even stronger adverse relationship. In no taxon, however, was pilodyn penetration significantly correlated with underbark volume, the growth trait of primary interest.

In all three taxa, pilodyn and mean density showed very similar genetic relationships with density variability traits, in all three taxa. However, pilodyn was consistently more strongly correlated with pith-to-bark gradient than was density, and in no instance was the correlation between $PILSTH^{-1}$ and SLOPE less than 0.9, significant at $p<0.005$. In the F_1 hybrid, the correlation between these traits was 0.98, indicating that selection for low pin penetration at age 12 is effectively synonymous with selection for increased pith-to-bark density gradient.

Table 5.10 Genetic correlation of $PILSTH^{-1}$ (inverse of mean south aspect pilodyn penetration) and DENS (area-weighted breast height density, age 12) with DBHOB, UBVOL, SLOPE and AVEDEV, in PEE, PCH and F_1 at Tuan and Beerwah sites.

Taxon	Trait	DBHOB	UBVOL	SLOPE	DEV
PEE	$PILSTH^{-1}$	0.03	0.06	0.9^{***}	0.79^{***}
	DENS	-0.04	0.03	0.66^{**}	0.75^{***}
PCH	$PILSTH^{-1}$	-0.57^{*}	-0.38	0.95^{***}	0.02
	DENS	-0.68^{*}	-0.84^{***}	0.85^{***}	0.02
F1	$PILSTH^{-1}$	-0.93^{***}	-0.08	0.98^{***}	0.51^{*}
	DENS	-0.71^{*}	-0.19	0.78^{***}	0.61^{***}

Note: DBHOB is diameter at breast height overbark; UBVOL is underbark stem volume; SLOPE is a measure of pith-to-bark variation; AVEDEV is a measure of localised or within-ring density variation; *, ** and *** denote correlations that differ significantly from zero, at the 0.05, 0.01 and 0.0005 levels, respectively.

5.3.4 Early selection and field screening for spiral grain in F_1

Area-weighted mean spiral grain angle (SGMEAN) was moderately to strongly heritable (*eg* h^2_{FS} =0.63±0.07), but area-weighted standard deviation of spiral grain angle (SGSD) was only moderately heritable (*eg* h^2_{FS} =0.46±0.07; see Table 5.11). In SGMEAN, the estimate of SCA variance was high, and was equal to approximately half of GCA variance; in SGSD, SCA variance was equal to approximately 0.3 of GCA variance.

Due to the high expense of taking multiple measurements of spiral grain, priority was accorded to assessing aspects of the inheritance and predictive value of individual-ring spiral grain measurements instead of cumulative, whole-stem measurements, at juvenile ages. The heritability of spiral grain angle in individual rings varied from year to year, ranging between low and moderate values, but tended to be lowest in the rings formed closest to the pith (SG4, SG5) and in the outermost rings (SG8, SG10) (see Table 5.11). The highest heritability was found at tree age 7, corresponding to growth ring 5 from the pith (see Table 5.11). The ratio of SCA variance to GCA variance varied unpredictably among the rings, but was greatest in the first and last measured rings (rings 2 and 8 from the pith); all estimates of this parameter were generally similar to or less in magnitude than their standard errors.

Type B genetic correlations were moderate to high for most spiral grain traits, tending to be higher in more strongly inherited traits, and higher for SGMEAN (r_B=1.00) than for SGSD (r_B=0.69±0.29). SGSD was strongly and significantly genetically correlated with SGMEAN, indicating that selection to reduce mean spiral grain would have a strong favourable correlated effect on spiral grain variability. Additionally, individual ring measurements of spiral grain in all years assessed were very strongly genetically correlated with SGMEAN, and with SGSD, although in most years the correlation with SGSD was not statistically significantly different from zero (see Table 5.11). This is probably due to the high within-family variation observed in SGSD and in most individual-ring measurements (Chapter 3), suggesting the need for large numbers of individuals per family when assessing genetic parameters for spiral grain.

An average measurement of spiral grain angle assessed on the outer surface of age 12 standing trees using the bubble protractor (PROT) was found to have low heritability (*eg* h^2_{FS} =0.40±0.06), and SCA variance exceeded GCA variance for this trait. However, parental values for PROT were highly stable across sites (r_B=0.94, and were strongly and significantly genetically correlated with SGMEAN.

Regression plots of family means, presented in Figure 5.5, were used to further examine the important relationships suggested by the high genetic correlations between SG4 and SGMEAN, and between PROT and SGMEAN. These correlations, estimated by regression of family means, were 0.817 and 0.744 respectively, which are congruent with the corresponding genetic correlations of 0.98 and 0.90, respectively (see Table 5.11). The relationships appeared to be reasonably strong, and were not simply due to outlying family mean values; however, particularly in the graph of SG4 vs SGMEAN (Figure 5.5), a strongly right-skewed distribution of family means was clearly evident, suggesting that the skewed distribution of spiral grain traits at the individual-tree level observed in Section 3.4 may also have a genetic basis.

The efficiency of early selection for SGMEAN based on individual-ring measurements of spiral grain angle at tree ages 4-10 is graphed in Figure 5.4. Although genetic gain per generation is greatest from selection at age 7 (29.3% genetic gain), genetic gain per year, or efficiency of early selection, is maximised by selection at age 4. However, because family assessments at age 4 were less stable across sites than assessments of subsequently formed rings, field screening or other measurement of spiral grain for the purpose of selecting progeny might best wait until at least age 5 from seed.

Table 5.11 Genetic parameters for individual-ring spiral grain angles, mean (SGMEAN) and standard deviation (SGSD) of spiral grain angles, and efficiency of early and indirect selection for SGMEAN.

	heritabilities				genetic correlations			genetic gain	
	$h^2_{HS_f}$ (se)	$h^2_{HS_m}$ (se)	h^2_{FS} (se)	$\frac{\sigma^2_{SCA}}{\sigma^2_{GCA}}$ (se)	r_B (se)	$r_{G:}$ SGMEAN	$r_{G:}$ SGSD	ΔG_{FS} %	
								direct selection	
SGMEAN	0.73 (0.13)	0.72 (0.14)	0.63 (0.12)	0.49 (0.43)	1.00 (0)	-	-	27.4	-
SGSD	0.24 (0.42)	0.72 (0.16)	0.46 (0.18)	0.29 (0.55)	0.69 (0.29)	0.86***	-	14.3	-
								early selection for SGMEAN	
								$\Delta G_{FS_{J:M}}$ %	$E_{FS_{J:M}}$ %
SG4	0.48 (0.25)	0.32 (0.32)	0.32 (0.18)	2.48 (2.20)	0.67 (0.28)	0.98***	0.85^{ns}	19.2	175
SG5	0.68 (0.13)	0.35 (0.27)	0.44 (0.14)	0	1.00 (0.00)	1.00***	0.84^{ns}	23.0	167
SG6	0.67 (0.16)	0.66 (0.18)	0.56 (0.14)	0.42 (0.47)	0.96 (0.16)	1.01***	1.10***	25.9	157
SG7	0.84 (0.07)	0.73 (0.11)	0.71 (0.08)	0	1.00 (0.00)	1.02***	0.79^{ns}	29.3	154
SG8	0.65 (0.17)	0.64 (0.17)	0.53 (0.15)	0.24 (0.58)	1.00 (0.00)	1.04***	0.80^{ns}	25.4	119
SG10	0.31 (0.34)	0.42 (0.28)	0.30 (0.20)	1.97 (2.24)	0.62 (0.35)	1.04***	1.01***	18.9	71
								indirect selection for SGMEAN	
								$\Delta G_{FS_{S:T}}$ %	$E_{FS_{S:T}}$ %
PROT	0.45 (0.25)	0.55 (0.23)	0.40 (0.18)	1.22 (1.23)	0.94 (0.25)	0.90*	0.75^{ns}	19.7	57

Note: SGMEAN is radial area-weighted mean spiral grain angle at age 12; SGSD is radial area-weighted standard deviation of spiral grain angles at age 12; SG4-SG10 are spiral grain angle in individual rings formed at approximate tree ages 4-10 from seed (rings 2-8 from the pith). PROT is bubble protractor field measurement at age 12 from seed. ΔG_{FS} % is the genetic gain from direct selection of the best 10% of full-sib families; $E_{FS_{J:M}}$ % is the percentage efficiency of early selection of full-sib families for SGMEAN based on individual ring measurements at each juvenile age, and $E_{FS_{S:T}}$ % is the percentage efficiency of indirect selection for SGMEAN based on PROT. $\Delta G_{FS_{J:M}}$ % and $\Delta G_{FS_{S:T}}$ % are genetic gain in SGMEAN from early and indirect selection, respectively; Asterisks *, ** and *** next to genetic correlations denote estimates significantly different from zero at the p<0.05, 0.01 and 0.0005 levels, respectively.

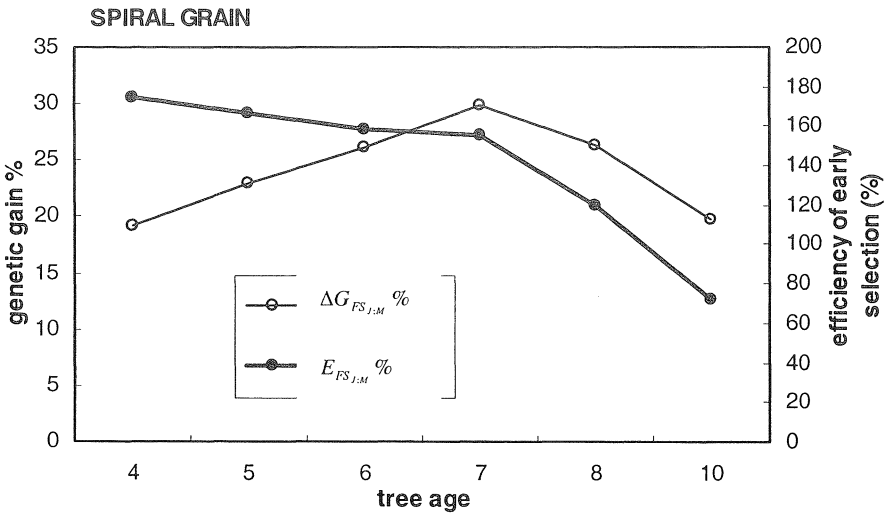

Figure 5.4 Percentage genetic gain in SGMEAN from early selection of the best 10% of full-sib families based on individual ring spiral grain angle at tree ages 4-10 ($\Delta G_{FS_{J:M}}$ %); percentage efficiency of early selection based on individual ring spiral grain angle, relative to direct selection on SGMEAN ($E_{FS_{J:M}}$ %).

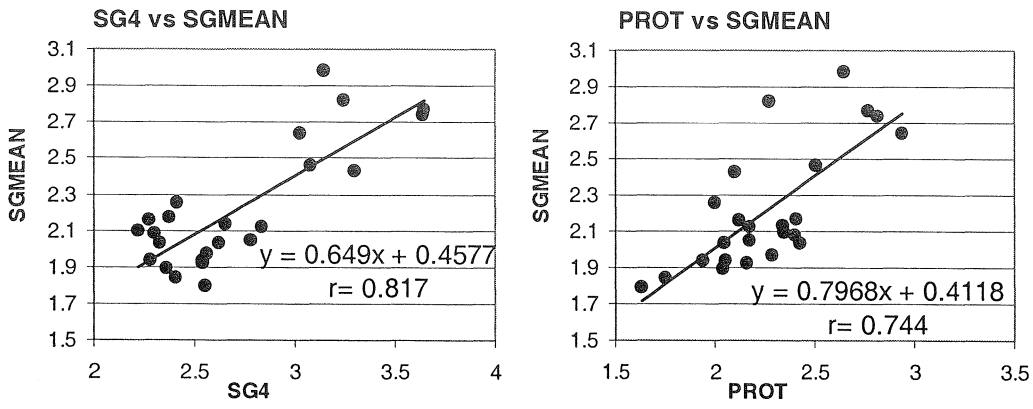

Figure 5.5 Half-sib family mean regression of SG4 on SGMEAN and PROT on SGMEAN, showing regression equation, and Pearson's correlation coefficient (*r*).

5.4 Discussion

5.4.1 Time trends in heritability

The reasonably constant heritability of stem basal area at successive tree ages 3-12 in PEE, PCH and the PEE×PCH F_1 hybrid contrasts with the common trend of increasing heritability of growth traits over this age range, in these and related taxa in previous studies (Hodge and White 1992; Dieters *et al.* 1995b; Dean *et al.* 1986; Balocchi *et al.* 1993; White and Hodge 1992; Li *et al.* 1996; Cotterill and Dean 1988). The more consistent heritability of basal area at different ages in the present study may be due to the measurement of basal area on an underbark basis, rather than on an overbark basis as in the studies cited above. Alternatively, it may be due to climatic or other environmental conditions specific to the progeny test examined. Of the few studies that have measured basal area underbark at successive ages, Matheson *et al.* (1994) also found that heritability varied little (0.13-0.18) between age 5 and age 14 from planting, in *Pinus radiata*. Where diameter and bark thickness are genetically and environmentally uncorrelated, or weakly correlated (*eg* Wei and Borralho 1998; Powell 2001, Crockford *et al.* 1990), measurement of growth traits on an overbark basis could potentially introduce large random variation into measurements of basal area and volume. For example, in a subset of trees examined in the current study, bark comprised an average of 0.33 of overbark basal area across the four taxa; this ratio had a phenotypic coefficient of variation of 17%. From calculations based on the results of an earlier study of this same trial (Powell 2001), bark comprised an average of 0.39 of overbark basal area, at age 6. Powell also found that the heritability of bark thickness often exceeded twice that of underbark diameter. These results together suggest, firstly, that selection on overbark diameter measurements may seriously compromise genetic gains in wood volume, through diverting selection pressure onto bark volume instead of wood volume. Secondly, the finding that bark forms a higher proportion of stem volume at earlier than at later ages suggests that overbark measurements may introduce greater random variation, and therefore deflate heritability estimates more seriously, at younger ages. Extensive further study of the indirect selection efficiency of overbark measurements for underbark traits is recommended.

In PEE, the full-sib family heritability (h^2_{FS}) of wood density remained reasonably constant with age; in PCH it increased steadily with age, and in the F_1, it increased slightly with age, at a rate intermediate between the two parental taxa. Further examination of the heritability estimates in the F_1 hybrid (Table 5.6) revealed that the PEE parent half-sib family heritability estimate (h^2_{HSf}) is constant with age, as in pure PEE; similarly, that of the PCH parent (h^2_{HSm}) increases with age, as in pure PCH. This finding reflects the strongly additive inheritance of wood properties in the pure species and hybrid populations indicated in Chapter 4, and further suggests that ontogenetic effects on the heritability of wood density are strong enough to persist in very different genetic backgrounds. The results accord with previous studies of time trends in the heritability of wood density in pure species, which typically show either constant or slightly increasing heritability over this range of stem ages (*eg* Harding 1995; Hodge and Purnell 1993; Vargas-Hernandez 1991; Hylen 1999; Hannrup *et al.* 1998).

In the F_1 hybrid, the heritability of individual-ring spiral grain measurements increased from age 4 (ring 2) through to age 7 (ring 5), and decreased thereafter to age 10 (ring 8). This trend is similar to that found by Harding *et al.* (1991) in PCH in Queensland, and Burdon and Low (1981) in *Pinus radiata* in New Zealand, in that the heritability of spiral grain was very low in the early rings, yet increased thereafter. The lower heritability at age 8 and 10 in this study corresponds with the decline in the heritability of spiral grain observed at later ages in other studies (*eg* Nicholls 1967, broad-sense heritability, *Pinus radiata*; Eisemann *et al.* 1990, narrow-sense heritability, *Araucaria cunninghamii*).

5.4.2 Importance of GCA and SCA effects

In most traits and at most ages, GCA variance was more important than SCA variance in both pure species and in the F_1 hybrid. This is consistent with other studies of genetic variances of growth and wood traits in pure species (*eg* Cotterill *et al.* 1987; Li *et al.* 1996; Kusnandar *et al.* 1998) and with studies of growth traits in most intraspecific and interspecific tree hybrid combinations (*eg* Gerhold and Park 1986; Kaya and Lindgren 1992; Blada 1992; Bouvet and Vigneron 1995; Volker 1995). No

studies of wood traits in interspecific hybrids are available for comparison with the current results.

In the F_1 hybrid, SCA variance for basal area increases strongly and steadily from age 3-12; by age 12, it exceeds average GCA variance. If the relative importance of SCA variance were to continue to increase at the same rate through to rotation age, greater genetic gain would be possible from selection for SCA effects than from selection for GCA effects, in the hybrid population. Most previous studies in both pure species and hybrids suggest that the importance of SCA variance in growth traits may variously increase or decrease at early ages, but commonly tends to decrease after approximately age 10 (*eg* Dieters *et al.* 1995b, *Pinus elliottii*; Balocchi *et al.* 1993, *P. taeda*; Matheson *et al.* 1994, *P.radiata*; Paques *in press*, *Larix* × *eurolepis* Henry) and is rarely of comparable magnitude to GCA variance at mature ages. Nevertheless, the observed strong increase in SCA effects in basal area to age 12 in the F_1 may particularly affect the efficiency of early selection of hybrid clones, and emphasises the need for separate early selection studies in clonal tests.

In spiral grain in the F_1 hybrid, SCA variance was of high though variable importance at different ages (see Table 5.11). Although no results are available for comparison in interspecific hybrids, in previous pure species experiments, existing evidence on the importance of SCA variance in spiral grain has been inconclusive. For example, Zobel *et al.* (1968) found little evidence of additive genetic effects, but strong non-additive genetic effects, in mean spiral grain in *P. taeda* measured at age 4 (nested design, 1043 trees, 52 crosses). However, Pederick (1971), in an unbalanced nested design with 22 crosses in *Pinus radiata*, also at age 4, found that additive effects were more important than non-additive effects for mean spiral grain. Costa e Silva *et al.* (2000) found low non-additive genetic variance for spiral grain in *Picea abies*. The mating designs in the three studies cited above did not include sufficient crosses to accurately estimate non-additive genetic variance; hence, the importance of SCA relative to GCA variance has remained poorly understood. The current study suggests that in the PEE×PCH F_1 hybrid, SCA variance may have a moderate to strong influence on mean spiral grain, though its importance may vary greatly from year to year in individual-ring measurements.

5.4.3 Juvenile-mature genetic correlations

The high juvenile-mature genetic correlations for basal area are consistent with previous studies of age-age correlations involving similar age ranges in these taxa. For example, in open-pollinated tests of PEE in Florida, Hodge and White (1992) found r_A=0.945±0.024 and 0.818±0.045 between height measurements, and overbark diameter measurements, respectively, at age 5 and age 10. In control-pollinated tests of PEE in Florida, Dieters *et al.* (1995b) found r_A=0.769±0.045 between age 5 and age 11 stem volume. Hodge and Dvorak (2001) and Hodge and Dvorak (1999) found similar results in 8-year-old tests of PCH and *P. tecunumanii*, respectively.

The high juvenile-mature correlations for wood density are also consistent with previous findings in *Pinus* (*eg* Hannrup and Ekberg 1998; Harding 1995; Hylen 1999; Williams and Megraw 1994). The high juvenile-mature correlations estimated in growth and wood density suggest a predominance of additive genetic effects in the traits of interest in the PEE×PCH hybrid and parental populations, that persist not only through different ontogenetic stages but also, considering the strong r_{ph} estimates for density presented in Chapter 3, in different genetic backgrounds. In PEE and the F_1 hybrid, the consistent heritability and consistently strong juvenile:mature correlations of both cumulative and individual-ring wood density through from age 3 to age 11 suggest the possibility that a common set of genes, or QTL, may be responsible for governing this trait through juvenile and mature phases of wood formation. The observed negligible effect of ontogeny on these genetic parameters for individual ring wood densities suggests greater promise for molecular marker studies in wood density than has been demonstrated for growth traits such as height and diameter increment, where QTL and their effects often vary greatly between successive increments (*eg* Lerceteau *et al.* 2001; Shepherd *et al.* in press). In PCH, juvenile-mature correlations of wood density were low for the early rings, but increased steadily to approximately 1 at age 6. This, and the observed increase in density heritability with age in PCH, suggests greater importance of ontogeny in determining wood density in PCH than in PEE, in both pure species and hybrid combination.

Juvenile-mature genetic correlations in tree basal area were lower in the F_1 than in PEE and PCH; also, the relative importance of SCA variance strongly increased with age in the F_1, but showed much less variation with age in PEE and PCH. These results suggest stronger influence of ontogenetic effects for basal area in the F_1 than in its parental taxa, reflected in the later optimum age of selection for basal area in the F_1. Further studies of early selection for growth characters in PEE×PCH hybrids in older genetic tests are necessary to examine the ontogeny of growth traits more conclusively.

The high genetic correlation between individual-ring grain angles and overall area-weighted spiral grain mean (SGMEAN) and variability (SGSD) indicates that trees with higher spiral grain angle in any particular year also tend to have higher overall grain angle, and higher variability in grain angle, from year to year (Table 5.11). The often non-significant correlations with SGSD reflect the high within-family variance in spiral grain traits, and the small number of parents in this study. In a study involving 27 open-pollinated PCH families on two SE QLD sites, Harding *et al.* (1991) also found strong genetic correlations of individual-ring spiral grain measurements with mean spiral grain at age 11 (*eg* $|r_A| = 0.93$ and 0.96 in rings 5 and 7, respectively), and moderate correlations with spiral grain variation. No other published studies appear to have evaluated age-age genetic correlations in spiral grain.

Several of the genetic correlations in this study exceeded one: this is not unusual in juvenile-mature correlations of wood properties (*eg* Harding 1995; Loo-Dinkins and Gonzalez 1991), due to the combination of very strong genetic relationships, and small parental and offspring sample sizes that cause large errors in the estimation of variances and covariances. Inflated age-age correlations may also be due to the analytical methodology used, as discussed in Section 2.3. The method used to estimate all genetic correlations in this thesis assumed absence of autocorrelation between trait measurements, which may not be reasonable in the case of repeated measurements performed at different ages on the same trees (Davidian 1998). Although several previous studies (Dieters *et al.* 2000; Apiolaza *et al.* 2000; Lu *et al.* 2000) have found minimal differences in age-age and other trait-trait genetic correlations estimated using univariate, multivariate and longitudinal data analyses, it is possible that the estimates in this thesis are upwardly biased by family and residual

autocorrelations among successive measurements; future work is planned on the same datasets to investigate this possibility. However, the strong genetic correlations between whole-stem wood properties and individual-ring wood properties at nearly all ages in this study suggest that the strong juvenile-mature relationships observed are likely to be real and not simply due to autocorrelation, which inevitably contributes more to age-age correlations of cumulative measurements.

5.4.4 Early selection efficiency

BASAL AREA

This study found that early measurements of basal area were of high value for predicting stem basal area at age 12. However, because the "mature" age in this study was only just in excess of half rotation age, the optimal selection age estimated from these analyses may not be optimal for full rotation age. The results can be interpreted to suggest that selection for basal area should wait until at least age 4 from seed in PEE and PCH, and at least age 6 from seed in the F_1 hybrid. These ages are consistent with, though generally slightly earlier than, those suggested by previous early selection studies of DBH, height and stem volume in temperate and subtropical species with mature measurements at near rotation age. For example, in first generation *Pinus taeda*, Li *et al.* (1996) found that selection for volume growth was optimal at age 6 from planting for mature age 20 years, although preliminary results from tests of second-generation *P. taeda* in the same study suggested that the optimum age might be earlier. Also in *P. taeda*, Gwaze *et al.* (1997) found that optimum genetic gain per year was achieved by selecting at age 3 from planting for age 22 height, although selection had to be delayed until age 10 due to late flowering of *P. taeda* in Zimbabwe. In *Pinus radiata*, King and Burdon (1991) estimated that optimum age for family selection for stem diameter was 7-8 years from planting, for mature age of 25-30 years, and Cotterill and Dean (1988) estimated 6.5 years from planting for 16-year volume. The current results need to be confirmed using rotation age data.

WOOD DENSITY

The results also indicate that in PEE, PCH and F_1, selection for whole-stem or individual-ring wood density at tree age 4 (approx. 2 rings from the pith) is likely to

deliver optimum genetic gain per year in age 12 average wood density. Early selection ages for wood density are also supported by the results of previous studies in related taxa. For example, based on the results of Harding (1995) in *Pinus taeda*, selection for the density of rings 1-5 from the pith (*c.* at tree age 6 from planting), would have yielded approximately 60% of the genetic gain per generation, or 230% of the genetic gain per year, in age 27 whole-core density relative to direct selection at age 27. Harding's study provides particularly strong evidence in support of early selection for wood density, because two sites were sampled, and the trees were retained until rotation age. Similarly, according to the results of Loo *et al.* (1984) in *Pseudotsuga menziesii*, juvenile-mature genetic correlations were so high that selection based on the wood density of the first two rings from the pith gave the same predicted genetic gain per generation in age 25 density as direct selection. Several recent studies in various pure species conifers (*eg* Hylen 1999; Hannrup and Ekberg 1998; Vargas-Hernandez and Adams 1992) have also suggested strong potential for selection for whole-stem density based on inner juvenile wood measurements.

The current results for both wood density and basal area must be interpreted conservatively, because the 'mature' age was only just in excess of half rotation age, and high genetic correlations between age 4 and age 12 do not guarantee high genetic correlations between age 4 and age 20. Furthermore, unless flowering precocity can be improved, selection at age 4 is not useful in progeny tests of PEE and PCH in Queensland, because first flowering does not take place until 6-7 years from seed – though some advantage could be gained by grafting selections into a breeding orchard at age 4 rather than at age 6. The current results are well supported by the literature in suggesting that selection for basal area and wood density at age 6-7 from seed for a rotation age between 17-25 years is likely to result in a strong increase in genetic gain per year relative to selection closer to maturity in PEE×PCH and parental taxa.

A novel finding of the current study is the strong potential for selecting for whole-stem density based on individual ring densities: in all taxa, the efficiency of early selection based on individual ring density at most juvenile ages was found to be as high or higher than for selection based on cumulative density at the same age. One important reason for the strong predictive value of individual-ring measurements was the assignment of rings based on tree age rather than cambial age. This ensured that

the individual rings being compared among trees and families were formed in a common environment (*ie* in the same year). Appendix 17 demonstrates that the heritability of individual-ring wood density measured based on tree age was consistently greater, on average and in most rings, than that based on cambial age (an adjustment of the same dataset). These data demonstrate the value of assigning tree ring labels based on tree age, where the genetics of individual-ring traits are of interest: for example, for predicting whole-stem characteristics, or for studies aiming to detect QTL. The lower heritability of cambial age assessments is due to the confounding effect of annual climatic variation on wood density comparisons among trees, as noted by Hylen (1999).

Convention in measuring wood properties has been to compare rings among trees based on their cambial age (explained in Section 3.3). Because of the strong ontogenetic effect of cambial age on mean ring density (Zobel and Jett 1995), this approach is advisable in trials with high among-tree or among-site variation in the year at which the apical meristem reaches breast height. Hylen (1999) provided an extreme example in a *Picea abies* progeny trial in Norway, in which ring 3 was formed in nine different years at a single site. However, in most temperate and subtropical trials, trees typically vary by no more than 1-3 years in the calendar year of their first-formed ring. In such circumstances, the assignment of ring number based on tree age does not substantially confound the ontogenetic trend, but does ensure that the often large year-to-year variations in wood density characteristics resulting from climatic fluctuations are not confounded. Where the possibility of selection based on individual-ring values is of interest, it is recommended that future studies of even-aged genetic tests with reasonably uniform early height growth adopt the practice of comparing rings based on tree age.

If the current results can be reproduced on a larger sample of genotypes and sites, the sampling of only a small piece of wood in the outermost ring(s) could provide a cost-effective alternative to increment coring or stem disking. Wood sampling could be carried out very quickly, for example using a spring-loaded device with a cutting head. The genetic correlation between individual-ring and whole-stem values in other important wood traits, such as microfibril angle, may therefore be worth investigating. Although point sampling does not allow assessment of radial variability, it may allow

large increases in selection intensity for traits highly correlated with point estimates, due to the cost saving per sample.

SPIRAL GRAIN

The high early selection efficiency of individual-ring measurements of spiral grain in the PEE×PCH F_1 hybrid is in close agreement with a previous study of PCH in Queensland. Predictions based on the results of this study and that of Harding *et al.* (1991) both indicate that an individual-ring assessment of spiral grain at tree age 7 will provide 90% or more of the genetic gain per generation possible from direct selection on mean spiral grain (at tree age 12). Both studies also indicate that large correlated reductions in spiral grain variability, a trait of likely economic importance in PEE×PCH (Harding *et al.* 2000) may also be possible from selection for low spiral grain in individual rings. This study and that of Harding *et al.* (1991) sample the progeny of 51 parents across 4 sites between them, lending weight to the conclusion that the marginal genetic gain per generation from direct selection on whole-tree average spiral grain relative to selection on individual-ring values is likely to be very slim indeed. When the comparison is made based on genetic gain per year, selection on individual-ring measurements at age 7 resulted in at least 150% of that from direct selection on mean grain angle at age 12, in both studies. Furthermore, the cost of individual-ring measurements has been estimated at 10% of the cost of multiple ring measurements (Sorensson *et al.* 1997a), who similarly concluded that little additional genetic gain could be made from selecting on multiple-ring means relative to individual-ring values. Methods for individual-ring measurements are discussed further in Section 5.4.5.

The correspondence between the results of this study and those of Harding *et al.* (1991) is surprisingly strong, with the exception of a slight disagreement between them on the optimum age for individual-ring selection in spiral grain. Based on Harding *et al.* (1991), selection on a single measurement at ring 3 from the pith (approx. age 5 from seed) would have resulted in only half the genetic gain per generation in mean spiral grain as would a single measurement at ring 5; the optimum age for early selection was hence a little later (ring 5; approx. age 7) than in the current study (ring 2; approx. age 4). These differences may be due to the different taxa assessed (PEE×PCH vs. PCH), the sample of families, or the different site or

climatic influences on the trees in the two studies, though both examined families from the same breeding population and similar pairs of SE QLD sites. No other estimates of the efficiency of early or indirect selection for spiral grain could be found in the published literature.

Extensive research on spiral grain screening using individual-ring measurements was conducted in New Zealand during the 1990's: Burdon and Low 1992, Cown *et al.* (1991), Sorensson and Lausberg (1995) and Sorensson and Lausberg (1996b) all found phenotypic correlations of between 0.5 and 0.9 between juvenile individual-ring and whole-stem mean grain angle in *Pinus radiata*. The corresponding genetic correlations are expected to be higher because group means are always less variable than individual measurements. However, these genetic correlations, and the efficiency of early or indirect selection on individual ring measurements of spiral grain do not appear to have been assessed; Sorensson *et al.* (1997a) comment on the need for estimates of these genetic parameters in New Zealand. However, a phenotypic study of spiral grain variation patterns in *P. radiata* (Sorensson *et al.* 1997a) found that rings 5-8 accounted for more than half of the total wood area with excessive spirality, and so the authors recommended that sampling take place in this area. Measurement at age 7 from seed, as supported by the results of both this study and Harding *et al.* (1991), conforms to this recommendation. This study suggests that selection may be possible at even earlier ages, largely due to strong age-age genetic correlations (Table 5.11), though this needs to be confirmed in a larger sample of families and sites. In the current study and in previous studies, spiral grain was compared among trees by comparing rings of common cambial age. As found for wood density (Appendix 17), the labelling of rings based on tree age is likely to increase the heritability of individual ring measurements, and hence their indirect selection efficiency for whole-stem measures, beyond the level reported in this study.

ADDITIONAL CONSIDERATIONS - EARLY SELECTION

More generally, the calculations for optimum age of selection in this study did not consider the effect of discounting the value of genetic gains obtained, nor the risk incurred in selecting at very early ages, in any trait. Discounting is likely to suggest a reduction in optimum selection age (*eg* Johnson *et al.* 1997), while stochastic simulation accounting for the risk of variable genetic parameters at early ages

(Magnussen and Yanchuk 1993) is likely to suggest an increase. Based on the results of this study and previous studies, selection at age 6-8 from seed, coinciding approximately with the age of first flowering in PEE and PCH, appears likely to provide reliable estimates of age 20 growth, density and spiral grain performance in the F_1 hybrid, PEE and PCH.

An important consideration for early selection regards the emerging practical reality of selecting at the seedling stage using marker-assisted selection (MAS). Increasing availability of technologies and marker types to facilitate MAS has placed a high premium on the discovery of major genes or alleles of large effect (Mackay 2001), not historically of great interest to breeders. In relation to this, an unusual and possibly informative pattern in the spiral grain data is the strongly right-skewed distribution of half-sib family means for both traits in the graph "SG4 vs. SGMEAN" (Figure 5.5). There appear to be two 'groups' of families, the smaller group having distinctly higher grain angles than the larger group; the right-skewed distribution of this trait is also observed at the phenotypic level (see Chapter 3). The same pattern has been observed in both family mean and individual-tree data in some previous studies (*eg* Cown *et al.* 1991; Sorensson *et al.* 1997a). The influence of a major gene locus is one known cause of skewed trait frequency distributions (Falconer and Mackay 1996); one possible explanation for the results is that the distinct group of seven parents with high means for spiral grain, visible in Figure 5.5, possess at least one copy of an allele of large effect, that the group of parents with lower means do not. Further examination of the data indicated that the within-family distribution of tree values were of a distinctly different shape in the group of families with high grain angles than in the group with lower grain angles. Though Sorensson *et al.* (1997a) do not specifically provide this explanation, they comment on increased interest in MAS for spiral grain traits in New Zealand after the discovery of the skewed frequency distributions. The hypothesis that major genes influence absolute spiral grain angle could be tested either using the individual-locus model of gene effects presented in Chapter 6 or, more conclusively, by molecular genetic analysis of a large number of progeny from crosses of parents from the high-spiral grain angle group with parents from the low-spiral grain angle group. Screening of candidate clones by marker-assisted selection at an early age may be highly effective if major genes are present, particularly given the moderate to high heritability of spiral grain (Kerr and Goddard

1997). If it can be successfully applied on a large scale, MAS has the potential to eliminate the need for costly clonal testing and assessment.

5.4.5 Field testing for wood properties

5.4.5.1 Pilodyn

The similar, moderate to strong heritability of pilodyn and density, and strong genetic correlation between these traits (see Table 5.7, Table 5.8) is the basis of the high indirect selection efficiency of pilodyn in this study. These findings are consistent with previous results from studies in a broad range of taxa, summarized in Table 5.12. Further to these results directly demonstrating high selection efficiency of the pilodyn are a large number of unpublished and informally published studies reporting a strong genetic relationship between pilodyn and density at either the family or clonal mean level (*eg* Cown and Andrew 1979; Dean *et al.* 1990; Villeneuve *et al.* 1987). Although the phenotypic correlation between pilodyn and density is typically much weaker, as found in this study, its genetic counterpart is, with few exceptions, very strong. Though the ability of the pilodyn to rank provenances for density is less certain and deserves further study (Hylen 1996; Muneri and Raymond 2000), the literature almost unanimously supports its ability to rank families within provenances. The strong and consistent pilodyn-density genetic correlation at both the half-sib and full-sib family levels in this study (Table 5.9), even with very small numbers of individuals per full-sib family (10 and 7 at the Beerwah and Tuan sites, respectively), suggests that the pilodyn may be useful for screening clones, and for accurately predicting the mean density of groups of trees in general, even when group size is small. Furthermore, the similar, high pilodyn-density correlation at the Tuan and Beerwah sites considered separately, and high type B genetic correlations for all pilodyn traits, are in agreement with the results of a large study of *P. radiata* in New Zealand (Cown 1982) suggesting good stability of pilodyn across sites. If the generally low G×E interaction for wood density (Chapter 3) and pilodyn on these two sites is indicative of more general trends in SE QLD, it may be possible to select for wood density based on pilodyn assessments on fewer sites than is necessary for growth trait assessment.

The high indirect selection efficiency of pilodyn, which uniformly exceeded 90% at the across-site level in this study, was highly robust to variation in both the aspect of pilodyn sampling on the tree stem, and the number of individual measurements taken (see Table 5.7, Table 5.8). The number of sampling aspects necessary to predict density is of high practical importance, because removal of bark and cambium is necessary for pilodyn sampling (Micko *et al.* 1982; Koch and Fins 2000), and so sampling on four aspects (Greaves *et al.* 1996), or even two, could be damaging or fatal to young trees. The current results support the findings of Greaves *et al.* (1996), that little extra genetic gain in wood density will be made by sampling beyond a single, carefully executed pilodyn assessment on a single aspect. The consistently high pilodyn-density correlations at the Tuan site (see Figure 5.3, Table 5.9) are surprising because of the high compression wood formation in PCH and F_1 at this site, although it was avoided during sampling. Further investigation of aspect-related variation is recommended on sloped and wind-prone sites, where cambial growth and wood properties are likely to be more anisotropic.

Table 5.12 Efficiency of indirect selection for density based on pilodyn pin penetration: review of the published literature

Study	species	no. and type of families[†]	basis[‡]	$h^2_{(PIN)}$	$h^2_{(DEN)}$	$r_{A\ (PIN:DEN)}$	$E_{(PIN:DEN)}$ %
King *et al.* (1988)	*Pseudotsuga menziesii*	26 FS (22×4 NCII)	ind.	0.80±0.26	0.90±0.28	-0.95	90
Sprague *et al.* (1983)	*Pinus taeda*	28 HS (OP)	ind.	0.46	0.44	-0.82	84
Yanchuk and Kiss (1983)	*Picea glauca*	40 HS (OP)	fam.	0.48±0.28	0.67±0.26	-0.80	68
Greaves *et al.* (1996)	*Eucalyptus nitens*	50 HS (OP)	ind.	0.60±0.01	0.73±0.09	-0.92	84
Wei and Borralho (1997)	*Eucalyptus urophylla*	90 HS (OP)	ind.	0.68±0.12	0.71±0.20	-1.00	98

Note: [†] FS=full-sib families, NCII=North Carolina II (factorial) mating design, HS=half-sib families, OP=open-pollinated; [‡] basis indicates the selection units to which the genetic parameter estimates apply, ind.=individual tree, fam.=half-sib family. $E_{(PIN:DEN)}$% is the indirect selection efficiency of selecting for density based on pilodyn pin penetration.

Early selection results indicate that selection on individual-ring density at ages 4-11 is approximately as effective as selecting on cumulative density at the same age, for improving age 12 density in PEE, PCH and the PEE×PCH F_1 hybrid. Given the fact that the pilodyn samples a localised point (*ie* one or two annual rings), and the high

correlation between pilodyn and overall density, the results suggest that pilodyn assessments at around age 4-5 may be a highly efficient method of screening candidate families and trees for wood density. Because most trees are not expected to reach around 8cm DBHOB until after age 5 from seed (Dieters[7], pers. comm.), pilodyn assessments at earlier ages are not likely to be practicable, even in the F_1 hybrid, which flowers as early as age 1 year from seed. This is because the tree bole needs to have sufficient strength to withstand the impact of the bark hammer and pilodyn without rebounding, and the branches of the live crown need to be far enough above breast height to allow access to the stem.

Pilodyn assessments were not adversely genetically correlated with growth in PEE, PCH or the PEE×PCH F_1. This contrasts with the previous results of Costa e Silva *et al.* (2000) and Wang *et al.* (1999), where pilodyn penetration was strongly influenced by growth ring width, and had to be adjusted to remove these effects. In PCH, the significantly lower adverse genetic correlation between pilodyn and underbark volume than between density and underbark volume suggests that growth and pilodyn penetration could be selected for concurrently, using a selection index, whereas growth and density could not. However, the very strong and significant correlation between pilodyn and SLOPE in all taxa indicates that selection for decreased pin penetration at age 12 will cause a correlated increase in the pith-to-bark wood density gradient. This is probably because the pilodyn most accurately measures the density of the outermost wood, which strongly affects SLOPE; pilodyn measurements at younger ages may not affect SLOPE as strongly. However, the results of Chapter 4 indicated that juvenile wood density and SLOPE were also highly correlated; the strong adverse correlation with pilodyn re-affirms the importance of assessing the economic value of changes in SLOPE.

The usefulness of the pilodyn for genetic improvement of density has sometimes been challenged based on the interpretation of studies that examined only the relationship between these traits at the individual-tree level. Raymond and MacDonald (1998) conducted a very detailed investigation of the phenotypic correlation between pilodyn assessments at a variety of stem heights with whole-stem density: the relationship was

[7] Dr Mark Dieters, Principal Geneticist, Queensland Forestry Research Institute

sometimes strong, but varied greatly among sites and species, consistent with the results of Smith *et al.* (1981) and other estimates of phenotypic density-pilodyn correlations. These results provide good evidence that the pilodyn is unlikely to be reliable for segregating logs into density classes at a mill, but their implications for breeding are less clear. In breeding, when selection on a screening trait is carried out at the within-family level, the correlated genetic gain in the target trait is estimated as a function of the within-family heritability in the screening trait, the within-family heritability in the target trait, and the additive genetic correlation between the traits. Correlated genetic gain from either family (*eg* Equation 5.1) or within-family selection on pilodyn penetration are therefore not reliant on the phenotypic correlation between pilodyn and density, which is consistently much lower and more variable than its genetic counterpart. Low phenotypic correlations *per se* between density and pilodyn are not clear evidence for limitations of the pilodyn as a screening tool under any selection strategy.

Most studies have found density-pilodyn phenotypic correlations in the range of 0.4-0.7. Early studies of PEE and PCH in Queensland (*eg* Smith *et al.* 1981) demonstrated that the pilodyn was of limited and inconsistent value for predicting individual tree density (*eg* r_P=0.483-0.743 for a range of sites at Beerburrum), but estimated the mean density of experimental populations reasonably well (within ±13-15 kg/m^3). The results of the current study extend the interpretation of these early studies to suggest that pilodyn may reliably predict density means of full-sib families, and the pilodyn-density genetic correlation may be high even with as few as 7 individual representatives per family per site (*eg* at Tuan Swamp).

The preliminary study of the effect of pin thickness described in Section 5.2 suggested that the thinner, 2.0mm pin achieved much better differentiation between trees than the 2.5mm pin. There are two ways of increasing the penetration of the pilodyn pin: using a smaller diameter pin, and using a more powerful machine (pilodyn penetrometers have traditionally been available in 6J, 12J and 18J models, of varying strike force, in Joules). Most studies in the literature have used the 6J model with a 2.5mm pin. This study used the 12J model with a 2.0mm pin; the increased penetration from this combination may be responsible for the higher indirect selection

efficiency than was achieved by previous studies. Unfortunately at this time only the 6J model is available from the manufacturers (PROCEQ 2002). The use of 2.0mm pins in place of 2.5mm or 3.0mm pins is strongly recommended, firstly because it increases the proportion of the stem radius sampled, and secondly because thinner pins result in a greater range of penetration, achieving improved differentiation between low density and high density trees (Villeneuve 1999). Use of the 6J model with 2.5mm or 3.0mm pins on very dense wood, for example, is unlikely to generate useful information. In view of the current results, it seems possible that cases in previous studies where pilodyn penetration was excessively influenced by growth ring width, and cases where the pilodyn did not rank provenances accurately, may have been due to inadequate pin penetration. The effect of different sizes and shapes of pin on selection efficiency deserves further investigation.

The effect of season of assessment was not examined in this study, although it has been observed to affect pin penetration in previous studies. However, season does not appear to affect the reliability of the pilodyn for ranking families for density (*eg* Cown 1980) except at subzero temperatures (Cheliak *et al.* 1984). A strong relationship between latewood characteristics and environmental variables such as temperature and rainfall (Cregg *et al.* 1988; Burdon and Low 1992) is often observed in *Pinus*. During assessment of the 2577 wood samples in this study, trees were observed to differ unpredictably in the response of their latewood characteristics to droughts. Where genotypes differ in their response to extreme climatic events by producing strongly differing latewood characteristics, pilodyn comparisons among genotypes conducted soon after such events may not accurately reflect whole-stem density. Longer-term investigations of pilodyn reliability at a series of tree ages are therefore recommended, to supplement the results from existing studies conducted in only two consecutive seasons (*eg* Cown 1980).

During fieldwork for this study, the importance of good operating technique with the pilodyn became evident. Operator effects were examined experimentally for five operators in a single trial by Cown and Andrew (1979), who found in an analysis of variance that the operator effect was statistically significant ($p<0.02$) for pilodyn, but non-significant for wood density. The pilodyn-density correlation, at the plot mean level, varied between 0.40^{ns} and 0.81^{**} among the 5 operators, demonstrating the

critical importance of technique, which was also commented on by Villeneuve *et al.* (1987) in a study of *Picea*. Based on the fieldwork for the current study, a set of recommendations for pilodyn operating technique were developed, and are listed in Box 5.1.

Box 5.1 Recommendations for operational use of the pilodyn

Recommendations for operational use of the pilodyn

- Use 2mm diameter pins
  - 2.5mm pins have traditionally been most often used in pilodyn studies. Thinner, 2mm diameter pins give better differentiation among trees, as found in this study and by Villeneuve (1999 unpublished).

- Train operators in consistency

"Operating the instrument was like shooting a bow: precision comes with constant release" (Villeneuve 1999 unpublished).

  - lean your weight onto the apparatus while firing, to avoid kickbacks;
  - take care not to move the instrument as the plunger is released;
  - on small stems, have someone hold the tree to prevent kickback;
  - remove a piece of bark large enough for the spacer pins to contact the wood;
  - ensure the spacer pins are vertically aligned, and pressed firmly against the wood;

- Consistently sample best aspect
  - note any consistent pith anisotropy (displacement from the centre) in the forest (*eg* on stumps) and choose aspect(s) for sampling accordingly, to avoid reaction wood - remembering that reaction wood is formed on the upper side of the tree in hardwoods and on the lower side in conifers. Measure at the same aspect on each stem.

- Sample representative wood
  - sample well clear of branches or other defects

Although the indirect selection efficiency of the pilodyn is unlikely to ever appreciably exceed 100%, its primary advantage is its lower cost. For an example where overall costs and number of selections are fixed, the pilodyn can be used to increase genetic gains by increasing the selection intensity, through increasing the number of candidates screened. Importantly, the decision between pilodyn assessment and direct assessment of density must trade off this increase in genetic gain through increased selection intensity, with the increase in risk incurred through indirect selection. A key factor in this decision is the non-linear relationship between proportion selected and selection intensity (*eg* Becker 1984); for example, a two-fold

increase in the number of candidates screened to produce a fixed number of selections will always less than double the genetic gain from selection, assuming the sample variance stays the same. However, the increase in genetic gain from using the pilodyn will be much greater where the planned selection intensity for density is low, than where it is high. To illustrate this point numerically, the following example assumes that pilodyn has 100% selection efficiency for density, yet is half as expensive, allowing evaluation of twice as many candidate trees to produce the same number of selections, holding overall cost constant. On this basis, if the pilodyn reduced the proportion selected from 50% to 25%, it would increase genetic gain by a factor of 1.6 (=1.271/0.798) relative to direct selection on density; yet if it were to reduce the proportion selected from 25% to 12.5%, it would increase genetic gain by a factor of only 1.3 (=1.647/1.271). Under this 'fixed total cost' scenario, marginal genetic gain from using the pilodyn therefore depends strongly upon the intended selection intensity for density, as well as on the relative cost of pilodyn assessment. Breeding programs that already use a high selection intensity for density will make little extra genetic gain by investing the same amount of money in pilodyn assessment. Conversely, in a breeding program where only half of the candidates assessed for density are culled off (50% selected), if pilodyn can be assessed at 8% of the cost of density (Greaves *et al.* 1995), and has 90% indirect selection efficiency, pilodyn would make 247% of the genetic gain possible from direct selection on density.

Weighted against the potential for these gains must be a consideration of the risk of using indirect assessments (*eg* Magnussen and Yanchuk 1993). The deterministic model used in this chapter does not factor in risk, which is difficult to assess and depends upon the reliability and representativeness of the genetic parameters. For the pilodyn, whose indirect selection efficiency has been known to vary with different sites, provenances and operators, risk can be minimised by rigorous evaluation, sampling a range of sites, genotypes and operators. As an additional decisionmaking tool, stochastic simulation and modelling may be used to take a probabilistic approach to estimating gains from indirect selection that factors in risk (*eg* Magnussen and Yanchuk 1993).

In summary, however, on the basis of this study and previous evidence, the pilodyn provides an excellent opportunity to assess wood density reliably and quickly in the

field, in PEE, PCH and PEE×PCH. In this study, pilodyn was highly useful for assessing density, regardless of the taxon, site or stem sampling aspect used. The main advantage of pilodyn over density assessment on wood samples is its lower expense; ancillary benefits include reduced damage to trees, and immediate availability of results for analysis, whereas laboratory measurement of wood properties can take months or years before data become available. Further investigation of operator, site and season effects is recommended, using a broader sample of genotypes.

5.4.5.2 Bubble protractor/Spiralite

Bubble protractor measurements of spiral grain at age 12 provided moderate indirect selection efficiency for age 12 whole-stem spiral grain (57%). However, this outer-ring measurement was taken at an age generally considered too late to reliably assess spiral grain in most fast-growing conifers (*eg* Nicholls 1967; Harris 1989). The high early selection efficiency of individual-ring laboratory measurements of spiral grain at tree ages 4-7 in the current study (175-157%), consistent with previous findings in PCH and in *P. radiata* (*eg* Harding *et al.* 1991; Sorensson *et al.* 1997a), suggests strong potential for spiral grain screening using a field measurement in a single ring at one of these younger ages. The small predicted marginal genetic gain from detailed radial assessments of spiral grain at 1.3m (discussed in section 5.4.4) seems unlikely to justify their high cost, which Sorensson *et al.* (1997a) estimate to be 10 times that of a field testing using a bark window assessment with the Spiralite®, a digital redevelopment of the bubble protractor recently purchased by the QFRI.

Besides the primary advantage of lower cost, which allows increased genetic gains through higher selection intensity, a further advantage of field testing is that small rectangular bark windows cause less damage to the tree than increment coring - a serious consideration when sampling young trees that may later be intended for mature age testing or seed orchards. Bark windows also provide a much larger area of observation, and so may in fact result in more accurate spiral grain estimates, than increment cores (Lausberg 1997). Additionally, results from field screening are available immediately for analysis along with other traits measured in the field, while laboratory measurements can take months or years to obtain, possibly delaying

breeding activities such as crossing. Sorensson *et al.* (1997a) estimate that a two-person crew can assess bark window spiral grain on 100 to 200 trees per day, depending on the terrain, and conclude that spiral grain is therefore the cheapest wood property to assess. In the current study, a two-person crew completed both pilodyn and bark window assessment on 200-300 trees per 8-hour day. The above are strong arguments for the use of field screening for spiral grain at breast height, although the optimum age for screening needs to be confirmed in larger progeny trials and in clonal trials. Finally, studies in *P. radiata* have indicated that spiral grain patterns can change and grain angle often dramatically increases higher in the stem (Cown *et al.* 1991), and so while routine screening may be carried out cheaply using the Spiralite®, final stage screening of select families and clones should also include destructive sampling and ring-by-ring assessments of spiral grain at several heights (Shelbourne[8] pers. comm.).

5.4.6 Field screening with truncation subsampling

Based on the current results, field screening using the pilodyn and bubble protractor can achieve nearly as much genetic gain per generation as direct selection on whole-stem density and whole-stem spiral grain at age 12. In this experiment however, field screening was carried out by a single experienced operator, with attention to taking precise measurements. In routine application of field screening, it is likely that several operators would take turns operating the screening tools, and the accuracy of the measurements may depend heavily on the technique of the operator (Cown and Andrew 1979). Additionally, the usefulness of the 6J model of pilodyn has not yet been confirmed in Queensland, and so must be viewed conservatively.

Given these elements of uncertainty in the genetic relationship between pilodyn and density, truncation subsampling of pilodyn measurements with direct density assessment may be a useful selection strategy for density in exotic pines in Queensland. Using this strategy, all or most trees in a genetic test would be assessed using the pilodyn; a proportion of the best-scoring trees would then be assessed for density, to confirm their superiority. The pilodyn is hence used simply to reduce the number of trees on which density needs to be directly assessed. Though this selection

[8] Dr Tony Shelbourne, Senior Geneticist, ForestResearch, New Zealand.

strategy only partially addresses the risk of type I selection errors (erroneous culling of high density genotypes), its primary advantage is in greatly reducing the incidence of type II selection errors (erroneous selection of low density genotypes). Based on the properties of the bivariate normal distribution, the following equation (Wu 1998) can be used to predict the combined genetic gain from selection for pilodyn and truncation subsampling for wood density, for the example of assessment at age 6:

$$E_{xy}(G_y) = (i_x h_x h_y r + i'_y \frac{1 - r^2 h_x^2 k}{\sqrt{1 - \rho^2 k}} h_y^2)\sigma_y \qquad [5.4]$$

where:

$E_{xy}(G_y)$ = genetic gain in breast height density at age 6 (trait y) resulting from the combination of indirect selection for pilodyn (trait x) on the full population, and direct selection for breast height density at age 6 on a subsample of the same population;

i_x = selection intensity on pilodyn;

i'_y = selection intensity on age 6 density in the subsample;

h_x = square root of the heritability of pilodyn;

h_y = square root of the heritability of age 6 density;

r = genetic correlation between pilodyn and age 6 density;

ρ = phenotypic correlation between pilodyn and age 6 density;

$k = i_x(i_x - a)$ where a is the value at the truncation point of the standard normal distribution curve corresponding to selection intensity i_x. These values can be obtained from tables of the standard normal distribution.

Although selection for pilodyn and density was used as an example in the above equation, the same methodology may be applied to spiral grain field screening and laboratory assessment. Genetic gain estimates based on Equation 5.4 may be biased however, as it assumes that the subsampled population is normally distributed, and does not differ in gene frequency or genetic correlation from the unselected population (Wu 1998). Simulations performed by Apiolaza *et al.* (1999) indicated that where only a small proportion of trees were subsampled for target trait measurement, the accuracy of predicted gains was poor. However, Equation 5.4 provides a method of estimating the combined genetic gain from this selection strategy, which is likely to be a useful framework for cost-effective wood property improvement in exotic pines in Queensland, and in other taxa.

5.4.7 Early and indirect selection in hybrid clones

Early selection is currently of particular importance in clonal testing in Queensland, as juvenile clones have not yet been successfully preserved using cryogenic storage. Currently, clonal tests are established 18 months after sowing seed into clonal hedges; tests are then evaluated for 6 years, and the best clones 'bulked up' for at least one year. This results in a total of 9 years from seed before tested clones can be deployed, and a maximum of approximately 14 years before clones become unusable due to physiological maturation, allowing a narrow window of only 4-5 years in which clones can be deployed (Dieters, pers. comm.). Assessment of wood properties at 4 years of age, rather than 6 years, would provide an extra 2 years of deployment for each clone. Results from the current study suggest that selection of half-sib and full-sib families for wood density and spiral grain can reliably be carried out at age 4 from seed in the F_1 hybrid.

If these results also apply to early selection of clones, evaluation of wood density and spiral grain in hybrid clonal tests may be reliably performed at age 4, using field screening with the pilodyn and spiralite. However, the optimum age for early selection in PEE×PCH may be different in clones than in seedlings. For example, the genetic differences among clones taken from a common set of full-sib families will be smaller than those among the unrelated half-sib progeny groups in this study, and so the ranking of clones may not stabilise until a later age (Greenwood and Volkaert 1992). Additionally, non-additive genetic variance, influential in basal area and spiral grain in the F_1 hybrid, is likely to affect the efficiency of early selection of F_1 hybrid clones in these traits, particularly in basal area, where SCA variance increased dramatically with age. Early selection for wood density among F_1 hybrid clones is likely to be more reliable, because of high heritability, high juvenile-mature correlations and low non-additive variance in wood density in the F_1 hybrid. These uncertainties need to be resolved by directly assessing the efficiency of early selection for growth and wood properties in PEE×PCH hybrid clonal tests.

5.4.8 *Improving the efficiency of wood improvement: summary and future possibilities*

The continuing trend towards shorter rotations in PEE×PCH and other conifers must be accompanied by juvenile wood quality improvement, if the quality and hence market share of solid wood products is to be maintained. Due to continuing reductions in the age at which trees are selected for growth characters, it is unlikely that mature wood characteristics and related traits such as latewood transition age can ever be directly selected for at acceptable cost in any tree improvement program. The results of this study suggest that selection for growth, wood density and spiral grain at age 6-7 will increase genetic gain per year by at least 50%, and in some cases by over 100%, relative to selection on the same traits at age 12, in PEE, PCH and F_1. Selection on individual-ring measurements of density and spiral grain was highly efficient for improving overall density and spiral grain at age 12, with the exception of measurements at age 3, which corresponds approximately to the first-formed growth ring. The selection efficiency of individual-ring measurements was improved by ascribing ring identities based on tree age instead of cambial age. Though selection at age 4 provided optimum genetic gain per year in all taxa and traits except basal area in the F_1 hybrid, it is not likely to be useful in PEE and PCH unless the time of first flowering can be reduced from the current age of 6-7 years. Selection at age 4 may be useful in the F_1 hybrid under certain breeding strategies, for example RRS and COMP, if interest were to be focussed solely on wood property improvement. If the current results also apply to clonal selection, selection at age 4 would increase the useful deployment period for tested clones from approximately 4-5 years at present, to 6-7 years.

The predicted increase in genetic gain from applying field screening instead of direct density and spiral grain assessments in exotic pine breeding in Queensland could not be calculated directly in this study, because it depends on such factors as the relative cost of the two methods, the intended selection intensity for direct measurements, and whether truncation subsampling for wood density is used. However, the strong indirect selection efficiency of the field screening methods, known large cost savings, and very low selection intensity for wood properties in Queensland until now suggests very strong potential for field screening. Substantial cost savings in pilodyn

assessment appear possible through sampling only one stem aspect, and a reduced subset of sites. Furthermore, if field screening can be performed at a young age, it may combine the high genetic gain efficiency of early selection with the high selection intensity possible with field assessments. Field screening has the unique potential to allow wood property improvement to proceed on a large scale: an activity rarely possible in any breeding program where wood properties have to be measured directly. Further studies of early selection efficiency and field screening are needed to verify these results in both seedling and clonal trials approaching rotation age, on a larger sample of genotypes. Larger experiments are particularly necessary to obtain reliable early selection information for basal area and spiral grain, which have large within-family coefficients of variation and so are difficult to examine conclusively with small numbers of trees per family and with few families. The significance of the current results lie in being the first to examine juvenile-mature correlations in hybrid wood properties, in the high efficiency of early selection on individual-ring values for density and spiral grain at young ages, and in the high efficiency of field screening methods for density and spiral grain.

This chapter and the one before it have investigated ways of improving the efficiency of PEE×PCH improvement, through selection in the F_1 hybrid and pure species parental populations. Chapter 6 will investigate the genetic basis of heterosis in PEE×PCH, and the possibility of improving its wood and growth characteristics using novel breeding strategies that employ forward selection within the interspecific hybrid population itself.

Chapter 6 - Genetic basis of heterosis and implications for breeding strategy

6.1 Introduction

The high cost of hybrid breeding relative to pure species breeding creates an imperative to identify the most efficient breeding strategy. Because of known genetic differences among taxa (*eg* between *Populus* and *Pinus*), a breeding strategy that is optimal in one hybrid taxon may be suboptimal or even dysgenic in other hybrid taxa. In the Queensland *Pinus elliottii* var. *elliottii* × *Pinus caribaea* var. *hondurensis* hybrid, as in other interspecific forest tree hybrids, little genetic information is available to support decisions between breeding strategies.

The results of analyses reported in Chapter 4, based on conventional statistical genetic methods, suggested that recurrent selection of parents based on their pure species cross performance (RSGCA) may in some traits provide similar genetic gains per selection cycle compared to more conservative strategies selecting parents based on the performance of their hybrid progeny (RRS). However, due to restrictive assumptions underlying these analyses, they were unsuitable for predicting the genetic advance from strategies involving forward selection in early generation hybrid populations. Their failure to accurately predict genetic gains from such strategies has been demonstrated in hybrids of numerous non-tree taxa (*eg* Moll and Stuber 1971 in maize). This is principally because these models are based on pooled statistical effects of genes measured across the whole population, on the assumption of a single random-mating population - an assumption that is not met in hybrid populations.

The distinction between additive and dominant Mendelian gene action and additive and dominant statistical effects of genes in populations is an important one for genetic modelling, and was explained in Section 2.2. Statistical effects of genes are derived from a regression of frequency-weighted genotypic values on genotype, and hence depend on allele frequencies and on the conditions of Hardy-Weinberg equilibrium and linkage equilibrium, in the progeny population. Because of the known large differences in molecular marker genotypes, and hence suspected large differences in genotypes at functional loci, among related tree species (*eg* Keim *et al.* 1989, Schmidtling and Hipkins 2001, Stokoe *et al.* 2000), assumptions of equilibrium are likely to be violated in populations generated by hybridising tree species. Estimates

of statistical effects of genes, and therefore genetic variances, will consequently be biased by an unknown amount. Mendelian gene action, however, can be described independently of gene and genotype frequency in the population, and the degree of linkage equilibrium in the population. Hence, models of Mendelian gene action, rather than statistical genetic variances, may provide a more reliable means of predicting the response of hybrid populations to both forward and other types of selection.

The reasoning behind this in respect to forward selection is simple. The progeny population derived from selecting and crossing amongst F_1 hybrid individuals will have an increased proportion of homozygotes relative to the maximally heterozygous F_1. Therefore, providing deleterious epistatic interactions do not occur in advanced generation hybrid populations, estimation of and comparison between the genotypic values of heterozygote and homozygote genotypes at functional loci can indicate whether a reduction in performance can be expected in advanced generation hybrids, relative to the F_1. Where interspecific heterozygous genotypes are clearly superior to homozygous genotypes (*ie* where overdominance or strong dominance and dominance-related epistatic gene action make a large contribution to hybrid performance), F_1R strategies, which focus on recurrently improving the maximally heterozygous F_1 generation, are preferable to advanced generation hybridisation (AGH) strategies. However, where dominance is partial, such that homozygous genotypes are superior, it may be possible to select for favourable homozygotes within an advanced generation hybrid population. Such individuals could, in theory, incorporate the most favourable characteristics of each parent species, surpassing any gene combinations possible in the F_1 or either pure species population (Namkoong 1979; Li and Wyckoff 1994). Strategies based on forward selection in hybrids have the potential to dramatically reduce the cost and generation interval of hybrid tree breeding, but their efficacy depends on the types of gene action underlying hybrid performance.

Knowledge of the predominant mode(s) of gene action underlying hybrid performance can also provide a basis for deciding between F_1R strategies, as an alternative to the method based on statistical gene effects used in Chapter 4. The strategy of Reciprocal Recurrent Selection was designed to allow genetic improvement regardless of the degree of (Mendelian) dominance or overdominance at

individual loci controlling the traits of interest. Comstock *et al.* (1949) showed that where partial dominance was the predominant mode of gene action, pure line selection (analogous to RSGCA in trees) was likely to make equivalent genetic gains to RRS. However, under complete dominance or overdominance, pure line selection yielded inferior gains. An understanding of the modes of gene action contributing to interspecific tree hybrid performance is therefore valuable both for guiding choices among novel and conventional breeding strategies, and for broadening scientific knowledge of the genetic consequences of hybridising genetically diverse populations.

The genetic gains that have been made in some crop hybrids demonstrate that progress can be made despite our ignorance of the genetic architecture of important traits (Cooper and Merrill 2000). However, theoretical studies and selection experiments have also demonstrated that large improvements in the efficiency of breeding may be possible where genetic architecture, particularly the mode of gene action influencing heterosis, is well understood (Comstock *et al.* 1949; Moll and Hanson 1984). In tree improvement, the high expense of crossing and long generation interval demand more prudent investment of resources than has traditionally taken place in crop hybrid breeding. An understanding of the gene action underlying heterosis in particular interspecific crosses will allow the formulation of long-term improvement strategies, the genetic advance from which is likely to far surpass that from the traditional haphazard exploitation of heterosis in trees.

Analytical methods to dissect quantitative variation at the level of the individual locus, or linkage group, in quantitative traits may provide further insight into gene action in hybrid populations. Some analyses developed in crop plants have estimated the genetic basis of heterosis in intraspecific hybrids based on advanced generation crosses of inbred lines (Hallauer and Miranda 1988), yet such populations are not available in forest trees. Methods based on analysis of a single generation of progeny have only recently been made possible by the exponential rise in computing power since the early 1960's, and the development of new molecular genetic tools that can identify chromosome segments using genetic 'markers'. However, molecular genetic technologies incur large up-front costs, and require data from large and unconventional field test designs (*eg* van Buijtenen 2001) which, in most cases, must be designed and established specially for the purpose, and maintained until close to

maturity (Lerceteau *et al.* 2001; Grattapaglia *et al.* 1995). Very few such experiments exist in forest trees. Furthermore, the ability of these methods to estimate gene action is still in development (*eg* Knott *et al.* 1997, Sewell *et al.* 2000). Recent quantitative genetic approaches such as those of Li and Wu (1996), Pong-Wong *et al.* (1998) and Wu and Li (2000) can use existing progeny trial datasets to estimate gene action at the level of individual linkage groups, potentially providing both useful information for hybrid breeding and preliminary information for genetic mapping.

This chapter has two aims: firstly, to construct a theoretical model of genetic architecture in the PEE×PCH hybrid and parental species populations, incorporating assumptions appropriate to interspecific hybrid populations, based on the model developed by Li and Wu (1996) in *Populus tremuloides* × *P. tremula.* Empirical variances and covariances estimated in previous chapters, in QFRI EXP674, will be mathematically equated with theoretical expectations based on the hypothesised model, to obtain estimates of the mode of gene action underlying heterosis in the PEE×PCH F_1 hybrid. Secondly, the results from the model will be discussed with reference to breeding strategies for PEE×PCH hybrids in South-East Queensland, and with respect to forest tree hybrid breeding more generally.

6.2 Materials and methods

The structure of the EXP674 progeny trial and the sample of it used in this study were previously described in Section 3.3. The genetic model developed by Li and Wu (1996) and applied in this chapter seeks to model the genetic basis of heterosis, based on empirical information estimated from pure species and hybrid populations. The model uses genetic information estimated at two hierarchical levels: the among-population level and the within-population level, and hence relies on genetic relatedness between the pure species and hybrid populations. In EXP674, the PEE and PCH progeny populations are both related to the PEE×PCH F_1 hybrid progeny population through common parents. The model also requires that statistically valid comparisons can be made among taxa and parents, and so their progeny must be grown together in multiple replicates of a field experiment, as occurs in EXP674 (see Section 3.3; Appendix 1). The PEE×PCH F_2 hybrid progeny population in EXP674 was excluded from the analysis in this chapter, due to its lack of common ancestry with the pure species and F_1 hybrid populations in this experiment.

The quantitative genetic model proposed by Li and Wu (1996) extends the model of Comstock and Robinson (1948) to incorporate assumptions appropriate for interspecific hybrids of outcrossing species, and to estimate gene action at the level of the individual locus, or linkage group. The model of Comstock and Robinson (1948), based on principles established by Fisher (1918), equates empirical variances estimated in genetic tests with theoretical expectations based on a simple genetic model, to estimate theoretical genetic variances. The extended model of Li and Wu (1996) equates empirical variances with theoretical expectations that are modified to account for the possibility of different alleles between the two parental populations of an outcrossing interspecific hybrid. The key difference between the two models, however, is that while the former estimates gene effects as a function of genotypic values and genotype frequencies assumed to be in equilibrium, the latter model relaxes this assumption by separately estimating individual-locus genotypic values and gene frequencies, under a set of simplifying assumptions based on results from molecular genetic studies.

6.2.1 Theoretical genetic model: assumptions

The genetic architecture of a population is typically complex, and depends on many variables (see Section 2.4). Some simplifying assumptions are necessary in order to model genetic architecture. The theoretical genetic model used in this study is based on the following assumptions:

1. *The set of alleles segregating in PEE may be entirely different to that segregating in PCH, or there may be some alleles in common.*

   The two species are both members of subsection AUSTRALES in the hard pines, are closely evolutionarily related (Dvorak *et al.* 2000; Schmidtling and Hipkins 2001), and until 1956 were considered a single species (Echols and Dorman 1962). However, molecular genetic studies using genetic markers commonly find largely different allelic systems between closely related species (eg Keim *et al.* 1989; Stokoe *et al.* 2000; Vaillancourt *et al.* 1995). Alleles at functional loci, particularly those affecting fitness-related traits, are expected to be more tightly conserved on average than markers, which are essentially random fragments of DNA from both functional and non-functional sections of the genome. Nevertheless, the probable different allelic systems between the species is also

evidenced by their substantially different morphology and performance in a variety of traits on common sites (eg Chapter 3).

2. *Genetic loci controlling the traits examined are common to the PEE, PCH and PEE×PCH hybrid populations, and alleles and genotypes segregate freely and randomly within and between the PEE and PCH populations.*

   The close evolutionary relationship of PEE and PCH, and studies in these and other closely related pairs of species (Shepherd *et al.* 2003; Stokoe *et al.* 2000) suggest that the same functional loci segregate in the two species: only the alleles at these loci differ. The assumption of random segregation in the hybrid implies that no segregation distortion (eg due to chromosomal aberrations or inter-specific genetic incompatibility) takes place during cross-fertilisation. There appear to be no karyotypic changes or changes in overall genome size between the two pure species and the PEE×PCH hybrid, indicating regular diploid inheritance in the hybrid (Williams *et al.* 2002), which has 12 chromosome pairs (2n=24), as have PEE, PCH and almost all other Pinus species (Khoshoo 1961). The results of a preliminary study of segregation distortion at two linked marker loci in two PEE×PCH F_1 hybrid crosses (Williams *et al.* 2002) suggest it is no more severe in interspecific than in intraspecific crosses. Though the proportion of filled seed is lower in F_1 hybrid controlled crosses than in pure PEE controlled crosses (Nikles and Robinson 1989), the high proportion of normal seedlings developing from filled seed and the low proportion of runts and deformed trees in planted PEE×PCH F_1 hybrid populations (Nikles and Robinson 1998, Powell 2001) suggest a low incidence of genetic incompatibility of PEE and PCH alleles.

3. *Any metric (measurable) trait is controlled by n independent 'loci'; these may be groups of linked loci that are assumed to act similarly to individual loci.*

   The model is constructed at the level of the individual locus, though its resolution is limited to individual linkage groups. In the F_1 hybrid population, each chromosome is a linkage group. Hence, where more than one locus contributing to a given trait exists on a chromosome, the detected 'locus' or linkage group may in fact encompass several loci. The maximum number of 'loci' or linkage groups detectable using this model in *Pinus* spp. is therefore 12, in the case that each of the 12 chromosome pairs contains an allele affecting the trait of interest.

4. *In any metric trait, the distribution of the genotypic values of loci contributing to the variation in that trait can be described approximately using a geometric series.*

   A variety of early and recent evidence from both quantitative genetic and molecular studies supports the hypothesis of Robertson (1967) that "the distribution of gene effects will probably be of an exponential kind (so that the smaller the range of effects specified, the greater the number of loci concerned)". There is strong evidence in the model species *Drosophila* from response to long-term selection experiments, which show steady change through generations from the fixation of alleles at polygenic loci, punctuated by sudden jumps due to the fixation of major genes (*eg* Caballero *et al.* 1991; Mackay *et al.* 1994). Numerous molecular genetic studies in a variety of taxa (*eg* Bost *et al.* 1999; reviewed by Mackay 1996) provide evidence that the pattern of individual-locus genotypic effects across loci may be modelled using simple continuous distributions. A geometric series allows a high degree of flexibility in the shape of the distribution, from strongly L-shaped distributions involving several major genes and a polygenic component, to flat distributions suggesting polygenic gene action with approximately equal effects of loci.

6.2.2 Theoretical genetic model: structure

Based on Mendel's first and second laws (that linkage groups segregate, and assort independently of each other), and the assumptions outlined in Section 6.2.1, the two pure species (PEE and PCH) populations and the PEE×PCH F_1 hybrid population can be described in terms of a theoretical genetic model. The model is identical in principle to that of Li and Wu (1996), though it has been extended to account for the possibility of totally different alleles between the two pure species populations. The model is first formulated at the single-locus level, and then accounts for the cumulative effects of multiple loci.

6.2.2.1 Single-locus level

If PEE and PCH populations each contain two alleles which may either be the same or different both within and between populations (*ie* the total number of alleles between populations may be between 1 and 4), the PEE alleles can be denoted A and a, at frequencies of p and q, and the PCH alleles may be denoted A' and a', at frequencies

of p' and q'. In the absence of segregation distortion, random mating among unrelated parents within the PEE and PCH populations will produce genotypes *AA*, *Aa* and *aa*, and $A'A'$, $A'a'$ and $a'a'$, respectively, in Hardy-Weinberg Equilibrium with respect to gene frequencies in each population. These genotypes are assumed to have genotypic values of a_1, d and a_2, and a'_1, d' and a'_2, respectively. Similarly, random mating between sets of PEE and PCH parents, where parents within sets are unrelated, will produce the genotypes: AA', Aa', $A'a$ and $a'a'$, assumed to have genotypic values D, d_1, d_2, and a, in ratios that can be predicted based on gene frequencies in the parental populations. These genotypes may be unique to the interspecific population, if the two parental populations possess entirely different alleles, or may also be found in the parental populations, if there are some alleles in common between the two populations.

For a single locus, under the above assumptions, the genotypes and genotype frequencies in the PEE, PCH and PEE×PCH F_1 hybrid progeny populations can be calculated based on mating arrays, and summarized using marginal and overall means of these arrays, as shown in Table 6.1, Table 6.2 and Table 6.3. Furthermore, the genetic relationship of individual PEE parents with the PEE×PEE and PEE×PCH progeny populations generated from them can be described as in Table 6.4 and Table 6.5. Due to the complexity of the calculations it is necessary to assume known gene frequency, with $p=q=p'=q'=0.5$, as in Li and Wu (1996).

Table 6.1 Genotypes, genotype frequencies and frequency-weighted genotypic means in progeny of intraspecific matings among PEE parents

Genotype code genotype frequency genotypic value	*AA* ¼ a_1	*Aa* ½ d	*aa* ¼ a_2	PEE-parental marginal frequencies and means
AA ¼ A_1	1/16 a_1	1/8 $(a_1+d)/2$	1/16 d	¼ $(a_1+d)/2$
Aa ½ D	1/8 $(a_1+d)/2$	¼ $(a_1+2d+a_2)/4$	1/8 $(d+a_2)/2$	½ $(a_1+2d+a_2)/4$
aa ¼ a_2	1/16 d	1/8 $(d+a_2)/2$	1/16 a_2	¼ $(d+a_2)/2$
PEE-parental marginal frequencies and means	¼ $(a_1+d)/2$	½ $(a_1+2d+a_2)/4$	¼ $(d+a_2)/2$	overall mean $(a_1+2d+a_2)/4$

Table 6.2 Genotypes, genotype frequencies and frequency-weighted genotypic means in progeny of intraspecific matings among PCH parents

Genotype genotype frequency genotype code	$A'A'$ ¼ a'_1	$A'a'$ ½ d'	$a'a'$ ¼ a'_2	PCH-parental marginal frequencies and means
$A'A'$ ¼ a'_1	1/16 a'_1	1/8 $(a'_1+d')/2$	1/16 d'	¼ $(a'_1+d')/2$
$A'a'$ ½ d'	1/8 $(a'_1+d')/2$	¼ $(a'_1+2d'+a'_2)/4$	1/8 $(d'+a'_2)/2$	½ $(a'_1+2d'+a'_2)/4$
$a'a'$ ¼ a'_2	1/16 d'	1/8 $(d'+a'_2)/2$	1/16 a'_2	¼ $(d'+a'_2)/2$
PCH-parental marginal frequencies and means	¼ $(a'_1+d')/2$	½ $(a'_1+2d'+a'_2)/4$	¼ $(d'+a'_2)/2$	overall mean $(a'_1+2d'+a'_2)/4$

Table 6.3 Genotypes, genotype frequencies and frequency-weighted genotypic means in progeny of interspecific matings between PEE and PCH parents

genotype genotype frequency genotype code	$A'A'$ ¼ a'_1	$A'a'$ ½ d'	$a'a'$ ¼ a'_2	PEE-parental marginal frequencies and means
AA ¼ a_1	1/16 D	1/8 $(D+d_2)/2$	1/16 d_2	¼ $(D+d_2)/2$
Aa ½ D	1/8 $(D+d_1)/2$	¼ $(D+d_1+d_2+a)/4$	1/8 $(d_2+a)/2$	½ $(D+d_1+d_2+a)/4$
aa ¼ a_2	1/16 d_1	1/8 $(d_1+a)/2$	1/16 a	¼ $(d_1+a)/2$
PCH-parental marginal frequencies and means	¼ $(D+d_1)/2$	½ $(D+d_1+d_2+a)/4$	¼ $(d_2+a)/2$	overall mean $(D+d_1+d_2+a)/4$

Table 6.4 Genotypic means and frequencies of marginal means of intraspecific and interspecific crosses of PEE parents

taxon frequency	*PEE* ½	*PCH* ½	PEE-parental marginal frequencies and means
AA ¼ a_1	1/8 $(a_1+d)/2$	1/8 $(D+d_2)/2$	¼ $(D+d_2+a_1+d)/2$
Aa ½ D	¼ $(a_1+2d+a_2)/4$	¼ $(D+d_1+d_2+a)/4$	½ $(D+d_1+d_2+a+ a_1+2d+a_2)/8$
aa ¼ a_2	1/8 $(d+a_2)/2$	1/8 $(d_1+a)/2$	¼ $(d_1+a+ d+a_2)/2$
Taxa marginal means	½ $(a_1+2d+a_2)/4$	½ $(D+d_1+d_2+a)/4$	overall mean $(D+d_1+d_2+a+ a_1+2d+a_2)/8$

Table 6.5 Genotypic means and frequencies of marginal means of intraspecific and interspecific crosses of PCH parents

Taxon frequency	*PCH* ½	*PEE* ½	PCH-parental marginal frequencies and means
$A'A'$ ¼ a'_1	1/8 $(a'_1+d')/2$	1/8 $(D+d_2)/2$	¼ $(D+d_2+ a'_1+d')/2$
$A'a'$ ½ d'	1/4 $(a'_1+2d'+a'_2)/4$	1/4 $(D+d_1+d_2+a)/4$	½ $(D+d_1+d_2+a+ a'_1+2d'+a'_2)/8$
$a'a'$ ¼ a'_2	1/8 $(d'+a'_2)/2$	1/8 $(d_1+a)/2$	¼ $(d_1+a+ d'+a'_2)/2$
Taxa marginal means	½ $(a'_1+2d'+a'_2)/4$	½ $(D+d_1+d_2+a)/4$	overall mean $(D+d_1+d_2+a+ a'_1+2d'+a'_2)/8$

Based on the mating arrays in Tables 6.1-6.5, theoretical expectations of the genetic relationships within and between populations can be expressed in terms of the single-locus genotypic values. For example, the covariance of half-sibs in the pure PEE progeny population can be algebraically calculated from Table 6.1 as the variance of the PEE-parent marginal means, weighted by their frequencies, around the overall pure PEE progeny population mean. This covariance can be simplified to the following:

$$\mathrm{cov}_{\mathrm{HS(PEE)}} = \frac{1}{32}\left(a_1^2 - 2a_2a_1 + a_2^2\right) \qquad [6.1]$$

Also from Table 6.1, the covariance of full-sibs in the pure PEE progeny population can be expressed as the frequency-weighted variance of full-sib family means around the overall PEE-population mean, which simplifies to:

$$\mathrm{cov}_{\mathrm{FS(PEE)}} = \frac{1}{64}\left(4d^2 - 4a_1d - 4a_2d + 5a_1^2 + 5a_2^2 - 6a_1a_2\right) \qquad [6.2]$$

Based on the mating arrays in Tables 6.2 and 6.3, the theoretical expectations of the covariances among half-sibs and among full-sibs can similarly be derived in the PCH and PEE×PCH F_1 hybrid progeny populations. Additionally, the genetic covariance resulting from common parents between the PEE and PEE×PCH populations, and between the PCH and PEE×PCH populations, can be calculated from Tables 6.4 and 6.5, respectively, as the frequency-weighted covariance between the two columns of genotypic values.

Lastly, the theoretical expectation of the mean genotypic difference between any two populations can be calculated simply as the difference between the overall means of those populations (see bottom right-hand corner, Tables 6.1-6.3). For example, the difference between the F_1 hybrid and PEE population means is:

$$\Delta_{G(F_1\text{-PEE})} = \frac{1}{4}(a - 2d + D - a_1 - a_2 + d_1 + d_2) \qquad [6.3]$$

The equations representing the theoretical genetic relationships described above, and their full derivations from the mating arrays in Tables 6.1-6.5, are presented in Appendix 18.

6.2.2.2 Extension across multiple loci

Extension of the theoretical genetic relationships described above to account for the effect of multiple loci controlling a trait is straightforward under the assumption that linkage and epistasis among loci (linkage groups) are absent or negligible in their effect, *ie* that genotypic values sum additively across loci. For example, for the case of the covariance among full-sib progeny in the PEE population:

$$\mathrm{cov}_{FS(PEE)} = \sum_{i=1}^{n} \frac{1}{64}\left(4d^2{}_i - 4a_{1i}d_i - 4a_{2i}d_i + 5a_{1i}^2 + 5a_{2i}^2 - 6a_{1i}a_{2i}\right) \qquad [6.4]$$

where i represents the i^{th} locus. However, the number of loci and the distribution of their relative effects on the trait are unknown; the trait could be controlled by many genes each of small effect (*eg* a polygenic trait), or by a few genes of large effect (major genes) in addition to a lesser polygenic effect. Although some traits do appear to be governed by a large number of polygenes, Thompson (1975) demonstrated that models with three loci, where two loci control 90% of the variation, could in fact produce continuous population distributions previously thought to result only from large numbers of loci. A recent molecular genetic study in PEE×PCH suggested that wood density and growth characteristics are under polygenic control (Shepherd *et al.* 2003). However, the sample size for this study was small, and other molecular genetic studies in various organisms including trees (Bradshaw and Stettler 1995) support the possibility of oligogenic control or an L-shaped distribution of gene effects across loci (Bost *et al.* 1999). An attempt to model the distribution of

individual-locus genotypic values across loci must therefore use a mathematical function sufficiently flexible to account for these possibilities.

If the locus described in Tables 6.1-6.5 can be considered a 'reference locus' at which individual-locus genotypic values are estimated, genotypic values can be considered to change at some measurable rate over the remaining n-1 loci. The general assumption that the rate of change across loci follows an inverse exponential curve that differs in slope for each genotype (*AA, Aa, aa, A´A´, A´a´, a´a´, AA´, Aa´, A´a, aa´*) allows for the possibility that at different loci, the relative values of the genotypes, as well as their rankings, may change. This can be expressed mathematically as a geometric series modelling the distribution of individual-locus genotypic values across loci (after Li and Wu 1996), as described in Table 6.6.

Table 6.6 Geometric series modelling the distribution of genotypic values across loci

Species and Genotype Locus:	1	2	3		*i*		*n*
Pinus elliottii (PEE)							
AA	a_1	ua_1	u^2a_1	...	$u^{i-1}a_1$	...	$u^{n-1}a_1$
Aa	d	vd	v^2d	...	$v^{i-1}d$	...	$v^{n-1}d$
aa	a_2	sa_2	s^2a_2	...	$s^{i-1}a_2$	...	$s^{n-1}a_2$
Pinus caribaea (PCH)							
A´A´	a'_1	$u'a'_1$	$u'^2a'_1$	...	$u'^{i-1}a'_1$	...	$u'^{n-1}a'_1$
A´a´	d'	$v'd'$	v'^2d'	...	$v'^{i-1}d'$	...	$v'^{n-1}d'$
a´a´	a'_2	$s'a'_2$	$s'^2a'_2$	...	$s'^{i-1}a'_2$	...	$s'^{n-1}a'_2$
PEE×PCH F_1 hybrid							
A´A	D	wD	w^2D	...	$w^{i-1}D$	...	$w^{n-1}D$
A´a	d_1	kd_1	k^2d_1	...	$k^{i-1}d_1$	...	$k^{n-1}d_1$
Aa´	d_2	ld_2	l^2d_2	...	$l^{i-1}d_2$	...	$l^{n-1}d_2$
a´a	a	ma	m^2a	...	$m^{i-1}a$	...	$m^{n-1}a$

Note: Adapted from Li and Wu (1996); $0< u, v, s, u', v', s', w, k, l, m <1$.

In Table 6.6, it can be seen that where the proportion coefficients (u, v, s, u', v', s', w, k, l and m, corresponding to each genotype) are less than 1, the genotypic values at loci 1...n decrease according to an inverse exponential curve whose slope is flatter with higher values of the proportion coefficient. Low values of a particular proportion coefficient indicate a strongly L-shaped distribution of genotypic values for the corresponding genotype. Loci with unusually divergent genotypic values (relative to the other loci) may indicate a 'major gene'. Many loci (large n) with similar variance among genotypes suggests polygenic control. The geometric series

therefore provides a flexible framework for modelling the distribution of genotypic values across multiple loci.

Equations expressing genetic relationships in terms of genetic parameters at the reference locus (*eg* Equations 6.1 and 6.2, Appendix 18) can be extended to include the effects of multiple loci, by summing the genotypic values across loci 1...*n*, for each of the genotypes presented in Table 6.6. Mathematically, this is done separately for each genotype, by integrating the distribution of genotypic values across loci shown in Table 6.6. For example, the covariance among half-sibs in the pure PEE population for the case of a single locus (Equation 6.1) can be expressed for the case of multiple loci of unequal effect as follows:

$$\mathrm{cov}_{\mathrm{HS(PEE)}} = \frac{1}{32}\left(\frac{(1-u^{n-1})(u^{n-1}+1)a_1^2}{(1-u)(u+1)} - \frac{2(1-(su)^{n-1})a_2 a_1}{1-su} + \frac{(1-s^{n-1})(s^{n-1}+1)a_2^2}{(1-s)(s+1)}\right) \qquad [6.5]$$

Based on Tables 6.1-6.6, it is possible to compile eleven equations (Equations 6.6-6.16) describing the theoretical expectations of covariances within and between populations, and mean differences between populations, expressed for the case of multiple loci of potentially unequal effect:

1. The covariance among half-sibs due to common female parent (variance among PEE female parents) in the F_1 hybrid population:

$$\sigma^2_{F(\mathrm{PEE\times PCH})} = \frac{1}{32}\left(\frac{(1-m^{n-1})(m^{n-1}+1)a^2}{(1-m)(m+1)} - \frac{2D(1-(mw)^{n-1})a}{1-mw} + \frac{2(1-(km)^{n-1})d_1 a}{1-km} - \frac{2(1-(lm)^{n-1})d_2 a}{1-lm} + \frac{(1-k^{n-1})(k^{n-1}+1)d_1^2}{(1-k)(k+1)} + \frac{(1-l^{n-1})(l^{n-1}+1)d_2^2}{(1-l)(l+1)} + \frac{D^2(1-w^{n-1})(w^{n-1}+1)}{(1-w)(w+1)} - \frac{2D(1-(kw)^{n-1})d_1}{1-kw} + \frac{2D(1-(lw)^{n-1})d_2}{1-lw} - \frac{2(1-(kl)^{n-1})d_1 d_2}{1-kl}\right) \qquad [6.6]$$

2. The covariance among half-sibs due to common male parent (variance among PCH male parents) in the F_1 hybrid population:

$$\sigma^2_{M(PEE\times PCH)} = \frac{1}{32}\left(\frac{(1-m^{n-1})(m^{n-1}+1)a^2}{(1-m)(m+1)} - \frac{2D(1-(mw)^{n-1})a}{1-mw} - \frac{2(1-(km)^{n-1})d_1 a}{1-km} + \frac{2(1-(lm)^{n-1})d_2 a}{1-lm} + \frac{(1-k^{n-1})(k^{n-1}+1)d_1^2}{(1-k)(k+1)} + \frac{(1-l^{n-1})(l^{n-1}+1)d_2^2}{(1-l)(l+1)} + \frac{D^2(1-w^{n-1})(w^{n-1}+1)}{(1-w)(w+1)} + \frac{2D(1-(kw)^{n-1})d_1}{1-kw} - \frac{2D(1-(lw)^{n-1})d_2}{1-lw} - \frac{2(1-(kl)^{n-1})d_1 d_2}{1-kl}\right) \quad [6.7]$$

3. The variance due to SCA effects in the F_1 hybrid population:

$$\sigma^2_{SCA(PEE\times PCH)} = \frac{1}{64}\left(\frac{(1-m^{n-1})(m^{n-1}+1)a^2}{(1-m)(m+1)} + \frac{2D(1-(mw)^{n-1})a}{1-mw} - \frac{2(1-(km)^{n-1})d_1 a}{1-km} - \frac{2(1-(lm)^{n-1})d_2 a}{1-lm} + \frac{(1-k^{n-1})(k^{n-1}+1)d_1^2}{(1-k)(k+1)} + \frac{(1-l^{n-1})(l^{n-1}+1)d_2^2}{(1-l)(l+1)} + \frac{D^2(1-w^{n-1})(w^{n-1}+1)}{(1-w)(w+1)} - \frac{2D(1-(kw)^{n-1})d_1}{1-kw} - \frac{2D(1-(lw)^{n-1})d_2}{1-lw} + \frac{2(1-(kl)^{n-1})d_1 d_2}{1-kl}\right) \quad [6.8]$$

4. The variance due to GCA effects in the pure PEE population:

$$\sigma^2_{GCA(PEE)} = \frac{1}{32}\left(\frac{(1-u^{n-1})(u^{n-1}+1)a_1^2}{(1-u)(u+1)} - \frac{2(1-(su)^{n-1})a_2 a_1}{1-su} + \frac{(1-s^{n-1})(s^{n-1}+1)a_2^2}{(1-s)(s+1)}\right) \quad [6.9]$$

5. The variance due to SCA effects in the pure PEE population:

$$\sigma^2_{SCA(PEE)} = \frac{1}{64}\left(\frac{4(1-v^{n-1})(v^{n-1}+1)d^2}{(1-v)(v+1)} - \frac{4(1-(uv)^{n-1})a_1 d}{1-uv} - \frac{4(1-(sv)^{n-1})a_2 d}{1-sv} + \frac{(1-u^{n-1})(u^{n-1}+1)a_1^2}{(1-u)(u+1)} + \frac{(1-s^{n-1})(s^{n-1}+1)a_2^2}{(1-s)(s+1)} + \frac{2(1-(su)^{n-1})a_1 a_2}{1-su}\right) \quad [6.10]$$

6. The variance due to GCA effects in the pure PCH population:

$$\sigma^2_{GCA(PCH)} = \frac{1}{32}\left(\frac{(1-u'^{n-1})(u'^{n-1}+1)a_1'^2}{(1-u')(u'+1)} - \frac{2(1-(s'u')^{n-1})a_2'a_1'}{1-s'u'} + \frac{(1-s'^{n-1})(s'^{n-1}+1)a_2'^2}{(1-s')(s'+1)}\right) \quad [6.11]$$

7. The variance due to SCA effects in the pure PCH population:

$$\sigma^2_{SCA(PCH)} = \frac{1}{64}\left(\frac{4(1-v'^{n-1})(v'^{n-1}+1)d'^2}{(1-v')(v'+1)} - \frac{4(1-u'v'^{n-1})a_1'd'}{1-u'v'} - \frac{4(1-s'v'^{n-1})a_2'd'}{1-s'v'} + \frac{(1-u'^{n-1})(u'^{n-1}+1)a_1'^2}{(1-u')(u'+1)} + \frac{(1-s'^{n-1})(s'^{n-1}+1)a_2'^2}{(1-s')(s'+1)} + \frac{2(1-s'u'^{n-1})a_1'a_2'}{1-s'u'}\right) \quad [6.12]$$

8. The covariance between common PEE parents in intraspecific (PEE) and interspecific (PEE×PCH) populations:

$$cov_{GCA(PEE,\,PEE\times PCH)} = \frac{1}{32}\left(-\frac{a(1-(mu)^{n-1})a_1}{1-mu} + \frac{D(1-(uw)^{n-1})a_1}{1-uw} - \frac{(1-(ku)^{n-1})d_1a_1}{1-ku} + \frac{(1-(lu)^{n-1})d_2a_1}{1-lu} + \frac{a(1-(ms)^{n-1})a_2}{1-ms} - \frac{D(1-(sw)^{n-1})a_2}{1-sw} + \frac{(1-(ks)^{n-1})a_2d_1}{1-ks} - \frac{(1-(ls)^{n-1})a_2d_2}{1-ls}\right) \quad [6.13]$$

9. The covariance between common PCH parents in intraspecific (PCH) and interspecific (PEE×PCH) populations:

$$cov_{GCA(PCH,\,PEE\times PCH)} = \frac{1}{32}\left(-\frac{d_1(1-(ku')^{n-1})a_1'}{1-ku'} + \frac{d_2(1-(lu')^{n-1})a_1'}{1-lu'} - \frac{a(1-(mu')^{n-1})a_1'}{1-mu'} + \frac{D(1-(wu')^{n-1})a_1'}{1-wu'} + \frac{d_1(1-(ks')^{n-1})a_2'}{1-ks'} - \frac{d_2(1-(ls')^{n-1})a_2'}{1-ls'} + \frac{a(1-(ms')^{n-1})a_2'}{1-ms'} - \frac{D(1-(ws')^{n-1})a_2'}{1-ws'}\right) \quad [6.14]$$

10. The difference between the genotypic mean of F_1 hybrid and PEE populations:

$$\Delta_{G(F_1\text{-PEE})} = \frac{1}{4}\left(\frac{a(1-m^{n-1})}{1-m} - \frac{2d(1-v^{n-1})}{1-v} + \frac{D(1-w^{n-1})}{1-w} - \frac{(1-u^{n-1})a_1}{1-u} - \frac{(1-s^{n-1})a_2}{1-s} + \frac{(1-k^{n-1})d_1}{1-k} + \frac{(1-l^{n-1})d_2}{1-l}\right) \quad [6.15]$$

11. The difference between the genotypic mean of F_1 hybrid and PCH populations:

$$\Delta_{G(F_1\text{-PCH})} = \frac{1}{4}\left(\frac{a(1-m^{n-1})}{1-m} + \frac{D(1-w^{n-1})}{1-w} + \frac{(1-k^{n-1})d_1}{1-k} + \frac{(1-l^{n-1})d_2}{1-l} - \frac{2d'(1-(v')^{n-1})}{1-v'} - \frac{(1-(u')^{n-1})a'_1}{1-u'} - \frac{(1-(s')^{n-1})a'_2}{1-s'}\right) \quad [6.16]$$

These equations were constructed using Mathematica®: their full derivation is presented in Appendix 19.

6.2.3 Empirical model

The computational intensity of the method required that only two traits, UBVOL (stem volume underbark) and DENS (area-weighted wood density at breast height), were selected for analysis in this chapter. Of the traits assessed in this study, UBVOL and DENS are expected to have the strongest impact on the value of wood produced from genetic improvement programs (Greaves *et al.* 2000). Furthermore, these two traits were expected to provide contrasting modes of genetic control due to their differing types and strengths of inheritance (see Chapter 4). Empirical estimates of the nine covariances and two mean differences represented in the eleven equations (6.6-6.16 above) were obtained from previous analyses, reported in Chapters 3 and 4. However, because the model is based on the relative values of the covariances and mean differences within and between the pure species and hybrid populations, it was necessary to analyse data that were not scaled to account for differences in variances between sites. Bartlett's homogeneity of variance test (Snedecor and Cochran 1983) was applied to the pooled data to check that the assumption of homogeneous variances between sites was reasonable. In the two traits examined, the variances at the two sites were not significantly different (p>0.05), and so it was considered reasonable to pool the data without scaling. The empirical covariances and mean

differences estimated from models described in Chapters 3 and 4, and used as inputs into the current model, are listed in Table 6.7.

Table 6.7 Model inputs: empirical covariances and mean differences estimated using models presented in Chapters 3 and 4

Equation	Empirical quantity	UBVOL	DENS
1	$\sigma^2_{F(PEE\times PCH)}$	0.74977	1.97488
2	$\sigma^2_{M(PEE\times PCH)}$	1.38936	1.63625
3	$\sigma^2_{SCA(PEE\times PCH)}$	1.50327	0.11043
4	$\sigma^2_{GCA(PEE)}$	1.98089	2.95964
5	$\sigma^2_{SCA(PEE)}$	0.31903	0
6	$\sigma^2_{GCA(PCH)}$	1.59324	1.28395
7	$\sigma^2_{SCA(PCH)}$	0.06835	0.06625
8	$COV_{GCA(PEE,PEE\times PCH)}$	0.71939	2.21591
9	$COV_{GCA(PCH,PEE\times PCH)}$	1.23618	1.46785
10	$\Delta_{G(F_1-PEE)}$	6.29590	-3.25211
11	$\Delta_{G(F_1-PCH)}$	0.84231	-0.47603

Note: Empirical values 1-11 correspond to the Equations 6.6-6.16 described in Section 6.2.2.2; UBVOL=underbark stem volume; DENS=area-weighted wood density at breast height.

6.2.4 Solving to obtain estimates of the unknowns

Equating the 11 empirical estimates of covariances and mean genotypic differences (Table 6.7) with their theoretical expectations in Equations 6.6-6.16 allows the equations to be solved simultaneously to obtain estimates of the unknown variables. The unknown variables comprise ten genotypic values at the reference locus (see Table 6.6: a_1, d, a_2, a'_1, d', a'_2, D, d_1, d_2, a), ten proportion coefficients (u, v, s, u', v', s', w, k, l, m) describing the distribution of the genotypic values across loci, and the unknown integer n (the number of loci or linkage groups). Excluding n, this total of 20 unknown variables cannot be solved using only 11 equations, as it is necessary to have the same number, or fewer, unknowns than equations in order to reach a solution. The total number of unknowns to be estimated, excluding the integer n, which can be deduced iteratively, can be reduced to 11 by imposing restrictions on the unknowns based on available information. Because there are numerous ways in

which the unknowns can be restricted, two sets of genetically plausible restrictions were proposed. These will be referred to as Scenarios 1 and 2. The first scenario is analogous to that used by Li and Wu (1996), and assumes that because of the suggested recent common evolutionary origin of PEE and PCH (Schmidtling and Hipkins 2001; Dvorak *et al.* 2000), they share a common recessive allele at each locus. The second scenario relaxes the assumption of common alleles between the two species, allowing for the possibility that the species have completely different alleles at some or all loci, though some restrictions are imposed on the proportion coefficients. The restrictions imposed under each scenario, and a general description of each, are given in Table 6.8.

Table 6.8 Restrictions placed on unknown variables under Scenarios 1 and 2

Scenario	Restrictions	Description
1	$a_2=a'_2=a$ $d=d_2$ $d'=d_1$ $s=s'=m=1$ $v=l$, $v'=k$	Emulates the model of Li and Wu (1996), assuming a total of 3 alleles segregating between the populations at each locus. A recessive allele is common to PEE and PCH populations at all loci, such that both pure species and hybrid populations have the same recessive genotype a_2. The genotypic value of a_2 is assumed constant across loci.
2	$a_2= a'_2$ $u=u'=w$ $v=v'=k=l=m$ $s=s'$	Allows for a total of 4 possible alleles segregating between the populations at each locus, but the genotypic values of homozygous recessive genotypes in the two pure species are set equal. All pure species and hybrid genotypes containing only wild type alleles have common proportion coefficients, as do all genotypes heterozygous for wild type alleles, as do all homozygous recessive genotypes.

In addition to these restrictions, the following constraints were applied to the unknowns to ensure the solutions were within reasonable bounds: $\{n, a_1, d, a_2, a'_1, d', a'_2, D, d_1, d_2, a\} \geq 0$; $a_1 \geq a_2$; $a'_1 \geq a'_2$; $D \geq a$; $0 \leq \{u, v, s, u', v', s', w, k, l, m\} \leq 1$. Solutions for the 11 unknowns in 11 equations were obtained by non-linear optimisation. The program Mathematica® Version 4 (Wolfram Research Inc. 1999) and an add-on program to it, Global Optimization 4.2 (Loehle 2002), were used to search the 11-dimensional parameter space for approximate solutions to the equations. The routine GlobalSearch in Global Optimization 4.2 uses a hill-climbing algorithm to find global minima (Loehle 2002). In order to adequately sample the parameter space and avoid local minima, the routine GlobalSearch was run at 50 randomly-selected starting points, for a fixed value of n (the number of loci). This procedure

was repeated for n=1...12. The accepted solution was that which minimised the function value, being the sum of the absolute values of the residual values for the 11 equations.

6.3 Results

The results of searches for approximate solutions to the equations for traits UBVOL and DENS under Scenarios 1 and 2 using GlobalSearch are presented in Appendix 20; in each instance, the best solutions, being those which minimised the function value and fell within the specified constraints, are indicated in the Mathematica output text.

6.3.1 Scenario 1 parameter estimates

The estimates of the six genotypic values and five proportion coefficients for UBVOL and DENS under Scenario 1 are presented in Table 6.9. The distributions of genotypic values across loci, being functions of the genotypic values and proportion coefficients in Table 6.9, are presented in Figures 6.1 and 6.2.

The results, particularly those for UBVOL, are not genetically plausible, and suggest that the assumptions of Scenario 1 are inappropriate for this dataset. Firstly, in the genotypic value distribution for UBVOL, from the 3rd locus in the series onwards, the value of the assumed common recessive genotype a_2 is in fact greater than the PEE wild type homozygote value a_1. At five other loci, a_2 is greater than all other genotypes except D, the single genotype which is exclusive to the hybrid population under this Scenario. The assumption of a common recessive genotype with constant genotypic value across loci in the pure species and hybrid population may therefore not be appropriate for this dataset. Additionally, the large overdominance displayed by the genotype D in UBVOL at loci 3-10 may in fact simply be the combined result of better parent heterosis in UBVOL (represented in Equation 6.16 above), and the assumption, under this Scenario, that D is the only genotype unique to the hybrid population.

Because of the apparent limitations of Scenario 1, it was considered necessary to relax the assumption of a common allele between the species at each locus, by assuming totally different allelic systems between the species. This assumption has previously been incorporated by Wu and Li (2000), though slightly different restrictions on the

unknown variables are used in this study due to the lower number of available equations. Allele frequencies remain fixed at 0.5.

Table 6.9 Genotypic values at the reference locus and proportion coefficients for Scenario 1, traits UBVOL and DENS

	UBVOL n=10 loci				DENS n=6 loci			
genotype	genotypic value		proportion coefficient		genotypic value		proportion coefficient	
PEE genotypes								
AA	a_1	8.06	u	0.232	a_1	7.69	u	0.761
Aa	d	6.65	v	0.472	d	5.07	v	0.644
aa	a_2	1.61	s	1*	a_2	0.89	s	1*
PCH genotypes								
$A'A'$	a'_1	7.05	u'	0.677	a'_1	6.77	u'	0.672
$A'a$	d'	6.31	v'	0.655	d'	4.67	v'	0.607
aa	a_2	1.61	s	1*	a_2	0.89	s	1*
PEE×PCH F_1 hybrid genotypes								
$A'A$	D	5.20	w	0.871	D	7.50	w	0.504
Aa	d	6.65	v	0.472	d	5.07	v	0.644
$A'a$	d'	6.31	v'	0.655	d'	4.67	v'	0.607
aa	a_2	1.61	s	1*	a_2	0.89	s	1*

Note: genotypic values are those at the first locus in the geometric series (the reference locus); in Scenario 1 the following restrictions are imposed, under the assumption of a common recessive allele between the PEE and PCH populations at each locus: $a_2=a'_2=a$, $s=s'=m=1$, $d'=d_1$, $d=d_2$; * denotes fixed values.

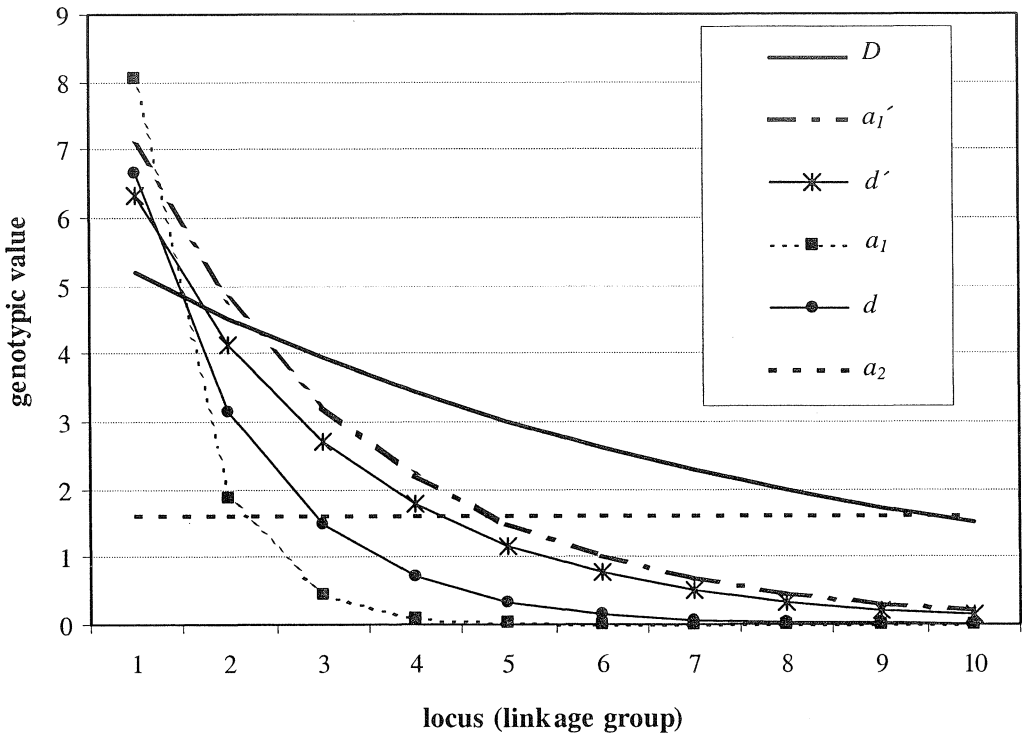

Figure 6.1 Individual-locus genotypic values at n=10 loci for UBVOL (underbark stem volume) under Scenario 1

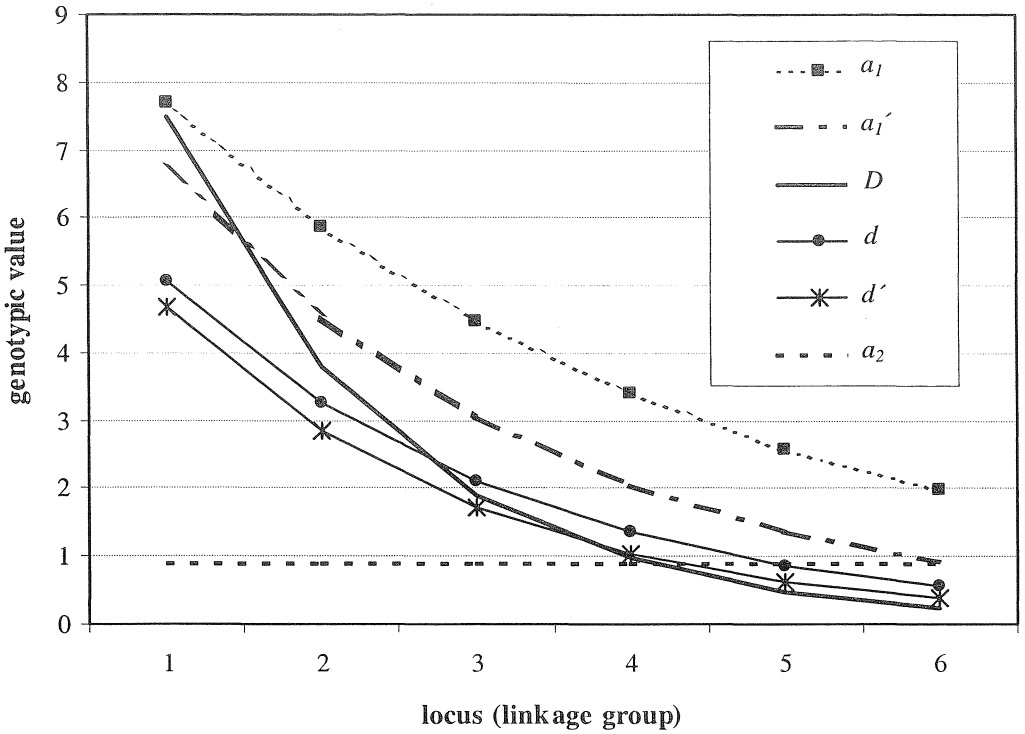

Figure 6.2 Individual-locus genotypic values at n=6 loci for DENS (area-weighted breast height wood density) under Scenario 1

6.3.2 Scenario 2 parameter estimates

The estimated genotypic values at the reference locus and at the other loci, and the estimated proportion coefficients, for UBVOL and DENS under Scenario 2 are presented in Table 6.2 and

Table 6.3, respectively. The distributions of UBVOL and DENS genotypic values across loci are plotted in Figure 6.3 and Figure 6.5, respectively. This set of solutions is genetically plausible: in both traits, the recessive genotype values a_2 and a_2' (set equal), and the double recessive hybrid genotype value a, are consistently lower than the double wild type genotype values, at all loci. The results for UBVOL and DENS will be examined separately in more detail.

6.3.2.1 Underbark stem volume

As visible in Figure 6.3, the superior genotype at all loci is the wild type homozygote A´A´ (genotypic value a_1') which occurs in pure PCH. The hybrid genotypes d_1 and d_2 (set equal) and D are also of high value, though inferior to a_1'. This suggests that although the hybrid demonstrates better parent heterosis overall (See Tables 3.5 and 3.6), none of the heterozygous hybrid genotypes themselves outperform homozygous segregants of PCH wild type alleles, A´A´ (a_1').

The primary question of interest in this study is the relative values of the various pure species and hybrid genotypes, because hybrid breeding strategy aims to increase the frequency of the most favourable genotypes in the deployment population. The area under each of the distributions plotted in Figure 6.3 provides a measure of the total, or cumulative, genotypic value of each genotype across all loci. An approximation of the integral of each curve can be obtained by summing the genotypic values across loci, for each of a_1, d, ...a. A comparison of these pooled genotypic values across loci, for UBVOL under Scenario 2, is presented in Figure 6.4. The higher genotypic values of PCH than PEE genotypes reflect the relative growth rates of these taxa. The hybrid genotypes have comparable overall mean performance to those of PCH, but are less variable than the pure species genotypes, reflecting the lack of homozygotes in the F_1 population. The hybrid genotypes d_1 and d_2 both contain a wild type allele from one species and a recessive allele from the other. Though inference is limited because they are set equal by necessity to solve the equations, their intermediate value between PEE and PCH wild type homozygous genotypes suggest that the wild type genotypes from one species are almost completely dominant over the recessive alleles from the other species. This suggests that dominance gene action is important in controlling growth in the hybrid, although it is not so important in the pure species populations. Nevertheless, the hybrid genotypes do not display overdominance over the better homozygote from the better parent (PCH).

The distributions of genotypic values across loci also provide some basic information about the relative influence of loci on genetic variation. Variation among genotypic values is highest at the reference locus, though it is also substantial at the remaining loci, suggesting that UBVOL is under polygenic control, with loci affecting the trait scattered across 6 chromosome pairs.

Table 6.10 Genotypic values at the reference locus, proportion coefficients, and genotypic values at n=6 loci for UBVOL under Scenario 2

genotype	genotypic value	locus 1	2	3	4	5	6	proportion coefficient	
PEE genotypes									
AA	a_1	15.54	9.72	6.08	3.81	2.38	1.49	u	0.626
Aa	d	11.69	6.81	3.97	2.31	1.35	0.79	v	0.583
aa	a_2	11.47	6.12	3.26	1.74	0.93	0.49	s	0.533
PCH genotypes									
A´A´	a'_1	17.32	10.84	6.78	4.24	2.65	1.66	u'	0.626
A´a´	d'	15.46	9.01	5.25	3.06	1.78	1.04	v'	0.583
a´a´	a'_2	11.47	6.12	3.26	1.74	0.93	0.49	s'	0.533
PEE×PCH F_1 hybrid genotypes									
A´A	D	14.55	9.10	5.70	3.56	2.23	1.40	w	0.626
A´a	d_1	17.21	10.03	5.85	3.41	1.98	1.16	k	0.583
Aa´	d_2	17.21	10.03	5.85	3.41	1.98	1.16	l	0.583
a´a	a	11.40	6.64	3.87	2.26	1.31	0.77	m	0.583

Note: locus 1 is the "reference locus"; the following restrictions are imposed on genotypic values under Scenario 2: $a_2=a'_2$, $d_1=d_2$; the restrictions: $u=u'=w$, $v=v'=k=l=m$ and $s=s'$ are imposed on the proportion coefficients. Individual-locus genotypic values are derived as per Table 6.6.

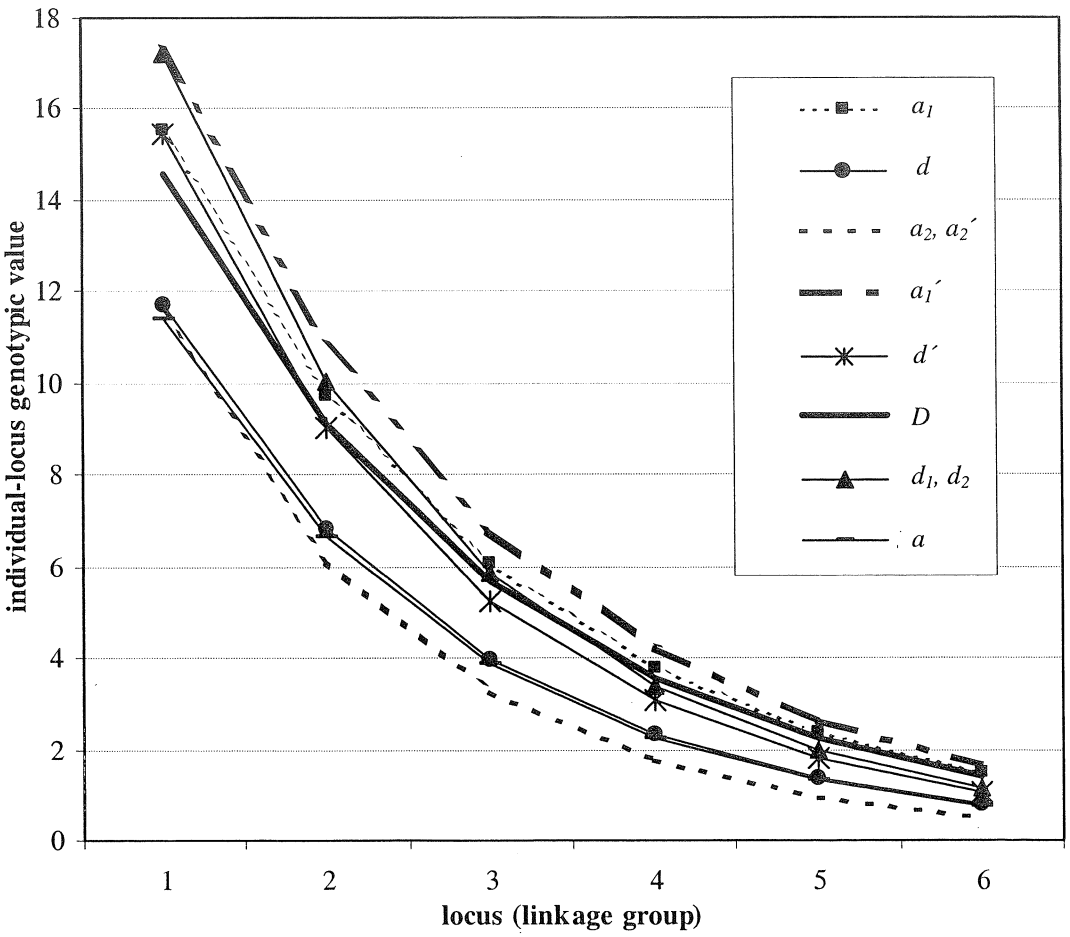

Figure 6.3 Individual-locus genotypic values at n=6 loci for UBVOL under Scenario 2

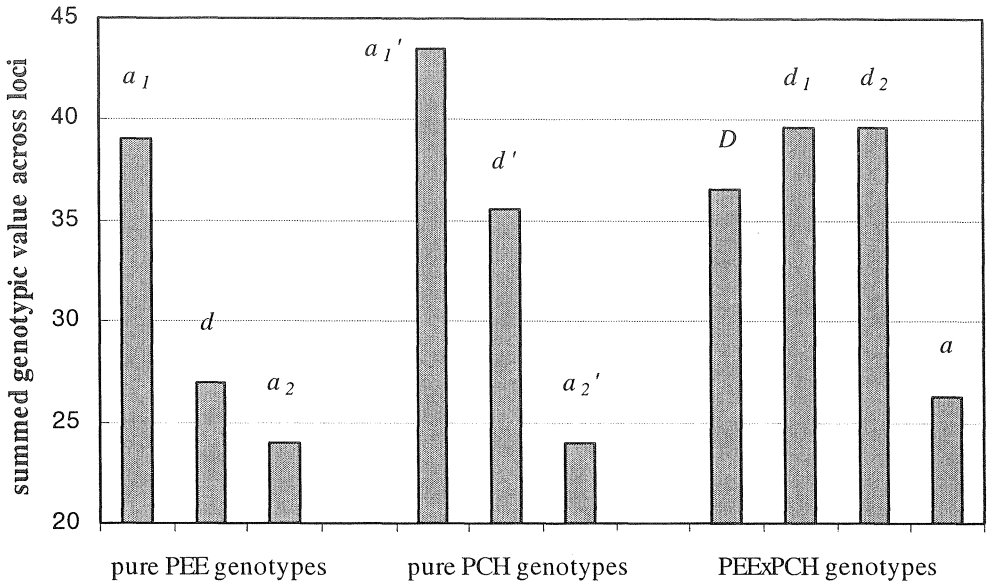

Figure 6.4 Integral of genotypic value distributions for UBVOL estimated under Scenario 2

6.3.2.2 Wood density

The distributions of genotypic values across loci for DENS are plotted in Figure 6.5. At all loci, the PEE wild type homozygote genotype value a_1 is superior to all other genotypes. The homozygous recessive genotypes are consistently the lowest performing, and the heterozygous (wild type/recessive) genotypes are generally intermediate between the homozygous genotypes, indicating strongly additive gene action at all loci. Changes in rank among the genotypes at different loci are few and slight.

The pooled genotypic values across loci for DENS presented in Figure 6.6 suggest a largely additive pattern of inheritance. The hybrid heterozygote value D is intermediate between the values of its respective homozygotes a_1 and a_1', as are the hybrid heterozygotes d_1 and d_2 between their respective homozygotes a_1 and a_2', and a_1' and a_2, respectively. No hybrid genotype outperforms the PEE genotype AA (a_1).

Dominance gene action in wood density in the pure species, indicated in Figure 6.6, is slightly higher than might be expected based on the largely additive model of inheritance for DENS suggested in Chapter 4. However, as in UBVOL (Figure 6.4), additive gene action accounts for a far greater proportion of the variation among genotypes than does dominance gene action.

The distribution of genotypic values presented in Figure 6.5 suggests that the various loci contributing to DENS are more likely to have unequal effects than are the loci contributing to UBVOL (Figure 6.3). This result suggests that DENS is more likely to have a major gene than UBVOL, although in common with UBVOL, it appears to be predominantly under polygenic control.

6.3.3 Commentary on interpretation of the results

The meaning of the individual-locus parameters needs to be clarified in order to prevent mis-interpretation. This model seeks only to uncover the genetic causes of the *differences* between and within the populations - not to measure the degree of genetic contribution to population or individual performance *per se*. A genotypic value of any given genotype at a locus is therefore not informative in itself - it is only informative relative to the other genotypic values at that locus and at other loci. The genotypic values do not indicate the contribution of a genotype at a locus to an individual's measurement in a particular trait. They indicate only the relative effects of the various homozygous and heterozygous genotypes. This information can be used to infer the type of gene action underlying genetically determined differences within and among the pure species and hybrid populations. It must also be emphasized that loci with high average genotypic values are not necessarily what would be considered 'major QTL'. Major QTL, or major genes (*eg* Mackay 1996), are loci at which large *differences* exist among the genotypic values of the genotypes present. The current model allows for the detection of major genes or polygenic control, because the different proportion coefficients for different genotypes allow the genotypic values to diverge or converge across loci (*eg* Figures 6.3 and 6.5).

Table 6.11 Genotypic values at the reference locus, proportion coefficients, and genotypic values at n=7 loci for DENS under Scenario 2

genotype	genotypic value	locus 1	2	3	4	5	6	7	proportion coefficient
PEE genotypes									
AA	a_1	19.49	11.93	7.31	4.48	2.74	1.68	1.03	u 0.612
Aa	d	16.26	10.08	6.25	3.87	2.40	1.49	0.92	v 0.620
aa	a_2	11.70	7.34	4.61	2.89	1.81	1.14	0.71	s 0.628
PCH genotypes									
A´A´	a'_1	16.63	10.18	6.24	3.82	2.34	1.43	0.88	u' 0.612
A´a´	d'	15.48	9.60	5.95	3.69	2.29	1.42	0.88	v' 0.620
a´a´	a'_2	11.70	7.34	4.61	2.89	1.81	1.14	0.71	s' 0.628
PEE×PCH F_1 hybrid genotypes									
A´A	D	17.36	10.63	6.51	3.99	2.44	1.49	0.92	w 0.612
A´a	d_1	15.14	9.39	5.82	3.61	2.24	1.39	0.86	k 0.620
Aa´	d_2	15.14	9.39	5.82	3.61	2.24	1.39	0.86	l 0.620
a´a	a	11.11	6.88	4.27	2.65	1.64	1.02	0.63	m 0.620

Note: locus 1 is the "reference locus"; the following restrictions are imposed on genotypic values under Scenario 2: $a_2=a'_2$, $d_1=d_2$; the restrictions: $u=u'=w$, $v=v'=k=l=m$ and $s=s'$ were imposed on the proportion coefficients. Individual-locus genotypic values are derived as per Table 6.6.

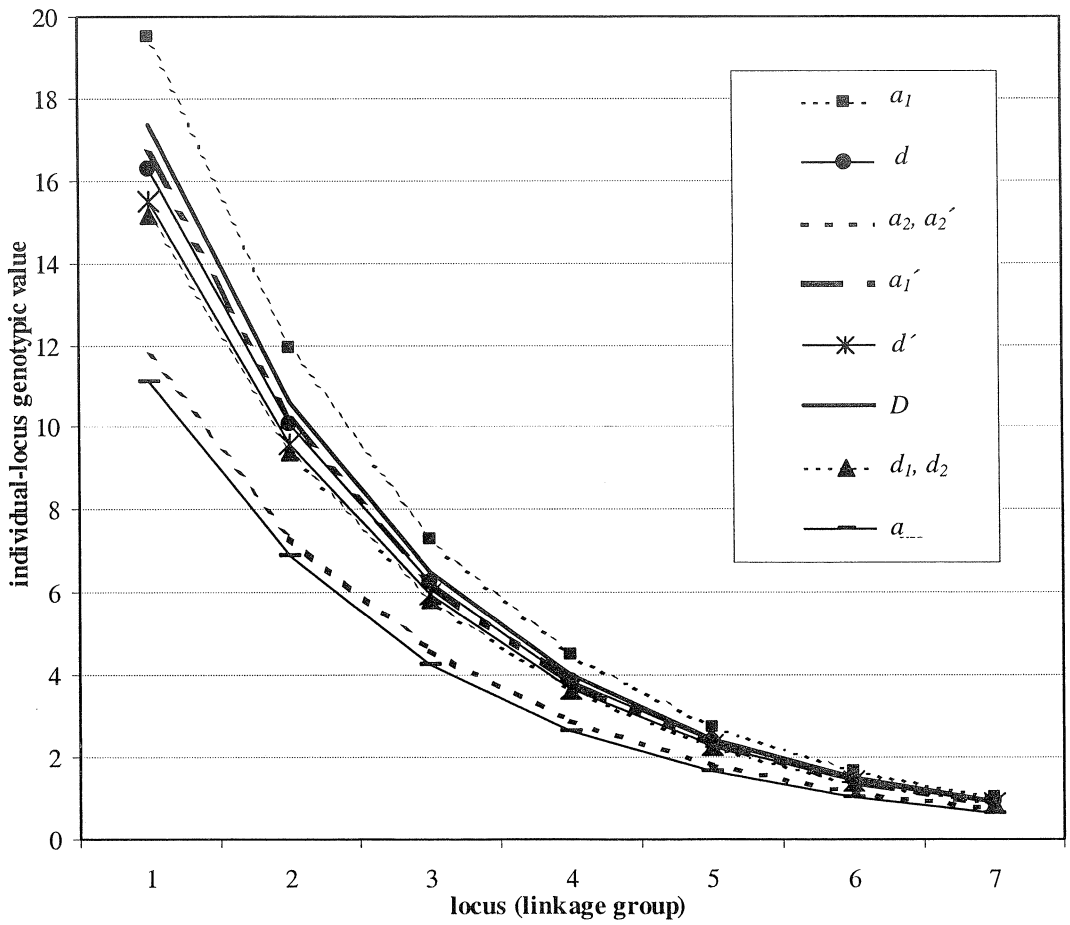

Figure 6.5 Individual-locus genotypic values at n=7 loci for DENS under Scenario 2

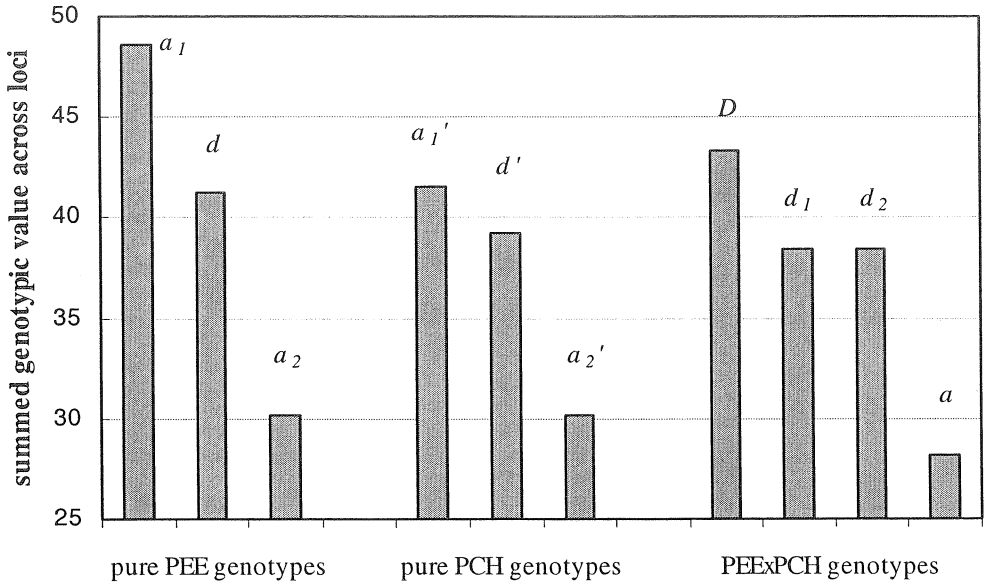

Figure 6.6 Integral of genotypic value distributions for DENS estimated under Scenario 2

6.4 Discussion

6.4.1 Assumptions of the model and interpretation of the results

This study is the first application of the model developed by Li and Wu (1996) to a complete dataset involving progeny of both parental pure species as well as their hybrid. However, because the number of equations and the number of unknown parameters to be estimated was the same, no degrees of freedom were available to estimate the variance of the estimates of the unknowns; the current results can therefore be considered only as preliminary. A planned future study using a maximum-likelihood approach to fit the model to the dataset directly (*eg* Wu *et al.* 2001) will allow estimation of the variance of the genotypic value estimates, accounting for the sampling error incurred in estimating the empirical covariances and mean differences from the data.

The assumptions of this model were restrictive, but necessary to permit characterisation of the pure species and parental populations using available data. The Scenario 1 assumption of a common recessive allele between the species at each locus appears to be unrealistic, as relaxation of this assumption in Scenario 2 produced a more genetically plausible result. However, the assumption of fixed allele frequencies at 0.5 in both PEE and PCH, applied in both scenarios, is also likely to be

unrealistic. Variable allele frequency could easily be incorporated into the model however, if additional independent empirical parameters could be estimated from this dataset. Ideally, it would be possible to account for multiple alleles at differing frequencies in each pure species population, and multilocus epistasis. The extended model of Wu and Li (1999) does this, but requires data from sophisticated experiments including clonal replication of full-sib families. The current results should be interpreted as a preliminary examination of gene action in the PEE×PCH hybrid using the best data available.

Although the assumption of no epistasis is probably unrealistic, this assumption is necessary in most studies using both molecular (*eg* Xiao *et al.* 1995) and quantitative (Kerr *et al.* 2000; Pong-Wong *et al.* 1998) genetic approaches due to the statistical difficulty of measuring interactions among numerous loci. However, simulation studies have demonstrated that when analysis of variance is applied, even where epistatic (additive×additive, additive×dominance, dominance×dominance) effects are present, and fitted into the model, much of the variance due to epistatic effects is in fact partitioned into the main effects (*eg* Lush 1945, Cheverud and Routman 1995). The additive and dominance effects estimated in this model are therefore thought to also include additive-related epistatic and dominance-related epistatic effects. As discussed in Section 2.4, for the purpose of breeding strategy design, the most important distinction is that between additive-related gene effects and dominance-related gene effects, and so the formal assumption of no epistasis in the current model is considered unlikely to result in misguided conclusions.

Abnormal chromosome behaviour and high phenotypic variability often found in F_1 interspecific hybrid tree populations (Potts and Dungey 2001; Griffin *et al.* 2000; Volker 1995) suggest that epistatic effects may be important in some hybrid populations. In such cases, the effects of individual-locus genotypes may have little influence on hybrid performance (Carson *et al.* 1996), and the assumption that individual locus genotypes act the same in pure species as in hybrid combination is unlikely to be realistic. In these cases it is probably not reasonable to apply models such as the one used in this study, due to the difficulty of incorporating realistic assumptions. The lower seed set of PEE×PCH crosses than PEE crosses (Nikles and Robinson 1989) indicates some type of incompatibility; however, this may be due to non-genetic factors such as issues associated with pollination and fertilisation, and so

does not in itself indicate segregation distortion. Evidence from a recent genomic study in PEE×PCH (Williams *et al.* 2002) showed no change in chromosome number or size, and suggested no change in the rate of segregation distortion, in the hybrid relative to the pure species parents. Furthermore, the results of this thesis indicate that in wood density traits, alleles behave similarly in interspecific as in intraspecific combination. Evidence of this was found in the similar strength of inheritance in pure species and hybrid populations (Table 4.4, Table 4.5), genetic correlations between pure species and hybrid populations approaching unity (Table 4.10 and 4.11), and in most cases, similarity of F_1 hybrid and mid-parent performance (Chapter 3). These results support the assumption of the genetic model fitted in this chapter, that alleles segregate freely between the pure species and PEE×PCH hybrid populations at a common set of loci.

6.4.2 Gene action

The results suggest that both stem volume and wood density are influenced predominantly by additive gene action, with some contribution from partial dominance. Dominance due to interspecific gene combinations makes a substantial contribution to heterosis in stem volume, but does not contribute to hybrid performance in wood density. Overdominance does not appear to occur at any locus in either trait in the hybrid population, and the best performing genotype for stem volume amongst the three populations is the wild type homozygote in the PCH population. The best performing genotype for wood density is the wild type homozygote in the PEE population. According to these results, heterosis in stem volume is not due to any particular outstanding gene combination in the hybrid, but is due to a moderate degree of partial dominance exhibited in all allelic combinations, at most loci. Hybrid wood density is genetically determined by additive contributions from PEE and PCH. Importantly from a theoretical perspective however, the estimates of additive and dominance gene action in this study are likely to be contributed to by additive-related and dominance-related epistatic gene action, respectively. The effect of this on the implications for practical breeding is unclear, but is expected to be minimal (eg Crow 1998, 1999).

The types of gene action suggested by the results of this finite-locus model corroborate results from conventional quantitative genetic analyses in previous

chapters. This is not surprising given that the model is based on the empirical data from these analyses, but the correspondence is worth noting. In UBVOL, dominance gene action makes a substantial contribution to hybrid performance, yet little contribution to pure species performance. This is consistent with the Chapter 4 result showing a greater proportion of SCA variance in the hybrid population than in the pure species populations, given that SCA variance is likely to result from dominance gene action. Family heritabilities of UBVOL and other growth traits in PEE×PCH were higher for parents of the better performing species, PCH, than for parents of the poorer performing species, PEE (see Table 4.4). This may result from the substantial contribution to heterosis in growth traits from dominant alleles donated by PCH, as indicated by the individual-locus model. These dominance effects cause progeny to more closely resemble the higher-performing parent (PCH), obscuring the effects of alleles contributed by the lower-performing parent (PEE). This may explain the higher heritability of PCH-parental effects than PEE-parental effects in the PEE×PCH population, even though the reverse was true in the pure species populations. Likewise, the stem volume performance of PCH parents in intraspecific crosses was more strongly correlated with their performance in interspecific crosses than was the case for PEE parents - a result that would also be expected if PCH alleles displayed dominance over PEE alleles in stem volume. The above evidence for dominance interactions in the hybrid is further supported by the observed moderate to strong SCA effects in growth traits in the hybrid population (see Table 4.6), and by the results of the individual-locus model indicating partial dominance caused by the PCH wild type allele (see Figure 6.4).

In wood density, the underlying mode of gene action, at least in the hybrid, appears to be almost completely additive (see Figure 6.6). This result is well supported by the results from previous chapters. In wood density traits in the hybrid, the family heritability of PEE and PCH parents were similar, and SCA variance was negligible. Additionally, the pure-hybrid genetic correlation was high and similar in PEE and PCH parents, and, at least in wood density component traits, the hybrid consistently displayed intermediate performance between the parents. These results from previous chapters form a considerable body of evidence to support the results of the individual-locus genetic model fitted in the current chapter.

The high heritability, negligible SCA effects, and negligible dominance gene action in wood density, and low heritability, larger SCA effects, and greater importance of dominance gene action in growth characteristics reflect trends found in these traits more generally in pure species populations of various taxa, and may reflect the different evolutionary processes to which these traits have been subject. The process of domestication has occurred comparatively recently for industrial tree species, and the genetic architecture of traits in breeding populations is unlikely to have changed much from natural populations. Theoretical evidence suggests that in traits closely related to fitness, such as growth rate, natural selection will tend to reduce additive genetic effects due to the Bulmer effect (see Bulmer 1985 ch.9), and accumulate beneficial dominant genes (Rieseberg and Carney 1998). In selectively neutral traits such as wood density however, additive genetic effects are likely to be larger, and dominance gene action less common. These theoretical expectations are empirically well evidenced in a variety of taxa and in both intraspecific and inter-specific cross populations (*eg* Cornelius 1994; Levin 1978). At the intraspecific level, they explain the high heritability of wood traits but low heritability and increased non-additive genetic variance of growth characters found in this study (see Table 4.3). At the interspecific level, they provide an explanation for why heterosis is greater (Tables 3.5 and 3.6), pure-hybrid correlations are lower (Tables 4.11 and 4.12), and dominance gene action is greater, for growth traits than for wood characteristics.

6.4.3 Number of genetic factors and distribution of factor effects

The results suggest that the genetic control of both stem volume and wood density involves a strong polygenic component. This is consistent with the results of a recent molecular genetic study in a PEE×PCH full-sib family, whose PCH parent was also used in EXP674 (Shepherd *et al.* 2003). In the current study, however, the pattern of distributions of genotypic values across loci differed for stem volume and wood density. While genetic variance in stem volume was reasonably evenly distributed across loci, the distribution was less even in wood density, suggesting the possible existence of one or more major genes for wood density. It is generally true of QTL mapping studies in tree species (reviewed by van Buijtenen 2001) that major genes are more commonly found in wood density than in growth traits (*eg* Kumar *et al.* 2000, Grattapaglia *et al.* 1996, Sewell *et al.* 2000). However, in PEE×PCH, Shepherd *et al.* (2003) found no QTL with very large effect for any trait, and putative QTL for

individual-ring widths explained a greater proportion of phenotypic variation in those traits than did putative QTL for individual-ring densities. However, Shepherd *et al.* sampled a relatively small progeny population (n=133 individuals), within a single F_1 hybrid full-sib family. It is possible that the single PEE and single PCH parent sampled in this study from the respective breeding populations may be either homozygous, or not carry alleles of large effect, at possible major gene loci. It may therefore be useful to search for QTL affecting wood density in other, larger populations of PEE×PCH.

Major genes, or QTL of large effect, are worthy of further investigation as they have the potential to produce large and rapid gains in hybrid breeding, and can be exploited using both conventional breeding methods and marker-assisted breeding. Simulation (*eg* Owen *et al.* 2000) and empirical studies (Owen *et al.* 1991, Owen 1996) indicate the importance of high selection intensity in order to bring about allele frequency changes at major gene loci, whereas lower selection intensity is likely to only make changes in allele frequency at polygenic loci. One way in which breeding programs can respond to the presence of a major gene is therefore to develop a nucleus breeding population or sub-population in which high selection intensity is applied to the major gene trait. In the case of PEE×PCH, rapid, short-term genetic gains in wood density would be highly desirable to improve juvenile wood density for clonal deployment over a 20-year rotation. Major genes can be more accurately targeted using marker-assisted selection (MAS; Lande and Thompson 1990; Lande 1992). Kerr *et al.* (1996) predicted that MAS could make an extra 25% genetic gain over conventional breeding where a single QTL was responsible for 20% of the genetic variance. However, genetic mapping is expensive, and the probability of success is usually not known until most of the investment has been made. Estimated distributions of QTL effects using quantitative genetic methods, such as applied in this study, may be useful in directing genetic mapping studies towards taxa and traits offering the highest probability of success for these technologies. Other quantitative genetic methods such as segregation analyses (*eg* Zeng *et al.* 1999) may further be able to identify pedigrees, parents or families segregating for major genes. Only limited interpretation of the results from the genetic model fitted in this study is possible, because the method used could not provide error estimates for the parameters. The working hypothesis that one or more major genes for wood density exist in this

population will be further tested using a maximum likelihood approach in a re-analysis of this data now in progress.

6.4.4 Implications of gene action for breeding strategy in PEE×PCH

The primary importance of additive gene action in both stem volume and wood density in the PEE×PCH hybrid and parental species suggests that genetic gains in PEE×PCH performance can be accumulated most efficiently through selection for alleles with strong additive effects. This can be achieved using a variety of breeding strategies. Half-sib or full-sib reciprocal recurrent selection (RRS) and recurrent selection for general combining ability (RSGCA) are the two most common conventional breeding strategies in hybrid crops and trees (see Section 2.2 for a full description). A third option is "composite" (COMP) hybrid breeding strategies, which are based on combined family and within-family selection using the hybrid itself as a base population, with the aim of creating genetically improved advanced generation hybrids for further breeding and deployment. Though gaining increasing popularity in livestock breeding (*eg* Bourdon 1999, Kinghorn 2000), COMP strategies have not traditionally been considered seriously by tree breeders (Dieters *et al.* 1995c). Of the above three strategy types, RRS can be used to select for both additive and non-additive gene action in the hybrid population. RSGCA and COMP are suited to select primarily for alleles that act additively and similarly in pure species and hybrid populations. The relative merits of these strategies will be discussed with respect to the genetic basis of variation in growth and wood density traits in the PEE×PCH hybrid and parental pure species populations, and practical considerations.

The primary importance of additive gene action and secondary importance of dominance gene action in UBVOL and DENS suggests that RRS may not be necessary in the PEE×PCH hybrid. Comstock *et al.* (1949) demonstrated using single-locus theory that where heterosis is due to partial dominance, rather than overdominance, the maximum genetic gains possible from pure line selection (PLS) and reciprocal recurrent selection (RRS) are equivalent. Given the much higher cost and longer breeding cycle interval of RRS, the current results therefore suggest that PLS, analogous to recurrent selection for General Combining Ability (RSGCA), will be more efficient than RRS for PEE×PCH improvement. This result is supported by the much higher selection efficiency in terms of genetic gain per year for both growth

and wood density traits from RSGCA than from half-sib RRS, reported and discussed in Chapter 4.

The value of RSGCA as a lower-cost substitute for RRS is additionally supported by empirical results in maize hybrids. A long-term selection experiment in maize intraspecific hybrids (Moll *et al.* 1978) realised comparable gains per generation from PLS and RRS over 8 generations of selection. This result was achieved despite strong heterosis in the hybrid, and only moderate pure variety-hybrid correlations of 0.63 and 0.72 in the first generation (Moll and Stuber 1971). In other maize populations, Martin and Russell (1984) similarly reported large gains in hybrid performance after several cycles of PLS. These results are surprising in view of the strong and much-studied influence of dominance on maize hybrid performance (*eg* Hallauer and Miranda 1988; Stuber *et al.* 1992). Most importantly, they suggest that it is possible to achieve similar results by exploiting different types of gene action in the hybrid population. In forest tree breeding populations, where additive genetic variation is typically far greater than in maize, the potential for exploiting additive effects is likely to be even greater.

Where gene action is mainly additive in the hybrid, selection in the pure species to improve hybrid population performance (RSGCA) effectively amounts to indirect selection (Namkoong 1979, p.103). This approach is unlikely to be as efficient as direct selection for the traits of interest, in the population of interest. Where genes act additively, it should theoretically be most efficient to select forwards in the F_1 population, under a COMP breeding strategy, achieving genetic gain through the accumulation of additive genetic and additive-related epistatic effects in an advanced generation hybrid (F_2, F_3...F_n) population.

6.4.4.1 Composite breeding: theoretical issues

Two common theoretical objections to advanced generation hybridisation are the possibilities of: (1) gains made through selection being eroded by the reduction in heterozygosity, and (2) segregation resulting in highly variable populations unsuitable for seedling-based deployment. At least in the two most economically important traits, the erosion of genetic gain seems unlikely in PEE×PCH composites due to the lack of observed overdominance, and the largely additive mode of inheritance (see Figure 6.4, Figure 6.6). Segregation may be detrimental, for seedling deployment, or

useful, if it can be exploited through clonal forestry. Though segregation is expected to be of low importance in most tree populations according to theoretical and empirical studies (reviewed by Rieseberg *et al.* 1999), the ongoing clonal deployment program in PEE×PCH could be used to propagate any outstanding segregants that may arise. The maintained or improved mean performance and similar phenotypic variance in unselected outcrossed F_2 hybrids relative to the (unrelated) F_1 hybrid population reported in Chapter 3 provides preliminary evidence that advanced generation hybridisation will not adversely affect population mean or variance in PEE×PCH, allowing for both steady recurrent gains from forward selection, and the option of seedling- or propagule-based deployment. This conclusion is also supported by the review of relevant theoretical genetic issues in Section 2.4. However, it is necessary to add the caveats that certain traits not examined in this study may be affected by segregation, and that where segregation occurs in two or more genetically independent traits, the frequency of 'normal' trees (non-segregants) declines at an exponential rate with increasing number of traits and with the proportion of "non-normal" segregants in each trait. Nevertheless these are not expected to present serious issues for PEE×PCH in Queensland.

Observations of severe hybrid breakdown in crops (*eg* Morris *et al.* 1999) and trees (*eg* Varghese *et al.* 2000; Brune and Zobel 1981) have often resulted from inbreeding (reviewed in Section 2.1), though the results have sometimes been erroneously interpreted as evidence against advanced generation hybridisation *per se*. Where outcrossing and even mild selection have been applied in advanced generation hybrids, hybrid performance has often been improved or maintained (*eg* Hyun 1974, Paques 2000, Paques 1989, Powell and Nikles 1996a in conifers; Grant 1966, Hallauer and Miranda 1988, p. 364, Lambert 1995, in crops; Shrestha 1996, Kinghorn 2000 in livestock; Robertson 1955). Based on the results of the current study, previous studies in the PEE×PCH hybrid and in other conifers, it is proposed that a regular pure species breeding strategy applied to UBVOL and DENS in a PEE×PCH hybrid base population, with the usual controls on inbreeding, will result in steady, economically valuable genetic gains.

The statement of Griffin *et al.* (2000) that "it is more likely that optimal genotypes will lie in more complex advanced generation and backcross combinations" is supported by evidence from evolutionary studies. Results from studies of population

variation, using a wide variety of investigative methods, in plants (reviewed by Rieseberg and Carney 1998; also see Stebbins and Daly 1961; Cruzan and Arnold 1993, 1994; Rieseberg *et al.* 1999), trees (Saylor and Smith 1966; Ledig 1986; Potts and Reid 1985) and animals (reviewed by Allendorf and Leary 1986; also by Mitton and Grant 1984; Ayala 1965), provide evidence for the contribution of hybridisation to microevolutionary processes in these taxa. Hybridisation is thought to have contributed to the evolution of a large proportion of species in both *Eucalyptus* (Blakely 1955 and Pryor 1957) and in *Pinus* (Saylor and Smith 1966). Evidence that currently existing species and/or natural subpopulations evolved, at least in part, from hybrid populations (see Arnold 1992 for a comprehensive review including nearly 200 research contributions) suggests strong potential for generating useful genotypes from hybrid populations using targeted artificial selection.

6.4.4.2 Composite breeding: practical advantages and potential issues

Hybrid improvement strategies based on advanced generation hybridisation, such as COMP breeding strategies, have several key advantages. The first is increased efficiency because only one breeding population is maintained, while RSGCA requires two breeding populations (one in each pure species), and RRS requires this in addition to an F_1 progeny population for progeny testing. A second advantage is the reduction in rotation length: while a breeding cycle of RRS may take up to 20 years in PEE×PCH, and RSGCA may take 10-12 years (Shelbourne 1993), a breeding cycle of COMP could be completed within around 8 years (though the first generation will take longer because of the need to produce many F_1 hybrid crosses). The reduction in cycle length is due to the faster growth, greater fecundity and flowering precocity, and ease of controlled pollination in the hybrid. A third and important advantage of COMP is that it allows direct selection in the population of interest on the sites of interest, whereas conventional strategies rely on indirect selection in related populations, which is unlikely to be as efficient (Namkoong *et al.* 1988). A fourth advantage is the increased range of deployment options possible in advanced generation hybrids. The fecundity and flowering precocity of the PEE×PCH hybrid can be used to provide cheap, seed-based deployment (Nikles 2000). The similar mean and phenotypic variance of the F_2 hybrid population to the F_1 hybrid and pure species populations both in Chapter 3 and in Harding *et al.* (1996) indicate that seedling forests of advanced generation PEE×PCH hybrids will have acceptable qualities for plantation forestry. Additionally, the clonal forestry program currently

operational in PEE×PCH, and emerging technologies such as embryogenesis, can fully capitalise on possible transgressive segregation in advanced generation hybrids. A fifth advantage of COMP breeding strategies is flexibility. A variety of breeding methods emphasising recombination and segregation, such as backcrossing, inbred lines, and marker-assisted selection for favourable homozygotes, could be used in a composite hybrid PEE×PCH population to generate individuals combining PEE-like wood density with PCH-like growth characteristics, for clonal propagation. The low and non-significant genetic correlation between growth traits and wood density in the PEE×PCH F_1 hybrid (Chapter 4) suggests that segregants incorporating both faster growth and improved wood quality will be attainable. A caveat is that genetic correlations estimated in the F_1 are biased by linkage disequilibrium and so may change as it dissipates. Marker-assisted selection could be used to maximum effect to identify favourable homozygous segregants in large elite families made possible by high seed yields in advanced generation PEE×PCH hybrids (Dieters and Nikles 1997).

An additional advantage worth noting is that COMP allows for a broad genetic base to be maintained in the breeding population, because gains are made by combined family and within-family selection. This is a preferable approach to that necessary in RRS, in which complete reliance on backward selection of parents in separate subpopulations can result in severe narrowing of the base population (Labate *et al.* 1999; Shelbourne 2000). Composite breeding also allows the possibility of infusing additional populations, such as improved pure species, or other species or varieties, at any time.

The most serious constraint to implementing COMP in favour of RSGCA will be the expense and time needed to create a sufficiently large number of unrelated F_1 hybrid families to form a base population for breeding. As in pure species breeding, a broad base population is necessary to maintain heterozygosity and avoid the detrimental effects of inbreeding on vigour (*eg* Nikles *et al.* 1999). Though the Queensland breeding program has ample numbers of PEE and PCH parents, this may be an issue in hybrid breeding programs where intensive backward selection using strategies such as RRS has substantially reduced the genetic base. The expense of developing an F_1 base population is likely to be compensated for in the short to medium term by the savings from maintaining only a single breeding population. Additionally, while the

F_1 base population is being established, the high r_{ph} estimates in this study indicate that genetic gain can be made by selecting superior pure species parents.

A second potential issue for COMP breeding strategies is the biasing effect of linkage disequilibrium on breeding values estimated in early generations of the hybrid composite (Namkoong 1979). Aside from the possible use of inbred subpopulations to create transgressive segregants, emphasis should be placed on outcrossing, to avoid detrimental effects of segregating recessive homozygotes, and recombination, to help restore linkage equilibrium. A useful strategy in PEE×PCH may be to place emphasis on selection for wood density in the first two generations of the composite, while applying only within-family selection, and mild family selection, for stem volume. Due to the strongly additive inheritance of wood density in the hybrid, bias in breeding values due to linkage disequilibrium is likely to be less than for growth traits. This approach would also meet the need to rapidly improve wood density, as necessary to allow reduced rotation length (Chapter 3), while maintaining or improving growth rates.

6.4.4.3 Integrating pure species improvement

A comparison of hybrid breeding strategies must also consider the extent to which the parents are deployed as pure species. RRS has been shown to yield inferior and unpredictable gains in parental populations (Keeratinijakal and Lamkey 1993; Moll and Stuber 1971; Moll *et al.* 1978), and so is likely to be suboptimal where pure species form the bulk of the plantation estate (*eg* Verryn 2000). In such cases, RSGCA may be preferable. In Queensland, PEE is not deployed operationally. Most of the estate in south-east Queensland is planted to PEE×PCH, with a smaller area of land planted to pure PCH in central and north Queensland. In the long term PEE×PCH is expected to account for at least 80% of the annual plantation establishment, with pure PCH accounting for less than 20% of the area planted each year. Given the high pure-hybrid correlation for growth and wood density in PCH parents (Chapter 4), and the suggested low importance of G×E across site types in Queensland (Kanowski and Nikles 1989), pure species selection in a state-wide (non-regionalised) population of PCH may yield cost-effective improvements in both PCH and PEE×PCH. However, a more efficient strategy may be to apply a COMP strategy

in the hybrid population, and breed separately in PCH (Li[9] pers. comm.). This strategy has the advantage of allowing direct selection for the traits of interest on the sites of interest, in both PCH and PEE×PCH populations. The COMP strategy would target only south-east Queensland, and pure PCH breeding would target central/north Queensland. This strategy may incur some risk if genetic gains in any trait in the composite hybrid are eroded due to the reduction in heterozygosity; however, RSGCA also carries the risk of inconsistent pure-hybrid correlations in some populations and sites, combined with the possibility of G×E for some genotypes across the two broad regions. RSGCA with regionalisation of the PCH population for south-east and northern regions may also be applied at the cost of maintaining an additional breeding population, though the problem of low r_{ph} of PEE parents for growth traits are still likely to compromise genetic gains in the hybrid, relative to the COMP approach.

6.4.4.4 Historical issues preventing composite breeding in maize hybrids

Composite breeding strategies are unconventional in the context of the hybrid crop breeding literature, except for the use of synthetic populations - usually stabilised mixtures of many inbred lines - to generate base populations for subsequent selection and hybridisation (*eg* Hallauer and Miranda 1988). Particularly given the scarcity of genetic information about hybrid trees, the reluctance of hybrid tree breeders to depart from breeding paradigms established in maize hybrids has been understandable. Nevertheless, when taking lessons from maize hybrid breeding it is necessary to distinguish between those that apply more generally to hybrids, and those influenced by characteristics and circumstances peculiar to maize and maize breeding. The large gains possible from exploiting dominance in maize were discovered early (Shull 1908), almost 30 years before the concept of experimental replication was introduced by Fisher (1930). Fast genetic gains, and the need for farmers to purchase new seed annually, motivated heavy involvement of private enterprise in maize breeding since the 1930's. While varieties of strong additive genetic merit can be easily propagated by the farmer, specific heterotic crosses cannot without incurring hybrid breakdown. This created a strong financial incentive to improve the heterotic component of yield rather than the additive component of yield, for marketing purposes (Smith *et al.* 1999). Since the early years of industrial maize improvement, breeders were hence compelled to maintain separate parental populations, rather than selecting for additive

[9] Dr. Bailian Li, Associate Director, North Carolina State University Tree Improvement Program

effects in a pooled population. It has been argued that if comparable resources were invested in programs selecting for additive genetic effects applying the principles developed by Fisher, similar or superior genetic gains could have been achieved (Namkoong *et al.* 1988).

A second notable feature of hybrid breeding strategy in maize is that it is constrained by the particular deployment strategy used, which is based on inbred lines. Organised hybrid maize improvement typically consists of two 'stages': firstly, the recurrent improvement of the pure varieties, through some type of recurrent selection for additive effects in the hybrid, and secondly, the generation of inbred lines from each population, followed by testing and deployment of the best hybrids between these inbred lines, to exploit non-additive effects. The need to keep the populations separate in the first stage is largely driven by the need to produce genetically divergent material for use in the second stage. In forest trees, the second stage does not occur, and is unlikely to ever be of importance because inbred lines are not feasible. Where non-additive gene action is unimportant relative to additive gene action, there is therefore no imperative to maintain the parental populations separately, and simple recurrent selection in the composite hybrid population is likely to be the most efficient strategy.

6.4.4.5 Summary of issues relating to composite breeding

In summary, the principal advantages of composites over alternative hybrid breeding strategies in trees are as follows:

- Only a single breeding population is required to improve the hybrid, whereas conventional hybrid strategies such as RRS involve up to three populations;
- Direct selection is applied on the traits of interest, in the population of interest, on the sites of interest;
- Recombination allows superior homozygotes not present in the F_1 hybrid population to be exploited;
- The breeding cycle may be shortened because the PEE×PCH hybrid flowers at age 1-2 rather than at age 6-7 in PEE and in PCH, and grows faster than one of its parents;
- Elite genes and genotypes can be more rapidly incorporated into deployment populations;

- Increased options for deployment strategies, which may use seed, vegetative propagules, clones, embryogenesis or other options;
- Seed set is much greater in PEE×PCH F_2 and advanced generation hybrids than in the F_1; seed yields increase from *c* 20 seeds per cone in the F_1 to over 80 seeds per cone in the F_2 (Dieters and Nikles 1997);
- Transgressive segregation, though likely to be infrequent, may generate additional variation for clonal selection, and where desirable, may be additionally stimulated using inbreeding.

The principal challenges to successful composite breeding will be:

- The resources and time taken to produce a sufficiently large base population of F_1 hybrids to avoid inbreeding in later generations;
- Accurate prediction of breeding values under linkage disequilibrium (less of a problem in predominantly additively inherited traits);
- The need to maintain outcrossing to avoid hybrid breakdown;
- Convincing breeders to establish experiments that depart from conventional breeding practice.

Shelbourne's hypothesis that "interspecific F_1 hybrids are genetic dead-ends" appears to hold true in highly heterotic hybrids displaying overdominance or pseudo-overdominance such as poplars (Bradshaw and Stettler 1995; Heilman and Stettler 1985; Li and Wu 1996; Wu and Li 2000), and in hybrids with severe crossing incompatibilities, poor seed set or low seedling viability (*eg* Potts and Dungey 2001). However, the evidence presented in this chapter, and corroborative evidence from previous chapters, suggests that it is not true of the PEE×PCH hybrid. Although the current results strictly apply only to the PEE×PCH hybrid, circumstantial but widespread evidence from the literature suggests that the superiority of many other 'complementary' hybrids may also be primarily due to additive gene action (see reviews by Martin 1989, Dungey 1999, Dungey 2001). As the majority of successful hybrid combinations in use today, particularly in *Pinus*, *Eucalyptus* and *Larix*, are generally complementary in nature, it is possible that breeding strategies in these hybrids may be made simpler and more efficient simply by targeting additive gene effects through recurrent forward selection in composite hybrid populations.

6.4.5 Needs for future research

Though quantitative genetic models such as those of Wu and Li (2000) and Kerr *et al.* (2000) can model the genetic basis of heterosis and predict the outcome of hybrid breeding strategies, respectively, it is likely that some of their assumptions do not reflect real conditions in hybrid breeding populations. Consequently, though these methods may provide some useful general guidelines for future breeding and empirical research, their results need to be verified with field experiments, if conclusive evidence for or against strategies such as RSGCA and COMP is to be produced. Some simple genetic test designs can provide highly useful information. Firstly, simple half-sib trials involving both pure species and hybrid progeny generated from large sets of common parents are necessary to verify pure-hybrid genetic correlations. Secondly, given the existing evidence supporting AGH, the testing of F_1 and outcrossed F_2 crosses of common ancestry should be a high priority for breeding programs working with complementary hybrids. Polycross matings involving a random sample of individuals in F_1 trials may be a cost-effective way to generate F_2 progeny for planting in yield trials along with seedlings and clones from the same F_1 families. Such trials will provide powerful tests of the usefulness of advanced generation hybrids, as the greatest increase in homozygosity will occur in the F_2, under random mating (Falconer and Mackay 1996), and probably also under outcrossing.

6.4.6 Conclusion and recommendations for future studies

The common ancestry and common test environment of the pure species and hybrid taxa in EXP674 allowed the integration of pure species and hybrid population parameters into a single genetic model. This model provided information on gene action and number, given a set of assumptions on other parameters of population genetic architecture drawn from the results of previous studies in these and other taxa. The results suggest that stem volume and wood density in the PEExPCH hybrid are not influenced by overdominance or pseudo-overdominance gene action. Partial dominance, and possibly dominance-related epistatic gene action, contribute to heterosis in stem volume, but the genetic control of wood density in the hybrid is due to additive, and possibly additive-related epistatic, gene action. These results corroborate those from conventional quantitative genetic analyses presented in Chapters 3, 4 and 5, and suggest that breeding strategies aiming to accumulate

additive genetic effects in the pure species and hybrid populations are likely to be the most efficient for improving PEE×PCH and other hybrids where a similar pattern of genetic control can be shown.

RSGCA and COMP are breeding strategies that focus on accumulating additive gene effects in hybrids. RSGCA, which involves breeding separately in the two pure species with hybrid crossing only for deployment, can be implemented quickly, but is disadvantaged by possible inconsistency of the pure-hybrid genetic correlation (Chapter 4) and compromised genetic gain as a result of indirect selection on hybrid performance. Implementation of COMP breeding strategies, which involve forward selection in the hybrid population, is challenged by the need to create a large F_1 hybrid base population to avoid inbreeding in subsequent generations, and possible bias in breeding value estimates in the early generations of breeding. However, these difficulties are likely to be outweighed by the large gains in efficiency from maintaining only a single breeding population for hybrid improvement, the ability to make direct selections in the population of interest, shortened breeding cycle due to faster growth, improved flowering precocity and fecundity, possible gains from cloning outstanding segregants, and quicker transfer of genetic gains from breeding to deployment populations. Based on the results of this study, a breeding strategy involving forward selection in an advanced generation composite hybrid population (*eg* Bourdon 1999) is therefore likely to be the most effective long-term breeding strategy for PEE×PCH, and for other complementary forest tree hybrids where similar genetic control can be demonstrated. Breeding to improve either or both pure species populations can be carried out separately, possibly also generating unrelated elite material to infuse into the composite population. To provide more conclusive evidence for the value of composite breeding strategies, there is a critical need to establish simple trials comparing F_1 and F_2 hybrids of common ancestry, in PEE×PCH and in other interspecific forest tree hybrid taxa.

Chapter 7 - Conclusions and principal findings

This study used conventional and novel quantitative genetic analyses to examine the genetic basis of variation in wood and growth characteristics in a progeny trial of 12-year-old *Pinus elliottii* var. *elliottii* (PEE), *Pinus caribaea* var. *hondurensis* (PCH), and their F_1 and F_2 (PEE×PCH) interspecific hybrids. The results were discussed with reference to appropriate breeding strategies for recurrently improving wood and growth characteristics in the PEE×PCH hybrid, and in interspecific tree hybrids more generally.

Studies of the inheritance of genetic differences are necessary to direct breeding strategy in populations of interest. In interspecific hybrids, complicated, conservative breeding strategies are necessary when the genetic causes of variation within and among pure species and hybrid populations are poorly understood. The cost of genetic gains from these strategies can be several times greater than for breeding pure species or for simpler hybrid breeding strategies that can be designed to capture specific types of genetic variation. Under the more typical breeding scenario of a fixed budget, an understanding of the genetic basis of hybrid performance may therefore increase several-fold the rate of genetic gain from breeding interspecific tree hybrids, as well as broadening scientific knowledge of the genetic consequences of hybridising genetically divergent populations.

The strong influence of wood properties on product value in most plantation conifers, particularly in fast-growing, short-rotation hybrid taxa, requires that hybrid breeding strategies are optimised not simply for improving wood volume, but for concurrently improving wood volume and wood quality. To achieve this, it is first necessary to evaluate the available pure species and hybrid resource, and the needs for improvement in important traits. Secondly, the genetic control of these traits, the genetic relationships among them, and the genetic relationships between pure species and hybrid populations, need to be evaluated. These parameters can be used to predict the genetic gains possible from applying conventional hybrid breeding strategies. Given the multi-population structure and long breeding cycle interval of conventional hybrid breeding strategies, methods to reduce the typically high cost of

wood property assessment and the late selection age for mature-stem wood properties are important research priorities. Lastly, breeding strategies based on forward selection in the hybrid population have the potential to dramatically improve the efficiency of hybrid breeding. Their likely efficacy can be assessed based on the results of genetic models developed specifically for interspecific hybrid populations, and depends on key parameters of genetic architecture in the hybrid population.

This study sought to address these key issues for PEE×PCH hybrids in Queensland. The principal conclusions from this study can be summarised as follows. Key conclusions from each component of the study are listed, followed by general conclusions.

7.1 Principal findings of each component of the study

7.1.1 Taxon level variation in PEE, PCH and their F_1 and F_2 hybrids (Chapter 3)

- Wood density of the PEE×PCH hybrid is much lower than PEE and similar to PCH, and needs to be improved by at least 30kg/m^3 in order to maintain the quality and value of the harvest at the proposed 20-year rotation relative to the current 28-year rotation. Additionally, moderate spiral grain angles in the inner growth rings of the hybrid may adversely affect wood value. Nevertheless, the superior growth, straightness and site adaptability of the hybrid cause it to be the preferred taxon overall;
- Radial wood density variability in the hybrid is intermediate between the highly variable PEE and the more uniform PCH. Wood density variability can be quantified using the proposed Radial Density Variability Index (RDVI), and may need to be reduced through breeding in order for proposed reduced rotation harvests to be profitable;
- Genetic improvement using some type of hybrid breeding strategy is the most promising way to improve the density and spiral grain of the PEE×PCH hybrid juvenile wood to an acceptable standard for industry. The economic importance of microfibril angle variation in the juvenile wood needs to be quantified.

7.1.2 *Family variation and genetic parameters in PEE, PCH and their F_1 hybrid: implications for conventional breeding strategies (Chapter 4)*

- Wood density and spiral grain are moderately to strongly inherited, and more strongly inherited than growth traits, in PEE, PCH and PEE×PCH. Neither wood property is substantially affected by genotype-by-environment interaction at the half-sib family level on the sites tested;
- Economically significant increases in wood density can be achieved by family selection in PEE, PCH and PEE×PCH, though this will cause substantial correlated increases in radial and within-ring wood density variability;
- Wood density and growth are strongly adversely genetically correlated in PCH, complicating concurrent improvement of these traits;
- The pure-hybrid genetic correlation (r_{ph}) is strong for wood density and growth traits in PCH, and strong for wood density in PEE, but only weak to moderate for growth traits in PEE;
- Selection for PEE×PCH hybrid performance based on pure species performance is highly efficient for improving wood density, and moderately efficient for improving growth characteristics – however in PEE this result is questionable because of the low r_{ph};
- The usefulness of recurrent selection for GCA separately in the two pure species (RSGCA) for improving hybrid growth performance needs to be confirmed in further studies with a larger sample of parents;
- The individual-tree heritability of a trait in a pure species population is a reasonably good predictor of the pure-hybrid genetic correlation (r_{ph}) in that trait, for the same set of parents.

7.1.3 *Age trends in genetic parameters and indirect selection for wood properties and basal area (Chapter 5)*

- Selection at age 4 provided optimum genetic gain per year for a mature age of 12 years in all taxa and traits except basal area in the F_1 hybrid, where selection was optimal at age 6;
- Selection for growth, wood density and spiral grain at age 6-7 will increase genetic gain per year by at least 50%, and in some cases by over 100%, relative to selection on the same traits at age 12, in PEE, PCH and PEE×PCH. The low

'mature' age in this study (12 years) limits the general applicability of the findings relative to early selection;

- The efficiency of early selection for wood density and spiral grain was approximately the same based on single-ring measurements as based on whole-stem measurements at the same age;
- Field screening for density using the pilodyn could achieve at least 90% of the genetic gain possible from direct selection on wood density, in all taxa;
- Field screening at an early age may exploit both the high genetic gain efficiency of early selection and the high selection intensity possible with field assessments, allowing effective large-scale breeding for wood properties with limited resources.

7.1.4 Genetic basis of heterosis in PEE×PCH F_1 hybrids and implications for breeding strategy (Chapter 6)

- Better-parent heterosis in stem volume in the PEE×PCH hybrid is not due to overdominance. Although partial dominance gene action contributes to stem volume in PEE×PCH, the superiority of homozygous genotypes to heterozygous genotypes, and primary importance of additive gene action, indicates that hybrid breeding strategies should focus on accumulating additive gene effects, either in the pure species populations or through selecting forwards in the hybrid population itself using a structured breeding strategy. Numerous theoretical and practical arguments favour the latter strategy;
- Wood density is predominantly under additive genetic control, though a low degree of partial dominance occurs at some loci. Useful variation in wood density can therefore also be most efficiently exploited through forward selection of outstanding recombinants in a composite hybrid population, with clonal deployment of outstanding tested individuals;
- The results provide evidence for the genetic basis of "complementarity" in the PEE×PCH hybrid, in which alleles provided by PEE confer increased wood density, and alleles provided by PCH confer improved growth; although neither trait is governed by overdominance, both better parent heterosis in stem volume and overall hybrid superiority can result from partial dominance genetic control.

7.2 Principal conclusions of the study

This study has demonstrated that the traits wood density, spiral grain and stem volume can each be improved through selection within and among PEE, PCH and PEE×PCH. Furthermore, these traits can be improved concurrently, except for the particular cases of density and stem volume in PCH, and spiral grain and stem volume in PEE×PCH. Though the adverse genetic correlations found in these instances are consistent with the results of some previous preliminary studies in these and other taxa, the sample size of 12 parents in each taxon in this study is inadequate to provide all but general indications of genetic parameters, particularly genetic correlations, which are subject to high sampling error. These correlations need to be investigated further, to verify whether the results in this small sample of parents apply to the wider breeding population.

There exists strong potential for integrating genetic improvement of wood quality into the Queensland breeding program by applying early selection and rapid, inexpensive field screening for wood density and spiral grain. Though more sophisticated techniques such as x-ray scanning for wood density and sonic testing for wood stiffness are in development, the pilodyn and bubble protractor provided accurate rankings of families in this study. Measurements using the former were robust to variations in site, taxon, aspect of sampling, and number of samples. These methods reduce the necessary duration of genetic testing, which will particularly increase the rate of genetic gain in conservative hybrid breeding programs such as that currently in use in Queensland, yet will also improve the efficiency of simpler hybrid breeding strategies.

There appears to be scope for simplifying hybrid breeding strategy in PEE×PCH. The findings of this study are at odds with Shelbourne's hypothesis that "F_1 interspecific hybrids are genetic dead ends" (Shelbourne 2000). This hypothesis is true if hybrid superiority is due to overdominance, or if advanced generation hybridisation is impracticable for technical reasons. While the former applies to some *Populus*

hybrids, and the latter is particularly true of some *Eucalyptus* hybrids, neither of the above appear to apply to the PEE×PCH hybrid.

The results of all components of this study provide evidence for the importance of additive, or additive-related epistatic genetic effects and gene action in PEE×PCH, particularly in wood properties, but also in growth. This suggests that breeding strategies focussing on accumulating genes with favourable additive effects are likely to yield more genetic gain than more complex (conventional) hybrid breeding strategies, for equal resource investment. However, this study only examined a small subpopulation of the Queensland PEE and PCH breeding populations, which represent only a small proportion of the genetic variability in these species. It is therefore uncertain whether the results can be extrapolated, either within this hybrid or to hybrids of other related taxa. The strongly contrasting results in some *Populus* hybrids, yet similar preliminary results in some other *Pinus* hybrids, suggest that the genetic causes of hybrid superiority, and consequently the most appropriate breeding strategy, may vary to a large degree according to genus. More comprehensive studies in other *Pinus* hybrids, and in hybrids of *Eucalyptus* and other genera, are necessary to confirm this trend.

This study substantially contributes to growing evidence from both animal and tree studies supporting a paradigm shift in breeding strategy for "complementary" tree hybrids: from hybrids as specialised problems for breeding, requiring expensive recurrent improvement of the F_1 hybrid population, to hybrids as useful general tools for breeding: as an attractive means for introgressing desirable genes, increasing genetic variation and contributing to genetic gain through the process of recombination and recurrent forward selection in composite hybrid populations (Li and Wyckoff 1994; Namkoong 1979). This approach will be inappropriate in highly heterotic hybrids, or in hybrids with a high degree of genetic incompatibility, as Shelbourne (2000) has emphasised. However, in taxa whose hybrid superiority is due to "complementarity", resulting predominantly from additive contributions from the parental species in a variety of important traits, recurrent forward selection in composite hybrid populations is likely to provide a powerful future tool for tree breeders.

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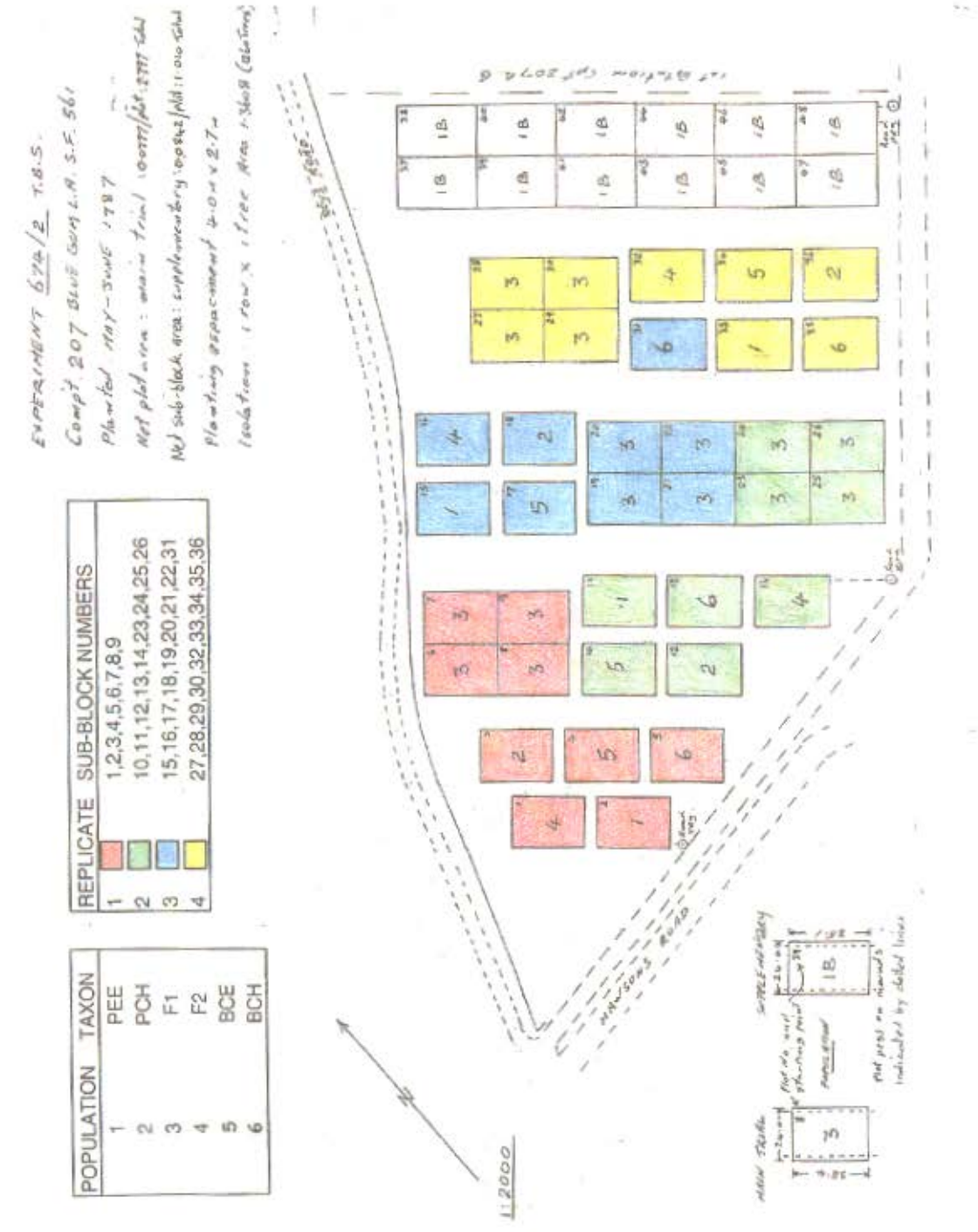
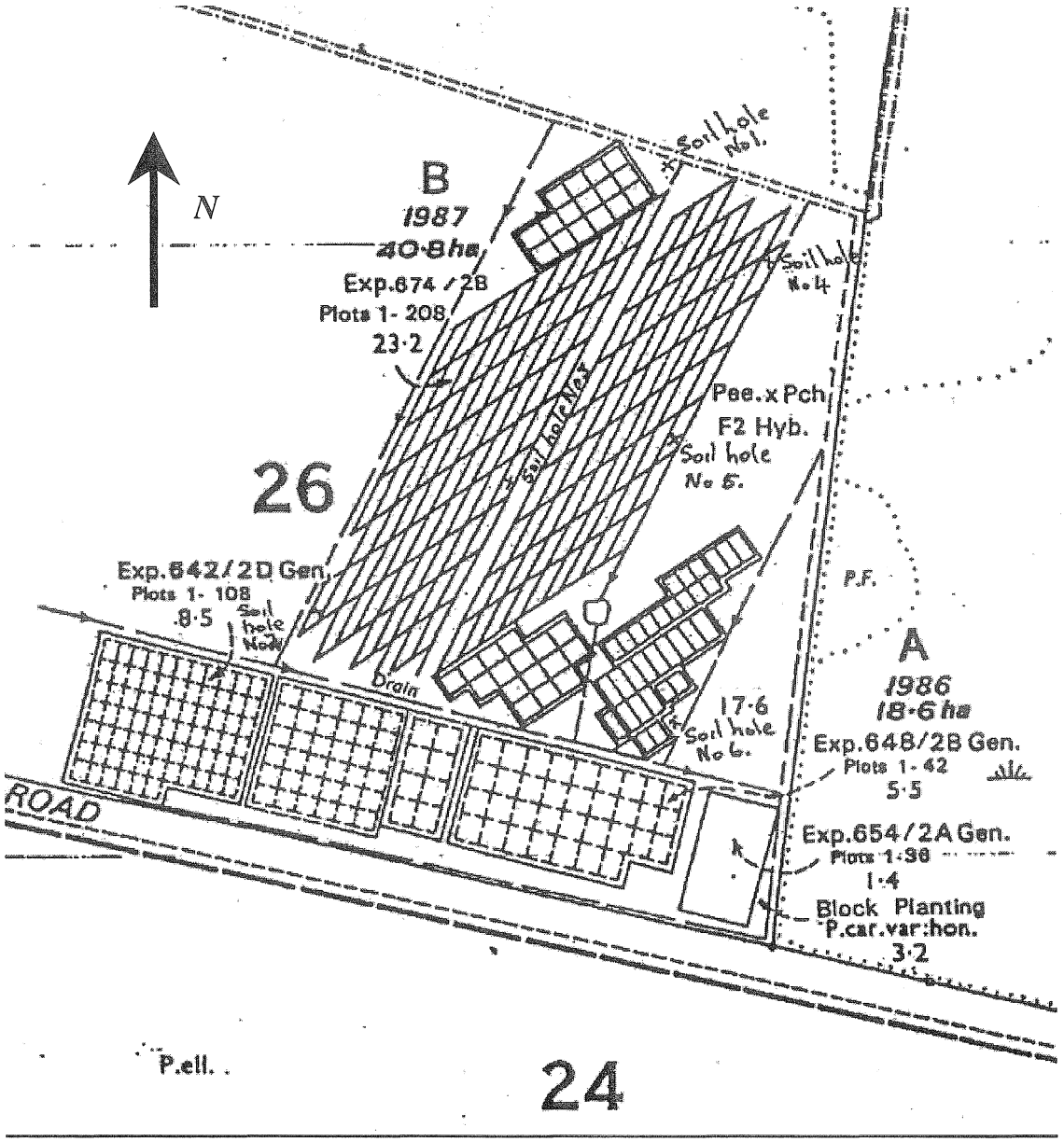
Appendix 1 Example layout of EXP674 replicates, showing replicates 1-4 at Beerwah site

Note: Coloured sub-blocks indicate components of EXP674 listed in Table 3.1; sub-blocks without colouring are part of a crossing experiment ancillary to the main design, and were not assessed.

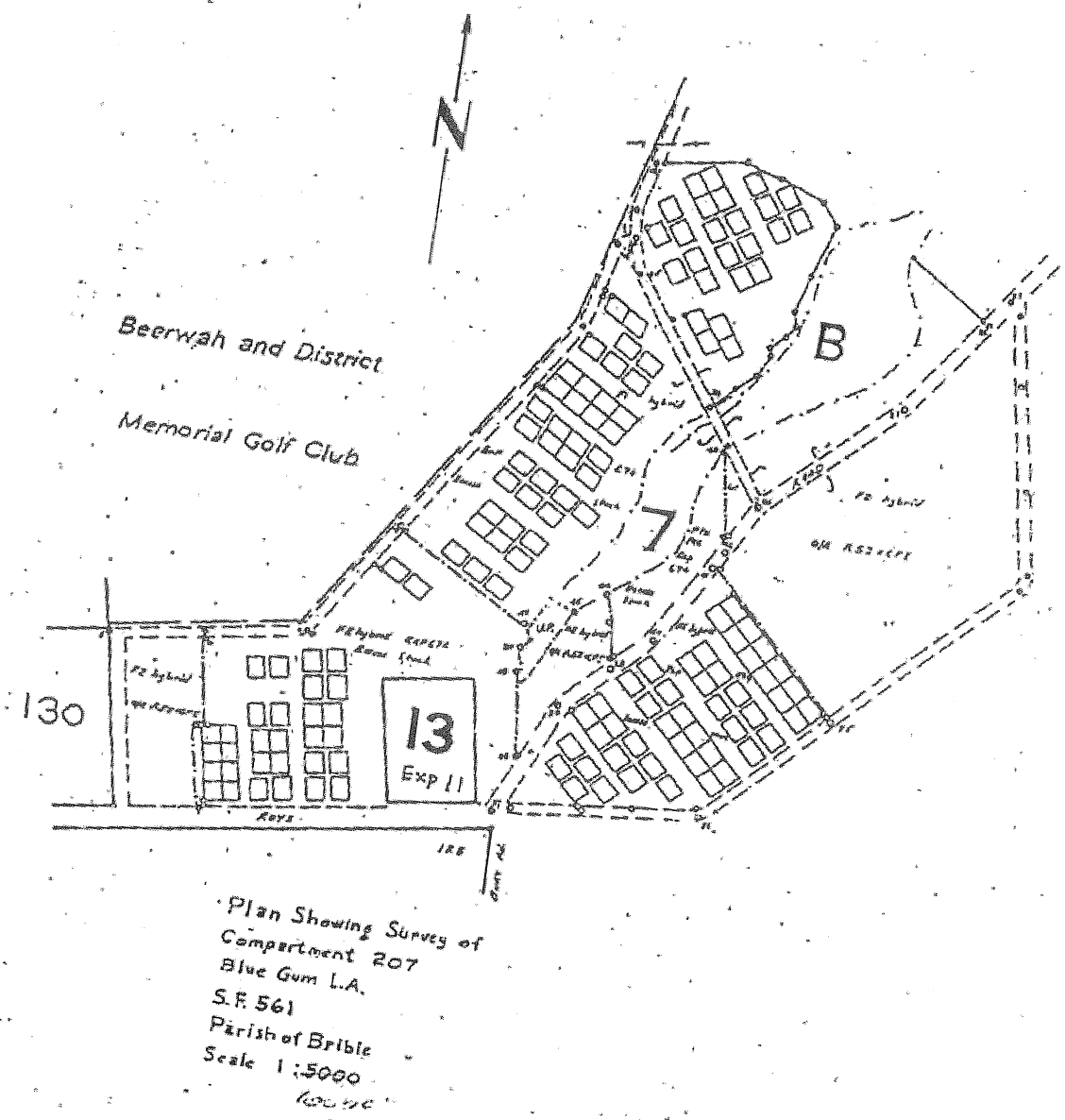


Appendix 1 (continued) EXP674 trial layout, Tuan site.

Note: Parallelogram-shaped boxes indicate 72-tree sub-blocks of EXP674. Rectangular and square boxes indicate blocks of unrelated QFRI experiments involving the same taxa at a similar age or younger.



Appendix 1 (Continued) EXP674 trial layout, Beerwah site.
Note: Rectangular boxes indicate 72-tree sub-blocks of EXP674. A small proportion of the boxes are plots of a crossing experiment ancillary to EXP674.



Appendix 2 User's guide for the CSIRO Forestry and Forest Products Yarralumla wood x-ray densitometer.

USER'S GUIDE FOR THE CSIRO FFP, YARRALUMLA WOOD X-RAY DENSITOMETER

by Dominic Kain

March 2001

Methodology developed by Mark Hall, Dominic Kain and Dr A.C. Matheson

LIST OF SOME TERMS USED AND THEIR DEFINITIONS

attenuation the process of x-rays being stopped/absorbed by a substance.

accuracy how close the measurements are to the true values of the quantities being measured (accuracy is determined by the sum total effects of precision and bias).

bias how far the mean of a set of measurements (estimates) of the same quantity deviates from the true value of the quantity

precision how closely a set of measurements of the same quantity are distributed around their mean - measured by repeatability

critical value the thickness of the first step of the wedge - derived from the wedge calibration (see Step 2) and used to estimate sample densities by using the calibrated wedge as a comparison

film calibration value calibration for individual films is carried out on a 0-255 scale - this standard scale allows correction for grayscale variation across the film, regardless of the grayscale range covered in the film image.

KV Kilovoltage of the x-rays: determines the intensity or 'cutting power' of the x-rays

MA Milliamps – determines the amount of x-rays produced. The effect of increasing the milliamps on film blackening is the same as increasing the exposure time: in both cases a greater number of x-rays hit the film).

masonite sheet a sheet of masonite used as a platform for preparing transparencies and exposing films. There should be two masonite sheets slightly larger than A3 size in the ANU x-ray chamber.

masonite target plate a larger piece of masonite positioned on the floor of the x-ray room, with short wooden legs. Masonite sheets should be placed on top of the masonite target plate during transparency transfer and during film exposure.

INTRODUCTION -REQUIREMENTS FOR SUCCESSFUL X-RAY DENSITOMETRY

As we have found out, having the actual equipment for a densitometer is only a preliminary step in developing a machine that gives reliable density estimates. The WinDendro density analysis package provided a good start, but required the following modifications before it would give both unbiased and repeatable estimates of density:

- Manufacture of a step wedge of similar x-ray attenuation properties to wood (Rudman 1969) - *provides an easy method of calibration;*
- A methodology for calibrating this step wedge to equate its x-ray attenuation properties with those of the wood samples of interest - *allows estimation of unknown densities of samples by comparison with a step wedge of known density properties;*
- A methodology for calibrating films based on a common scale (0-255 grayscale calibration) - *allows accurate density estimation even without scaling to gravimetric densities, & allows for background correction for film variation;*
- A methodology for correcting density estimates for observed background variation on x-ray film images - *increases the precision of estimates by standardizing variation across the x-ray plate*

We also developed:

- A method for collating and performing calculations on WinDendro output files to omit time-consuming file handling and spreadsheet operations.

To help run these features, find the following files in the 'D:\RADIATA\WinDendro tools package' directory:

- New CSIRO Densitometer Manual.doc (electronic version of this manual)
- Film calibrator - 4 step.xls (film calibration spreadsheet)
- Film calibrator - 3 step.xls (film calibration spreadsheet)
- Wedge calibrator.xls (wedge calibration spreadsheet)
- Summ.exe (WinDendro output collation program)
- Ringer.exe (WinDendro output collation program)

Find also next to the WinDendro computer and scanner, a disk box labelled 'Dominic's calibration samples'.

Densitometers in general should not be relied upon to give accurate assessments of whole-sample basic density. However, using the protocol described in this manual, we were able to predict whole-core basic densities with high precision and minimal bias, without scaling densitometric estimates to gravimetric densities. Although scaling may improve the accuracy of the estimates under some circumstances, it does not appear to be essential. At very least, gravimetric measurements should be performed on a subset of samples, to check the densitometer's predictions.

NOTE: if planning to start densitometry within the next couple of days, it is advisable to place the calibration set in a conditioning room immediately. Samples of 2mm thickness take 2 days to condition when spread apart on a bench in a room at constant temperature

and humidity (20°C, 65% r.h. recommended). Conditioning takes much longer (up to 2 weeks) if samples are stored in groups - *eg* with a rubber band).

ALSO NOTE: we developed the following procedure for softwood samples of 2mm thickness. When using the procedure with hardwoods and/or samples that deviate substantially from 2mm thickness, it may be necessary to test some of the steps in this procedure (where indicated in the text) to make sure they are appropriate for your material. It may also be necessary to create a new set of calibration samples other than the set supplied with this manual (see disk box labelled 'Dominic's calibration samples'). As this testing/calibration should preferably not be carried out using samples that are a part of a study, it is best if you have some 'spare' samples to work with - these should have undergone all of the same treatment procedures (*eg* extraction, sawing) as the study samples.

STEP 1. PREPARATION OF WOOD SAMPLES AND GRAVIMETRIC DENSITY ASSESSMENT

This section assumes that you have 12mm increment cores or flitch samples.
We recommend a sawn thickness of 2mm for the wood samples to be x-rayed. This gives a reasonable trade-off between statistical sample size (too thin might be an inadequate sample), necessary exposure time (usually longer for thicker samples) and precision of measurement and identification of individual ring boundaries (excessively thick samples result in a more blurred trace that is smoothed at the peaks - poor definition on ring boundaries). Refer to the CSIRO twin-bladed saw manual or other saw manual for instructions on how to slice samples to 2mm thickness. The samples should be sawn as wide as possible (preferably at least 7mm in width).

GRAVIMETRIC DENSITY ASSESSMENT

Assessment of gravimetric density may be carried out either on whole cores or on 2mm flitches, there are advantages either way. When the assessment is carried out with proper care, it is probably better to use 2mm flitches. However, for accurate estimates it is critical that the sawn flitches have consistent width and thickness along their length, on both axes; *ie* even if the 2mm thickness is constant along the length of the sample, if the sample is cut irregularly such that it becomes wider at, say, the juvenile wood end than the mature wood end, the gravimetric density of that sample would be seriously biased downwards.

Measurement of gravimetric density on a sample requires estimates of two quantities: its 'green' volume, and its oven dry mass, where:

$$\text{specific gravity} = \frac{\text{oven dry mass}}{\text{green volume}} \qquad (1.1)$$

where: (specific gravity = basic density / 1000)
It is generally more convenient to express basic density as specific gravity, which is a unitless measure. Our experiments indicate that gravimetric density may be measured accurately (no bias, and acceptable precision as measured by repeatability of

measurements) either on whole cores or on flitches cut from cores, when measurements are performed carefully using the following procedures.

Volume measurement

The cheapest and most accessible method for measuring volume is the Archimedian (water displacement) method. Instructions are as follows:

⇒ soak the samples in water for around 4 to 5 days (or until the samples sink) before taking measurements - we want to measure the green, or saturated volume ↵
⇒ when ready to take measurements, set up a water bath, weighing scales and a retort stand to hold the sample while it is lowered into the water bath ↵

It can be quite difficult to find suitable containers that will not exceed the tare limit of the scales, when filled with water). Phil Evans' 'Down to Earth' container works well - stored at the ANU wood lab). This vessel is not suitable for very long samples, though. Alternatively, a measuring cylinder can be used and the samples inserted vertically. Either way, a needle, either mounted in a dissection pin or tied to a piece of nylon fishing wire, and held by a retort stand, is used to hold the sample.

⇒ fill the water bath with enough water to allow for the sample to be fully submerged without touching the sides of the bath, making sure this is within the tare limit of the weighing scales ↵
⇒ add several drops of 'Teepol' (a soil wetting agent - available in genetics lab, above the sink) or other wetting agent into the water bath and dissolve in the water, making sure bubbles do not form, or at least are not present during sample immersion. ↵
⇒ tare the water bath, then after drying the sample carefully (see notes below), submerge the sample in the water bath. The sample volume, in cubic centimetres, is equal to the value in grams shown on the weighing scales. ↵
⇒ water spillages are common so record measurements in pencil, or if entering straight into a computer, keep it a safe distance away. ↵

The accuracy of the estimates, especially with small samples, particularly depends upon whether the measurements are performed consistently. Most importantly, to maximise repeatability (precision), each sample should be dried off to the same extent. Important: beads of water on samples make a measurable difference to the volume result, and I recommend that each sample be dried by smearing against the fingers (and then drying fingers on paper towel) until no beads of water are visible on any parts of the sample.

That some method such as this be followed, for which the repeatability of measurements has been carefully evaluated by each individual experimenter, is particularly critical when measuring 2mm flitches. To do this roughly, do the following: each experimenter should pick a sample of 10 or so flitches of different sizes, and measure the volume of each, recording the results. Repeat this exercise twice so you end up with three measurements of each sample, and calculate the mean for each sample. Now make sure that the highest minus the lowest, all divided by the mean, is less than 0.05; if not, repeat the exercise until you're lower than 0.05 on all flitches. If you want to get more technical about it and calculate standard errors etc., see Box 1.1.

Testing our version of the gravimetric method by repeatedly evaluating the same samples (repeatability test) we found good repeatability (consistent estimates), in fact better than that from a method based on measuring the dimensions of sawn 7mm*2mm samples at various points with a very accurate pair of automatic calipers. However, the Archimedian method was only superior when it was performed by carefully and consistently removing water drops from the surface of each 2mm flitch.

Oven dry mass measurement

Oven dry mass is more straightforward to measure than volume, as it does not involve liquids. The samples should be placed in an oven for 24 hrs at 105 degrees C. We did not experience any deformation of the 2mm samples during this drying procedure. However, if thicker samples, or samples of other species are to be used, it is recommended that this drying schedule first be checked using some test samples that are not a part of a study. Some practitioners have recommended that samples should be allowed to cool down in a sealed dessicator prior to measurement. It is pointed out here that the air inside a dessicator takes days to reach a condition of equilibrium with the gel crystals - which are far less hygroscopic than freshly oven dried wood samples. Allowing samples to cool in the dessicator therefore allows them to take up substantial amounts of moisture, which defeats the purpose of taking oven dry measurements.

A method that gives more consistent results (better repeatability) - and is easier to perform, goes as follows. Place Pyrex beakers with flat rims in the oven alongside the samples, allowing them to heat up. Then place, say, 6 samples at a time in a hot beaker before covering with a glass petri dish and taking them to the weighing scales, using gloves. This way the samples are kept hot and dry until they are measured. However, as changes in temperature affect the operation of weighing balances, the samples should not be placed directly on the balance. Taring a plastic cup (upside down) or other light, rigid object, and placing the sample on top of this for weighing, minimises the effect of heat on the operation of the balance. Oven dry mass should be measured in grams.

Box 1.1

Why does repeatability matter?

Repeatability matters because poor repeatability of measurements will inflate the error term in analysis of variance of genetic trial data, generally resulting in deflated genetic parameters including all types of heritability. If only means of large groups of samples (*eg* family means) are of interest, and not variances, then repeatability of measurements is of little consequence - it'll all just average out. But if variances are of interest (other than large group mean variances), then poor repeatability is a serious issue, due to the additive property of variance components. The error variance due to poor repeatability is independently distributed to other sources of error variance, and so will just add right on to those sources of variance, possibly even doubling the total error variance.

How do we measure repeatability, and what is an acceptable value?

Repeatability should be measured in terms of the standard error of measurements. The 'acceptable' value of this standard error varies depending on the experimental design, but as a general guide, it is suggested that the standard error on repeated measurements of gravimetric (basic) density on the same sample should be within ±0.002 specific gravity. For repeatability of density values estimated by densitometry (after overall core values

have been scaled to core basic density, an acceptable standard error value might be more like ±0.004 specific gravity, in view of the complications involved with densitometric measurement.

Using the oven dry mass and green volumes for each sample, calculate the specific gravity of each sample (can be done easily using a Microsoft Excel spreadsheet).

STEP 2. ESTABLISHING A SET OF WEDGE CALIBRATION SAMPLES

If you are evaluating plantation softwoods, you can probably use the existing set of calibration samples - that will save the procedure of developing a calibration set. If evaluating other material, use the following procedure to develop your own calibration set. Select a set of samples that range in density from the lowest to the highest density that will be evaluated during the study. The wedge calibration samples should be:

- the same type of wood and sample preparation as used in the study
- preferably *not* samples that are actually a part of the study (a good idea is to save cores that were rejected -*eg* missed the pith - and use broken-up parts of these as wedge calibration samples)
- small parts of cores rather than whole cores, in order to increase the density range
- made up of as wide a range of densities as possible (include some samples that are all juvenile wood and some that are all mature wood).
- between 20 and 50 samples (should be able to fit on a single x-ray plate)
- free from aberrations for example holes, needle traces, chunks missing
- constant thickness along <u>all 3 axes</u>
- conditioned to the same temperature and moisture content as the samples to be x-rayed in the study (recommended: ANU conditioning room, Forestry Engineering Wing - a constant 20°C, 65% r.h.- obtain permission from Phil Evans or Peter Beutel)

The wedge calibration samples should have their gravimetric density measured extremely carefully: the density estimates for every sample in the study are going to be based on the density of these calibration samples so it's important to get them right. The volume and oven dry mass of these samples should each be measured 2 to 3 times, and the measurements averaged for each sample, to ensure that the estimates are accurate.

When beginning X-raying (step 3 -instructions below) - <u>the wedge calibration set should be one of the first films (plates) to be made, as no other plates can be properly evaluated using WinDendro until the wedge calibration has been completed.</u>
nb it is preferable is all of the calibration set can be x-rayed on a single plate - however it would not be a problem if the set was large enough so as to cover several plates. Be sure to take the utmost care at all stages of the procedure where the calibration samples are involved. I recommend doing a couple of exposures of the calibration samples so that you can pick the best film images for the calibration.

Note: a 'good' film image is one whose grayscale appears consistent across the film; it does not have serious marks, dark spots or light spots or streaks across it; the label of the

sample is clearly visible (or write it on in permanent marker), and the samples are not overlapping or hanging off the edges.

STEP 3. X-RAYING OF WOOD SAMPLES

Box 3.1

Notes on film transportation and handling

Film issues are of primary importance in obtaining accurate density estimates. Film exposure to light and x-rays are major issues. As x-rays and light have the common effect of blackening the film, yet greatly different effects upon the density results, it is *critical* that these two sources of blackening are not confounded with each other, otherwise errors in density estimation will result. The only way to achieve this is to ensure that *no* light whatsoever comes into contact with the film. Some steps to achieve this are as follows:

1. ensure that at any stage of the handling process, films are left naked in the room, even under a safelight, for the absolute minimum amount of time possible. Film manufacturers generally recommend that for optimum results, film should not be exposed to safelight conditions for more than 1 minute. Although this is difficult where arrangement of a large number of samples in the darkroom is required, try and minimise the contact of the film even with safelights.
2. ensure that no light comes into contact with the film during transportation between darkrooms. Films should be transported in between white cardboard sheets, in a film box. The film box should be masking taped at the seam, before transportation, and should be carried in as light-proof a plastic bag as possible (two layers of black plastic garbage bags works reasonably well).
3. turn the safelight off during film exposure to x-rays. This can be done from the control room.
4. keep <u>all</u> lights in the control room *off* during film exposure and handling, close the control box lid, and ensure that all doors are kept closed as much as possible.

Best not to keep a black plastic bag on the inside of the film box, as is done with boxes of new film - this causes handling difficulties, and our experience suggests this may result in scratching of films especially when the bag becomes worn and dirty.

The film and development process is highly sensitive to dirt and impurities on the surface of the x-ray film. Handle the film only while wearing latex gloves. Be careful not to bend or crease the film in any way, or put it on a dirty or abrasive surface. Films should be laid only on the smooth masonite sheets, which should regularly be wiped clean of dust and grit with a dry cloth.

EXPOSING FILMS

Follow the x-ray room procedure (on the reverse side of the door) for warming up and using the machine. See John Kane (head technical officer) for clarification on any points, and for instruction on the first time of using the x-ray generator. Be sure to have an X-ray monitoring badge on at all times, and don't leave it in the emission chamber!

The film box contains three sheets of white cardboard, forming two inner compartments where film may be kept. Looking at the box from the front (labelled/cut-away side), the unexposed films should be kept in the front compartment, and transferred to the back compartment after x-ray exposure. This ensures that no films are double-exposed.

Place some prepared, conditioned wood samples (*ie* your wedge calibration set if these are your first film exposures), along with the Rudman calibration step wedges, on a piece of x-ray film on the target plate in the emission chamber, following the notes provided below.

Box 3.2

Notes on sample placement

We recommend placing the 2mm thick wood samples on cellulose acetate (general transparency) sheets, on the smooth side of the masonite sheets provided. This allows the identity of the samples to be labelled on the acetate sheets using permanent overhead markers- although these labels will not properly show up on the film, they can later be transferred to the film or inputted into a spreadsheet along with the sample data. The use of a lead or other metallic-based pencil or pen ink would be of great benefit in transferring the label onto the film automatically, however we were unable to identify a useable pen with these properties. There is some room for improvement in the technique used to place and identify samples. Ensure you write, onto the transparency sheet, the identity of each sample, and importantly, the identification number for the plate. Two transparency sheets should be used per masonite sheet - a separate number should be used for each transparency. The large size Cronex medical grade film will easily fit two transparencies with samples onto it. Remember to place the corresponding lead numbers provided over the top of the transparency sheet ID numbers before exposing the film - this puts a permanent label onto the x-ray film for later identification. Also importantly - ensure that the calibration wedge, and samples, are all placed perpendicular to the long axis of the transparency. The development and scanning process tends to put in some grayscale variation lines parallel to the long axis - these error lines can be accounted for more effectively by background correction if they run perpendicular to the long axis of the sample. Also - make sure that the calibration wedge is on each and every transparency being exposed, and that it is placed towards the centre of the film and not at the edge of the film. Avoid placing wood samples too close to the edge of the transparency or edge of the film - this may result in blurring on those samples.

After placing the samples, and carefully labelling the transparencies, turn the lights off in the emission chamber. The film is <u>extremely</u> sensitive to light and so every effort should be made to ensure that light does not come into contact with the film - any exposure could seriously bias the density results, yet the effect would be almost impossible to detect. In the darkroom, with the safelight (red light) ON, untape the film box and remove a sheet of film, wearing latex gloves. Place the film on the smooth face of a masonite sheet on top of the masonite target plate, and place the other masonite sheet with the transparencies and samples, on top of the target plate, adjacent to the masonite plate with the film on it. Keeping the safelight on (and all doors closed of course), carefully slide the transparency sheets over on top of the film on the adjacent masonite sheet, ensuring that the wood samples stay in place and that there is a minimum, say, 5mm gap between samples. Sliding the transparencies onto the top of the film in the dark

can be a fiddly process, but works ok once you get used to it and it avoids having to arrange samples and write labels in the dark.
nb the transparency sheets are very uniform in thickness and density, and thin sheets will attenuate very few x-rays - so there is no problem in leaving the transparency sheets on top of the film during exposure.

Exit the emission chamber, ensuring no light enters the chamber. Remember to bring the film box and one masonite sheet out with you. Close the sliding door, and, keeping the emission chamber and control room lights off, set the machine to irradiate the samples at the desired settings. The optimal settings are different with varying film and sample parameters, and can be time consuming to determine. To avoid this costly process, we recommend using the same parameters we have used, if you are irradiating 2mm softwood pine samples. These are:
13.5kV, 20mA, 9 minutes. This was with 2mm thick samples and 14 x 17" Cronex Medical Imaging Film (previously I think some type of Kodak Scientific Imaging Film (X-OMAT AR) may have been used).

Box 3.3

Some rough guidelines if you do have to vary the above parameters for whatever reason
Likely reasons you may need to change the above parameters may include: having samples that deviate from the 2mm thickness, and using different types of film.
- Sample thickness has a large, though somewhat predictable effect on the appearance of the x-ray image. With thicker samples, either the kV or the exposure time, possibly both, may need to be increased.
The kV is the wavelength of the x-rays: a measure of the intensity. The mA and the exposure time both determine the amount of x-rays being given off; mA and exposure time have the same effect. Doubling the exposure time yields the same effect on the film appearance as doubling the mA, and vice versa (*nb* the effect of either would be to double the degree of film blackening).
The effect of changing the kV is less easy to predict, and experimentation is required. Certainly increasing the kV will increase the film blackening - it will also decrease the contrast in blackening between earlywood and latewood, and it will tend to make the relationship between grayscale and density more linear. Increasing the kV too much should be avoided except perhaps with very thick samples, as it may reduce the ability of the system to accurately differentiate between wood of different densities.

The major criteria for a 'good' film image are:
1. a clear image with minimal blurring (this is best achieved by keeping the kV as low as possible)
2. minimum of grayscale spots, striations or gradients across the scanned film image. These can be observed and measured using Adobe Photoshop "Threshold" analysis.
3. an image with a large range of film grayscale values covered by the difference between earlywood and latewood (the difference between mean earlywood and mean latewood should be around/at least, say, 50 grayscale points).

A larger grayscale range facilitates more precise density determination - if the range is too small, it will only permit a very poor resolution of differentiation between wood of different densities.

Take care in determining acceptable settings for your material - these settings must be kept constant throughout your whole study.

While a film is exposing, a good idea is to bring out the spare masonite sheet and prepare the another set of transparencies with samples and labels for the next exposure. You will need to make regular trips to the conditioning room in the engineering wing to get freshly conditioned samples (say every couple of exposures).

After a film has finished being exposed, re-enter the emissions chamber, taking care to ensure no light is let in at any time. Pull the film out from under the transparencies (wear latex gloves at all times when handling the film), open the film box lid and place the exposed film in the back compartment of the box. Close the lid tightly and turn the light on ready to set more prepared samples in place for the next exposure.

Collect the transparency sheets afterwards and bring them to CSIRO along with the films - until a lead ink pen becomes available (not likely!), there is no other way of identifying the sample placement on the films.

When transporting the film box outside of the control chamber, tape up around the opening with masking tape, and carry inside black plastic bags.

Shut down the ANU densitometer according to the procedure on the reverse of the control room door. Remember to turn off the water - the pump unit has been known to leak large quantities.

STEP 4. DEVELOPING FILMS

Follow the instructions on the wall in the CSIRO darkroom for turning on and warming up the AGFA film developer. Ensure that the three bottles on top of the machine contain a sufficient amount of fluid (each should be at least about 1/8 full to develop several films). Charlie Bell is in charge of the developer (as at 2001) and can give instructions on how to use it. After the machine is warmed up (~8 minutes), turn the darkroom safelights on and close the doors.

Under safelight conditions, remove the film box from the black plastic bags or other cover, and remove masking tape from the film box to allow for removal of the lid. Remove the lid, and remove a single film for development. Feed the film into the developer via the metal input tray. We recommend feeding a single blank, unexposed, undeveloped film through the developer before developing any films for study - this acts to clean any dirt or dried fluid off the rollers. Allow the blank film to be developed, and examine it for blotches or streaks, before feeding any study films through. The rollers inside the developer may need to be examined or cleaned if they are consistently leaving black marks.

When developing films, wait until the film has completely passed through the developer and is sitting on the output tray, before turning on the fluorescent light in the darkroom.

STEP 5. CHECKING AND SCANNING IN FILMS

The films are fragile and the development process is sensitive to any dirt and impurities on the film surface. Occasionally, aberrations such as black scratching occur in the film image - if these obscure the image of any individual samples, it may be necessary to re-do that film exposure for the particular samples affected. So check the film image, either by holding up to the light or on a light table, before scanning in. Also note: any amount of water or other liquids on the films, either before or after developing, will ruin that part of the image. Be sure to keep the films dry, clean and free of lint.

After cutting out the films to just over A4 size, we found a useful system was to file the films away with their corresponding transparency sheets. CSIRO A4 size orange folders were good for keeping the film and transparency sheet together. Label each folder on the outside with the scan number and any other useful information. Hint: before placing the transparency into the folder, wipe it clean of dust and dirt using a cotton cloth (or on trouser leg). Otherwise the film will attract the dust onto it's surface - this will show up during scanning.

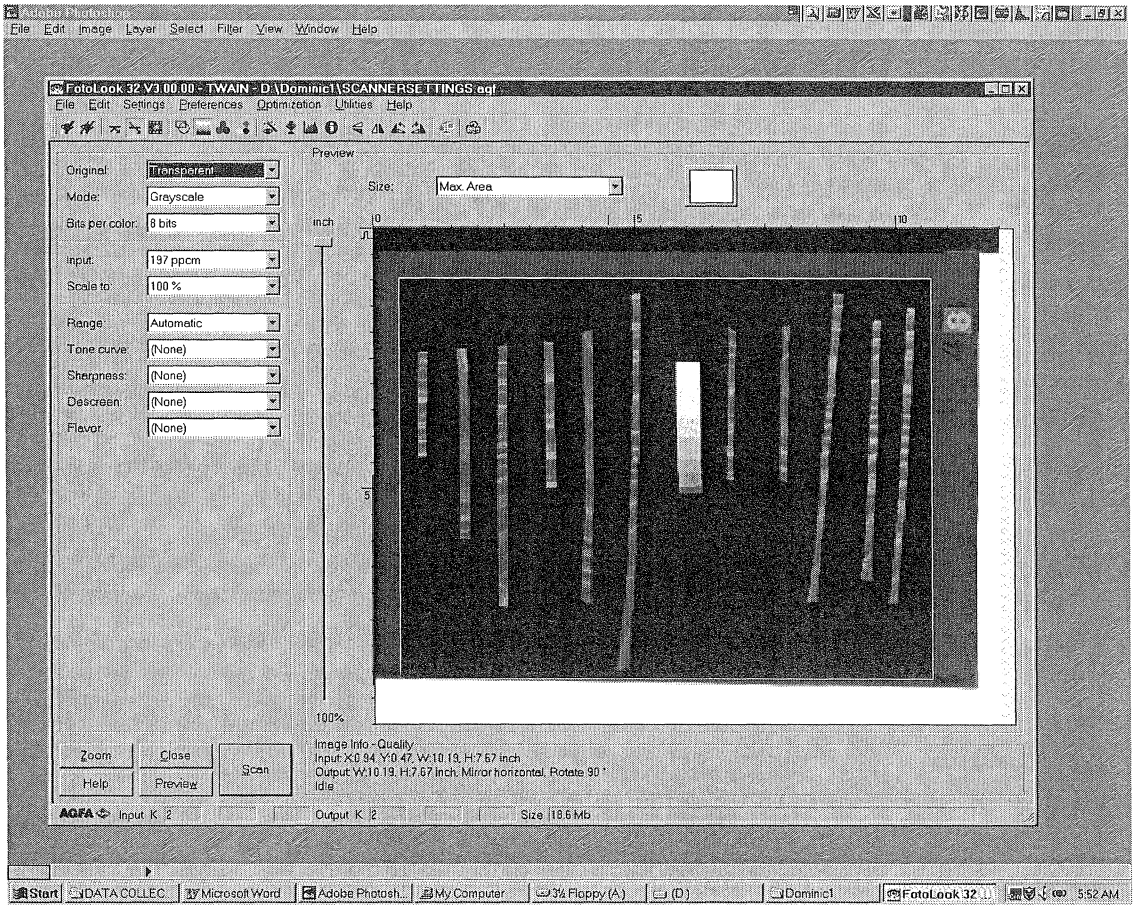
To scan in the film, first cut the film, using scissors or a cutting table, to a dimension that will fit onto the scanning tray. Wipe the film free of dust, and make sure that the film is pressed hard up against the glass of the scanner. It may be necessary to place small heavy objects around the perimeter of the film to hold it down. If the film is sticking up even slightly at the edges, a blurred image of samples in the vicinity may result and you will have to re-scan. Ensure that the calibration plate(s) film image and scanning are as perfect as possible.

To scan a film image, follow the instructions below:

- Open Adobe Photoshop
- Click on File menu → Import → Twain32 - the AGFA FotoLook window should open. Check that the following settings are selected:

- Scanning area: Maximum Area
- Source: Transparent (not reflective)
- Resolution: (we have found that 197ppcm is adequate, this produces images around 20MB)
- Optimization: Quality (not speed)
- All other settings should be at defaults / 'automatic'

The window should look similar to the one below, although the contents of the preview window will vary depending on what was scanned last:



Click on PREVIEW to preview the image - this takes 10-20 seconds.

On the preview image, drag the marquis to select the area to be scanned into the final image, and click on SCAN.

After the scanned image file "Untitled-1" has been created (2-3 minutes), save the file in your images directory as a TIFF file with PC configuration.

CHECKING X-RAY EXPOSURE SETTINGS

It is recommended, on the first films taken, to scan the images in using FotoLook or Photoshop, then with the images open in Photoshop, perform a 'threshold' analysis on the image. Go to Image →Analysis → Threshold on the toolbar, and examine the resulting plot, which should be very roughly shaped like a normal distribution. By moving the pointer from left to right on the plot, take note of at which grayscale levels earlywood and latewood disappear/come into view on the screen. The objective of this is to ensure that there is an adequate range (preferably >50 grayscale points) between earlywood and latewood grayscale. This will help increase the precision of density estimation.

OTHER CHECKING PROCEDURES

The threshold analysis is also used to check that there is not too great a range of grayscale values represented in the film background. Excessive grayscale (blackening) gradients across the image, worse still striations or blotches, will contribute to the error in density estimation. Under ideal conditions, the entire film background would be of uniform and low grayscale value.

Check that the samples/sample segments close to the edge of the film have been scanned in correctly. By moving the threshold pointer around the area between the background and the sample frequency distribution, see whether a flared pattern of grayscales results around the ends of samples close to the edges. This indicates blurring, or poor scanning. If present, re-scan, referring back to the first part of Step 5.

A decision must also be made on how many steps of the wedge to use when performing film calibrations. Steps on the wedge should not be included if they fall way outside the range of densities represented in wood samples on the plate. Decide on this by using the threshold tool in Adobe to cross-check between the wood and the acetate steps. Although in the maritime pine, slash pine and Caribbean pine material used in our study we found that the latewood density never exceeded the density of the third step of the wedge (three layers of acetate material), it may be the case with denser wood or thicker samples that the fourth wedge step needs to be used, to encompass the range of wood density variation encountered. To decide on this: while sliding the pointer along the threshold graph from left to right, compare the threshold appearances of the wedge steps with those of the latewood. If the latewood does not show (as white) past disappearance of the third wedge step, then the film background plus three wedge steps only need be used.

If working with softwoods, it is unlikely that use of any more than the third acetate wedge step would be necessary. In some cases, the third step of the wedge has been observed to add a degree of nonlinearity to the relationship between grayscale and density – specifically, this tends to occur when the grayscale values are very high (film may be slightly under-exposed). It should be noted here that the entire methodology of this manual is premised on finding a linear relationship between density and grayscale over the range of densities being assessed (this has been observed to hold without exception over hundreds of x-ray plates so far produced). However, where the third step of the wedge results in very high grayscale values, resulting nonlinearity may necessitate omission of this step from the calibration procedure. The film calibration regression would then be based on only three points: the film background, and the first and second steps of the wedge. I have written both 3-step and 4-step film calibration spreadsheets (FILM CALIBRATOR-3 STEP and FILM CALIBRATOR-4 STEP) which can be found in the RADIATA: \WINDENDRO USERS TOOLS directory. Use the instructions in **step 6** to help fill out the spreadsheet with your grayscale values.

STEP 6. ASSESSING DENSITIES ON AN X-RAY FILM IMAGE

The first step when assessing densities of samples on any film (wedge calibration set or otherwise) is to calibrate the film image (separate from calibrating the wedge). Each film image you assess, including the wedge calibration plate, must first be calibrated using the

film calibration spreadsheet **'film calibrator.xls'**. This spreadsheet contains density details for the acetate step wedge, which it matches up with wedge grayscale values that you input from your film. '**Film calibrator.xls**' then produces a regression of grayscale on density, with intercept zero, and outputs the FILM CALIBRATION VALUE (= the density value corresponding to 255 grayscale for your film). The film calibration value (**FCV**) should normally be between 3 and 4. **FCV** for your film is then inputted into WinDendro's 'Light Calibration Parameters - Advanced' window to complete the film calibration.

COMPLETING THE FILM CALIBRATION

⇒ Open WinDendro by clicking on the blue WinDendro icon in the top right hand corner of the screen. ↵

⇒ Click on CANCEL and then on OK to enter the program ↵

⇒ Click on the blue disk icon in the top left hand corner to bring up the 'open file' window ↵

⇒ Find the directory that your calibration plate image is in, and open the TIFF file ↵

⇒ Find the calibration wedge on the image and select Density → Start Calibration ↵

⇒ Draw a small marquis about the size of a calibration step on the blank film in front of the thinnest step of the calibration wedge. WinDendro will immediately tell you the grayscale value for this area. Record the value on paper and click on NEXT ↵

⇒ Draw a marquis on each of the first three steps of the wedge (first two steps if you are using a 3-step calibration), recording the grayscale values for each on paper ↵

⇒ Open the **'film calibrator –4 step.xls'** spreadsheet and enter in the grayscale values you have written down, in the first column of blank spaces headed 'grayscale'. The spreadsheet should produce an approximately linear regression line, and the **FCV** is shown highlighted in yellow. ↵

⇒ It is advisable to make background correction adjustments for the wedge. This is done by creating a small marquis on each side of each step of the wedge, and obtaining an average background value for that step. Enter these values alongside the wedge step values in **'film calibrator..'** in the 'background' column. Notice that the **FCV** changes slightly, and the regression line usually becomes more linear, after this adjustment. Check that the regression line in the plot is linear or almost totally linear.

You should now decide on whether you will use the 3-step or the 4-step film calibration. If your films consistently show non-linearity of wedge regression caused by the 4th step, then you should probably use the 3-step regression. However, if the non-linearity due to 4th step occurs only on occasional plates, you may simply need to re-do those exposures. If your line is linear across all 4 steps, then use the 4-step calibration. There are separate spreadsheets written for 3-step and 4-step, in the WinDendro Users Tools directory in D:\Radiata. See end of **step 5** for a discussion of 3-step vs 4-step calibration. *nb* the 3-step calibration program works slightly differently – it constructs a regression and plots it up on the screen. After entering in your grayscale values, you have to enter in the slope value (shown next to the plotted regression line) into the appropriate cell in the spreadsheet. The spreadsheet then calculates your FCV.

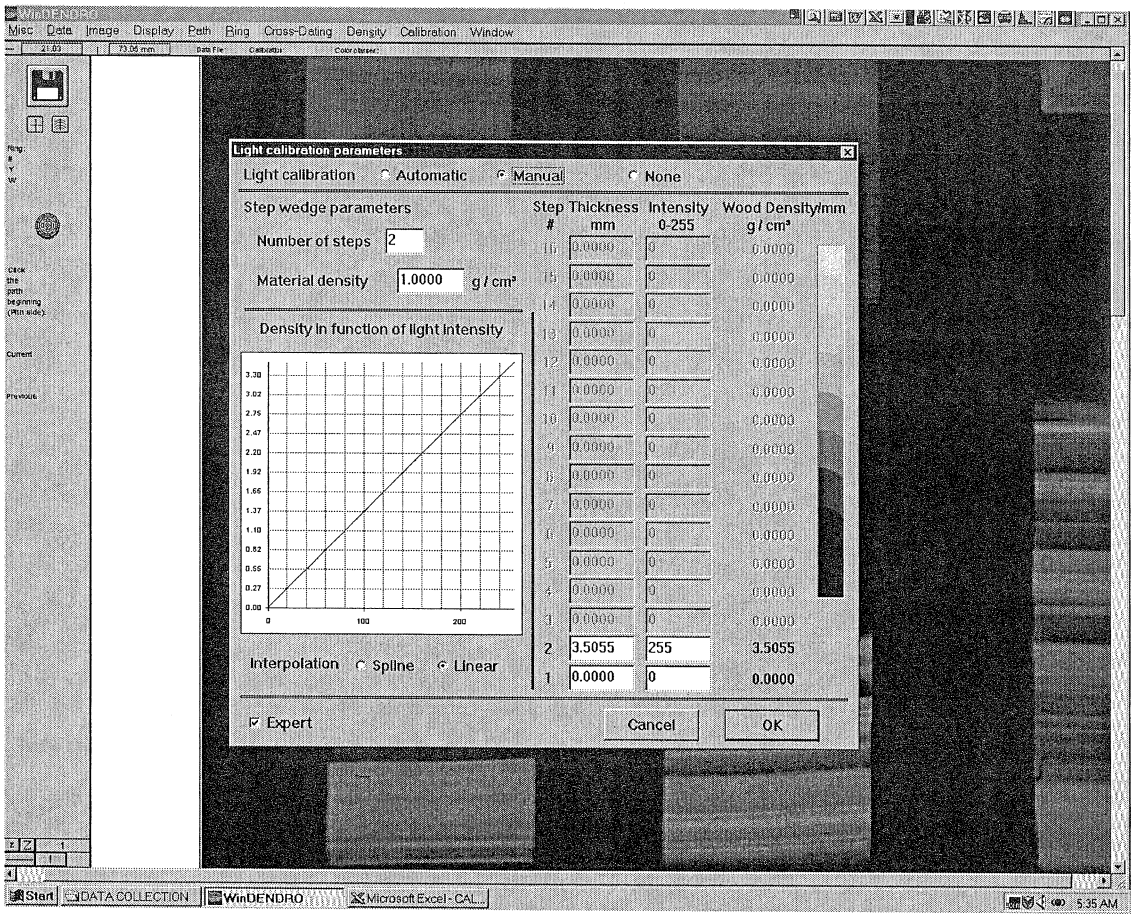
⇒ Assuming the line was linear: You now have your final **FCV** for that film.↵

Recommended: save the modified film calibrator.xls for each film in a subdirectory devoted to that particular film. Later on you can save the WinDendro individual sample assessments for that film in the same subdirectory.

⇒ Return to WinDendro and click on CANCEL calibration ↵
⇒ Go to Density → Light Calibration Parameters, to input your **FCV** into WinDendro.
⇒ First, ensure the following settings are in place:

- Light Calibration: Manual
- Number of steps = 2
- Material density = 1.0000 g/cm^3
- Interpolation: Linear
- [v] Expert
- Step 1: Thickness (mm) = 0.0000, Intensity = 0
- Step 2: Thickness (mm) = **<input your FCV>**, Intensity = 255

Your screen should look something as follows:



⇒ This has told WinDendro to perform a two-step calibration of the film with two points on the regression, 0 and 255 grayscale. Input your **FCV** as the 'thickness' equivalent for 255 grayscale (thickness = density as far as x-rays are concerned). ↵

⇒ Now click on 'OK' to input your film calibration into WinDendro. You're now ready to evaluate the density of samples on that film. ↵

SAMPLE ASSESSMENT

⇒ A blue instruction notice on the left hand side of the screen should read: 'click the path beginning pith side' ↵

⇒ Click to form the path beginning at the pith end of your sample. Now click to designate the path ending at the bark end of your sample. A red trace line with green ring indicators should appear on your sample. Now click on the green rings icon on the top left of the screen, and then on the black cross icon on the top left of the screen. ↵

⇒ Find a clear space on the blank film next to your sample, and mark in a trace parallel to your original sample trace, on the blank film. ↵

⇒ Click again on the green rings icon, and proceed to mark in the rings on your sample trace as instructed in the WinDendro manual. ↵

Some tips - keyboard shortcuts make WinDendro much faster and easier to use:
- zoom in/out using the + and - keys, to help position rings more accurately
- change the contrast using shift+j, shift+k, shift+l to get a better view
- move around the image using the up/down and left/right keyboard arrows
- move around quickly using the page up, page down, home and end keys
- press ENTER rather than clicking on OK at prompts.
- drag and drop ring boundaries by holding down shift while you do it
- alter the angle of ring boundaries by holding down shift while you drag and drop either end of the ring boundary to swivel them.
- see WinDendro manual for more complete instructions.

⇒ Once you have marked in the rings on your sample trace, now click on your background trace and mark in rings in approximately the same (parallel) positions. nb the purpose of the trace is to correct for localised grayscale variations on different parts of the film. ↵

⇒ Click on the green rings (top left of screen) icon to finalise the ring positions, then click on Data → New File, enter <your sample filename>, and click on OK. ↵

⇒ Now click on Data → Close file and hit YES (press enter). ↵

⇒ Now click on Path → Cancel Analysis, and repeat 'SAMPLE ASSESSMENT' instructions for every sample on your calibration (or routine) plate. ↵

COLLATING DATA

The above procedure, repeated for all samples on a plate, will have generated a large number of .pxb and .txt output files in a single folder. Colin Matheson has written a program that performs the background correction calculations in a large number of .pxb files at once, and sorts the density data into a single text file. Once you have all your .pxb files for a film in one folder, run the program "**summ.exe**" using the following instructions:

⇒ In windows explorer, place a copy of summ.exe into the folder containing the data files you want to compile.

⇒ Open a command prompt (MS DOS simulator) window ↵

⇒ Type in the path name for the subdirectory in which the files for collation are stored: for example: **D: radiata\pxbpro~1\19** ↵

nb the second folder here in the pathname is actually named "pxbprocessing" - names longer than 8 characters must be abbreviated as above when using MS DOS.

⇒ type in **dir *.pxb > pxb.txt** ↵

⇒ now open pxb.txt in Excel and edit out everything except for the filenames complete with their extensions. Save the resulting file as **pxb.dat**. ↵

⇒ return to the command prompt window and type **summ.exe** to run the program. ↵

⇒ now open the file '**results.out**' - this should contain a list of mean densities for the calibration samples. The file also contains other values - disregard these for the moment. Check that the mean values make sense (*eg* not outside the boundaries of 0 and 1).

STEP 7. CALIBRATING THE WEDGE

The file '**film calibrator.xls**' (both 3 and 4-step versions) contains some density values for the wedge steps, (in the first column) which are used as constants to calibrate each film to a common base. However, before we begin evaluating study samples, we must fine-tune these wedge density values so that they apply to the specific material of interest. The value highlighted in **red** in '**film calibrator.xls**' is referred to as the wedge critical value (**WCV**). This is the density of the first step of the wedge. As the other steps are only multiples of the first, the first can be considered critical.

The same WCV is used for every film of a given study. Between studies where different material is being evaluated, the WCV should be adjusted by performing a wedge calibration using the '**wedge calibrator.xls**' spreadsheet. We do this as follows:

⇒ Open '**results.out**' in Microsoft Excel. Copy the first two columns (sample label and average density) into the first two columns of the '**wedge calibrator.xls**' spreadsheet. Now find the basic densities for the calibration samples (obtained previously), and input these into the third column, alongside their corresponding densitometric estimates. ↵
⇒ Now construct a regression between the densitometric and gravimetric estimates:
⇒ Go to Tools → Data Analysis → Regression ↵
⇒ Input **Y** range: highlight **DENSITOMETRIC** data cells ↵
⇒ Input **X** range: highlight **GRAVIMETRIC** data cells ↵
⇒ **mix these the wrong way around & the ENTIRE calibration will be useless!**
⇒ Output range: select E6 ↵
⇒ click on OK ↵

Look at the regression output, and read the **Instructions** sheet of the '**wedge calibrator.xls**' spreadsheet for an explanation of the results. Most importantly, the R-square value should preferably exceed 0.98, and the Xvariable coefficient (X Variable 1 - Coefficient) should be noted.

⇒ To calculate the new WCV (wedge critical value), perform the following calculation:

$$\textbf{NEW WCV} = \frac{\textbf{OLD WCV}}{\textbf{X variable coefficient}}$$

⇒ Now input the new WCV (density value for the first step of the wedge, highlighted in RED) into the "**film calibrator.xls**" spreadsheet. The density values for the subsequent steps should change accordingly (multiples of the first step).

You have now completed a single wedge calibration. If your R-square value from the WEDGE CALIBRATION SPREADSHEET **equalled or exceeded 0.98**, and your X

coefficient satisfied **0.95<Xcoeff<1.05**, then you are ready to evaluate study samples - proceed to step 8. IF YOUR SUMMARY STATISTICS DID NOT SATISFY THESE CRITERIA, PERFORM THE ENTIRE WEDGE CALIBRATION PROCEDURE OVER AGAIN.

***I don't need to recalibrate*: proceed to step 8.**

***I need to recalibrate*: where should I re-start the procedure from?**

Here are some hints:

Usually, your R-square value should be pretty good (around 0.98 or higher - if not, see paragraph below for solutions). More commonly, the problem will be in the regression slope deviating from 1. If this is the case, you can probably keep your original calibration plate film images, and need only re-start from **step 6** - re-calibrate the film(s) with your newly revised/corrected **film calibrator.xls** spreadsheet. Make sure you have entered your new WCV and saved a new copy of the file - (*eg* 'film calibrator2.xls'?). Assess the sample densities on the calibration plate, once again enter these into the wedge calibrator spreadsheet and perform the regression as you have already done.

An R-square value of substantially less than 0.98 may be due to any of the following factors:

- excessive grayscale variation, irregular grayscale patterning or dark/light spots/heavy striations on your film plate (solution: re-do your calibration plate, starting from **step 3**).
- poor scan (make sure all parts of the film are pressed against the glass and not lifting off, otherwise blurring/poor estimates may result) (solution: start again from **step 5**).
- incorrect operation of WinDendro (eg failure to create a background trace line) (solution: graph the regression you have constructed, using the chart feature in Excel, and check any data points that deviate substantially from the trendline).
- too few calibration samples (ideally you should have 20-50, the more the better as long as they are of good quality (solution: see **step 2**).
- calibration samples do not cover a wide enough range of densities (solution: see **step 2**)

Note: if you do not have serious problems, around 1 to 2, sometimes 3 runs of the calibration procedure are usually adequate.

STEP 8. SCANNING OPERATIONAL SAMPLES

The procedure for scanning operational samples is to follow steps 3-5 for producing and checking your scans, and then follow step 6 through exactly for each film image to produce and collate the density evaluations.

Depending on the type of density information required, different file formats can be accessed. There is a choice between pixel based output, which gives raw density averages and Radial Variability Index parameters; and a ring based output, which gives ring, earlywood and latewood averages and other traits based on growth ring measurements.

Things to remember:

⇒ always double check that you have changed the calibration value in the 'light calibration parameters' window to the appropriate value for that film (as calculated by film calibrator.xls spreadsheet) before evaluating any of the samples on that film. Also check that other parts of the light calibration parameters window are filled in correctly (*eg* all zeros for the first step, 255 grayscale for the second step, no third step, material density = 1, etc.)

⇒ save a different copy of your film calibrator spreadsheet with the settings in it for each individual film.

COLLATING OPERATIONAL SAMPLE DATA

Pixel-based data may be collated using the program summ.exe as described in step 6. Where ring-based data is required, the programs RINGER.EXE or RINGREV.EXE may be used to collate the .txt files, which contain ring data. To use the program, follow the same instructions as given in step 6 for collating .pxb files, but instead use the command:

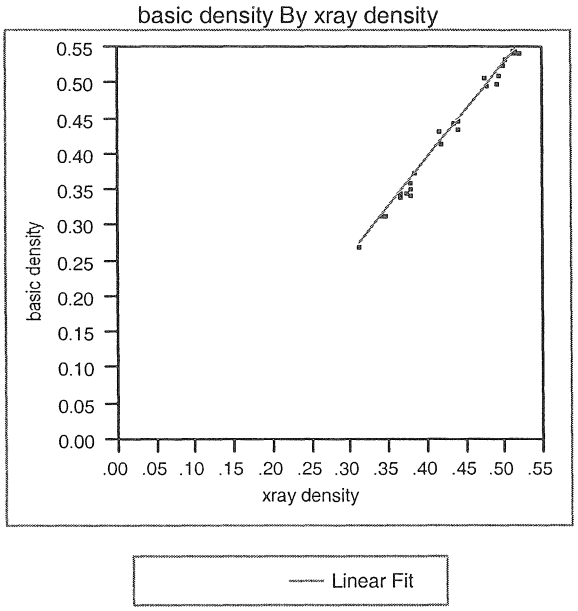
- **dir *.txt > txt.txt** - to create a text file containing the filenames of .txt files. After editing in Excel, save the file as '**txt.dat**'.

Collating a large number of files will place all of the data in a single text file which may be opened in Excel, edited and used for data analysis. The same goes for pixel data collated using SUMM.EXE.

If you wish to scale the densitometric ring measurements to gravimetric density (recommended in most cases) - you will need to create the file 'gravpxb.dat' containing the sample identities in one column, and the sample gravimetric densities next to them in another column. They will need to be sorted into the same order as in the txt.dat file. Run RINGREV.EXE - it will give you the option of whether to scale to gravimetric density or not. To scale: select lower case **y** and press ENTER. The program will give you a series of output traits in separate files - a separate file for each trait. You can open these output files (.out) in excel, then copy them into the same spreadsheet, side by side, if this is the format you want your data in for analysis using SAS, GENSTAT or other statistical program. Besides the standard WinDendro output traits, some other traits are calculated- these are in files 'oneg', 'twog' ... 'teng'. The names of the traits are given in column 2 when you open the file.

Appendix 3 Linear regressions used to calibrate the CSIRO FFP Yarralumla x-ray densitometer

CALIBRATION 1 - performed 2nd December 2000



Linear Fit
basic density = -0.1488 + 1.35435 xray density

Summary of Fit

RSquare	0.989996
RSquare Adj	**0.989561**
Root Mean Square Error	0.00874
Mean of Response	0.419818
Observations (or Sum Wgts)	25

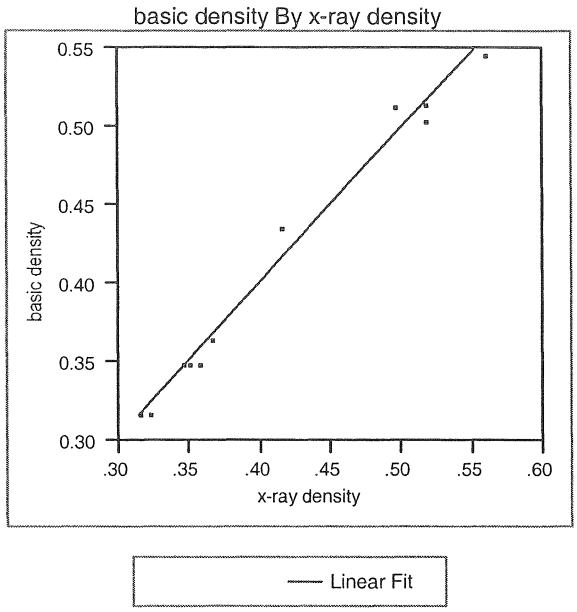
Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	1	0.17385564	0.173856	2276.084
Error	23	0.00175682	0.000076	Prob>F
C Total	24	0.17561247		<.0001

Parameter Estimates

Term	Estimate	Std Error	t Ratio	Prob>|t|
Intercept	-0.148764	0.012045	-12.35	<.0001
xray density	1.3543527	0.028388	47.71	<.0001

CALIBRATION 2 - performed 3th December 2000



Linear Fit
basic density = 0.00746 + 0.98201 x-ray density

Summary of Fit

RSquare	0.985037
RSquare Adj	**0.983374**
Root Mean Square Error	0.011557
Mean of Response	0.414944
Observations (or Sum Wgts)	11

Analysis of Variance

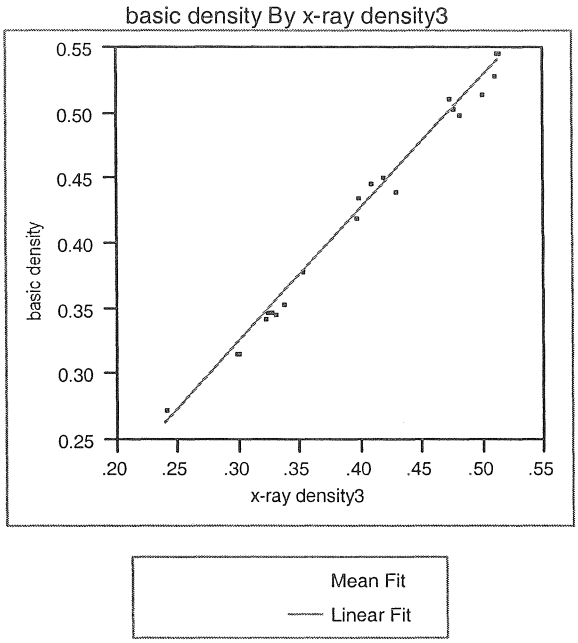
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	1	0.07912737	0.079127	592.4750
Error	9	0.00120199	0.000134	Prob>F
C Total	10	0.08032935		<.0001

Parameter Estimates

Term	Estimate	Std Error	t Ratio	Prob>|t|
Intercept	0.0074637	0.017099	0.44	0.6728
x-ray density	0.9820128	0.040344	24.34	<.0001

Note: this was a trial calibration and so included only a subsample of the calibration set

CALIBRATION 3 - performed 3th December 2000



Linear Fit
basic density = 0.01883 + 1.01886 x-ray density3

Summary of Fit

RSquare	0.990493
RSquare Adj	**0.990018**
Root Mean Square Error	0.008529
Mean of Response	0.42015
Observations (or Sum Wgts)	22

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	1	0.15156953	0.151570	2083.762
Error	20	0.00145477	0.000073	Prob>F
C Total	21	0.15302430		<.0001

Parameter Estimates

Term	Estimate	Std Error	t Ratio	Prob>|t|
Intercept	0.0188297	0.008978	2.10	0.0489
x-ray density3	1.0188607	0.02232	45.65	<.0001

Note: three samples were removed from the calibration set due to cracks

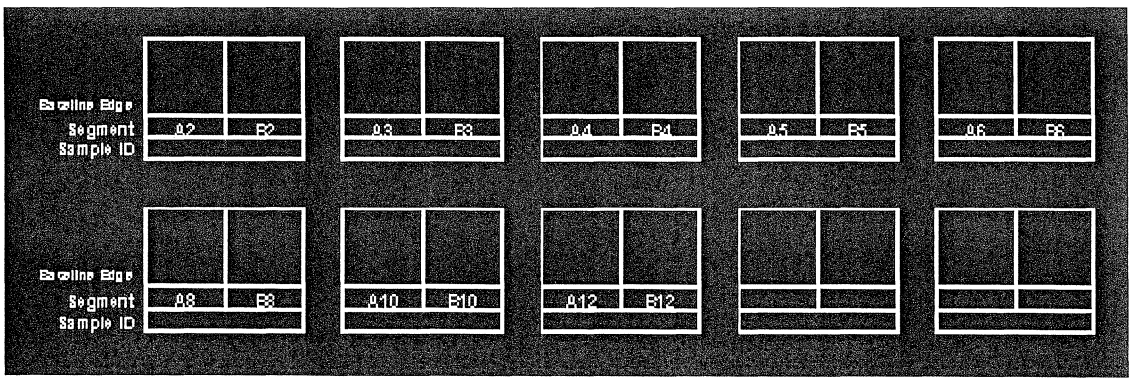
Appendix 4 User's manual for spiral grain measurement using ImageProV.4.1 - by Terence R. Copley and Jennifer J. Smout

MEASURING SPIRAL GRAIN ANGLES WITH ImageProV4.1

Preparing the Segment Rings for Image Capture:

(from section 6.4.8. Wood Quality Manual)

- Samples may be in the form of either a diametral strip or whole 12mm diameter core.
- Sample cores must be cleanly and continuously planed on at least one or both sides (see instructions for use of Makita planer).
- The upper surface must be smooth and level (this is used as the base-line for measurement).
- Trim ends of sample if 'burred', ensuring base line is not affected.
- Sort samples into numerical order and place in plastic containers.
- Soak samples thoroughly, especially if previously oven-dried.
- Remove sample from water and remove excess water with towel.
- Mark annual rings at outer latewood boundary, keeping 'base line' surface uppermost.
- Mark samples into segments of alternating rings, starting at Ring 1 nearest the pith or as stipulated in the working plan for the project.
- Clearly mark each segment with sample number for both A and B radii.
- Cut sample into marked segments.
- Number and mark the inner end of each segment, numerically from the pith, for both radii i.e. A1/B1, A2/B2 etc.
- It is most important to maintain the same upper and lower surface (base line) throughout i.e. keep sample number on top surface of each segment.
- Check to ensure correct orientation is maintained.
- Detach a thin sliver of the ring to be measured (approx 1.0 - 1.5mm thick)
- Mark the outer surface of the ring and the base line with a dot of indelible pencil to maintain the correct orientation of the sliver.
- Place the ring segment in the appropriately identified section of the "Spiral Grain Segment Proforma" template with the base line in the correct position on the form.



(Path = F:\WPP\WQG\PROJECTS\TEMPLATES AND FORMS\Spiral Grain Segment Proforma)

Capturing and Saving Images Using the Nikon *CoolPix 990* Camera.

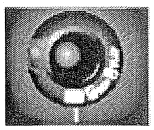
Have the camera mounted on the adjustable camera stand with the power-pack connected to the camera and turned on at the wall socket.

Transferring Images from Nikon *CoolPix 990* Camera to the Computer Directory.

After a sequence of images have been taken, they need downloading from the *CoolPix990's CompactFlash Memory card* to the SPIRAL GRAIN PICTURES directory and into the appropriate sub-directory corresponding to the sample identification for which the images belong.

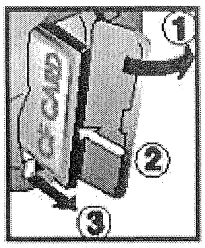
- In the *F:\Wpp\Wqg\Projects\ SPIRAL GRAIN PICTURES* directory, create new folders and rename them to that which represent the Tree/Sample number of the spiral segments that you have just captured the images of.
- Ensure the camera is **OFF**
- Remove the *CompactFlash Memory card* from the *CoolPix990.*

Inserting/Removing the Memory Card

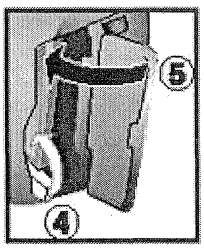


1 Turn the camera off
Turn the mode dial to the off position.

2 Insert the memory card
Open the card-slot cover (1) and insert the card (2) oriented as shown in the ▲ INSERT label on the underside of the cover, sliding it in until it is firmly in place at the back of the slot and the eject button pops up (3).

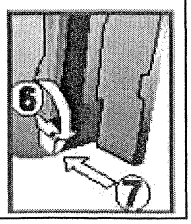


3 Close the card-slot cover
Fold the eject button back into position (4) and close the card-slot cover (5). If the button is not folded over when the cover is closed, closing the cover may partially eject the card, causing errors in recording photographs or during playback.



Removing memory cards

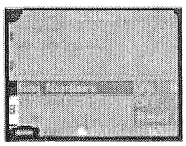
Memory cards can be removed without loss of data when the camera is off. To remove memory cards, turn the camera off and open the card-slot cover. Stand the eject button up (6) and press it down (7) to eject the card.



- Insert the *CompactFlash Memory card* into the **"Datafab" Image Reader** drive located on the right-hand side of the keyboard under the monitor.
- Open 2 copies of *Windows Explorer*. On one copy, locate and open the directory eg. path = *Image Card Reader\Dcim\100Nikon*..... which will show the spiral grain segment images that you have captured. On the other copy of *Windows Explorer*, locate the directory to where you will transfer the images to e.g. path = *F:\Wpp\Wqg\Projects\ SPIRAL GRAIN PICTURES*.... or into an appropriately created tree no. folder.
- Select appropriate pictures by highlighting and holding down button – drag and move across to correct tree No folder. – when it is highlighted release pictures to copy them across.
- Continue this process until all pictures have been moved to correct tree folder. Keep a note beside tree No. of the last photograph no. as a reference. Double click on a photo image to open and view that it is the correct tree. If photos are placed incorrectly – click on tree No. folder to open photos and then delete the incorrect photos.
- After double clicking on tree Nos. folder to ensure photos are present and correct, delete image files through Windows Explorer and this will clear the card as well. (control A to select all the image files).
- Remove *CompactFlash Memory card* from the card reader.

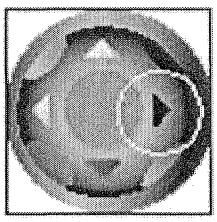
Reset the Numbers on the card

File Numbering



Photographs taken with the COOLPIX 990 are stored as image files. Each file is assigned a name consisting of "DSCN" plus a four-digit number assigned automatically by the camera. Although no two photographs in a single folder will have the same file name, photographs in different folders may share the same name, causing confusion when the files are copied to a computer. This can be prevented using the options in the **Seq. Numbers** submenu.

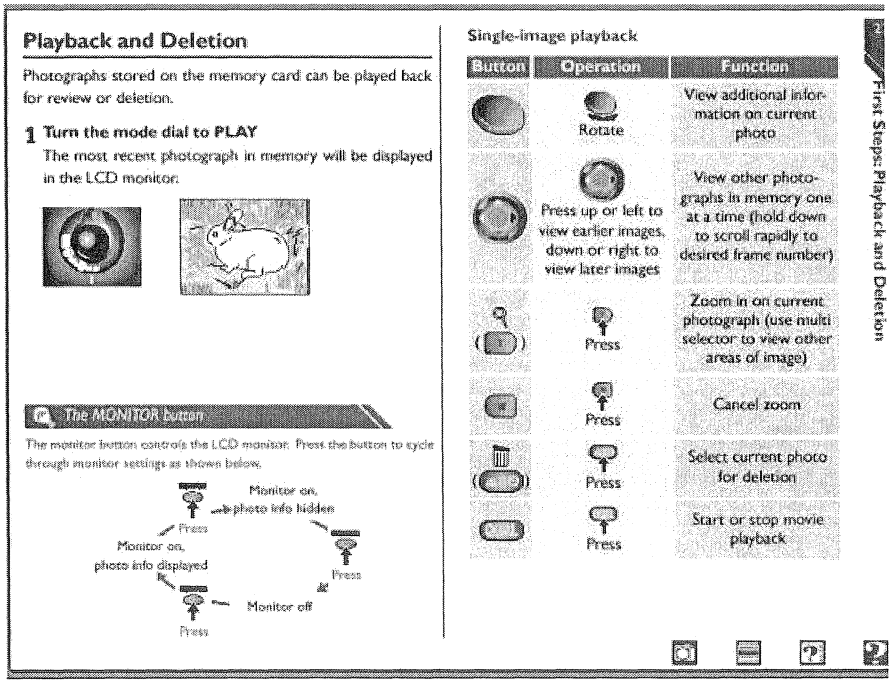
Option	Description
ON	When new folder is created, numbering will continue from last number used. All files will have unique names.
OFF	When new folder is created, numbering will begin from 0001. Files in different folders may have same name.
Reset	Resets sequential numbering to lowest number available on card



Insert the card into camera – automatic (A), press menu – press arrow (▼) down to *Seq. No.*, once highlighted set into place by pressing appropriate arrow-(▶),

arrow down(▼) to *reset*, once highlighted set into place by pressing the correct arrow (▶) and then press menu off and shut down camera if not required.

To clear the card while still in the camera (delete images).



Playback and Deletion

Photographs stored on the memory card can be played back for review or deletion.

1 Turn the mode dial to PLAY

The most recent photograph in memory will be displayed in the LCD monitor.

The MONITOR button

The monitor button controls the LCD monitor. Press the button to cycle through monitor settings as shown below.

Monitor on, photo info hidden → Press → Monitor on, photo info displayed → Press → Monitor off → Press → Monitor on, photo info hidden

Single-image playback

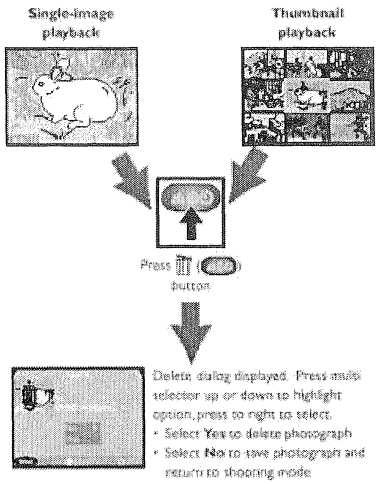
Button	Operation	Function
	Rotate	View additional information on current photo
	Press up or left to view earlier images, down or right to view later images	View other photographs in memory one at a time (hold down to scroll rapidly to desired frame number)
	Press	Zoom in on current photograph (use multi selector to view other areas of image)
	Press	Cancel zoom
	Press	Select current photo for deletion
	Press	Start or stop movie playback

First Steps: Playback and Deletion

Thumbnail playback

Button	Operation	Function
	Press	Press once to display menu of nine thumbnail images, twice to display four thumbnail images, a third time to return to single-image playback
	Rotate	Scroll through thumbnails page by page
	Press up, left, down, or right	Highlight thumbnail. Use ▦ button to view highlighted thumbnail at full size.
	Press	Select highlighted thumbnail for deletion

Deleting photographs



Switch to play, press menu, *play back menu* heading will come on screen, (▼) down to *delete*, OK this by (▶). (▼) down to *all images*, OK this by (▶) ,then press (▼) for *yes* , OK this by (▶).

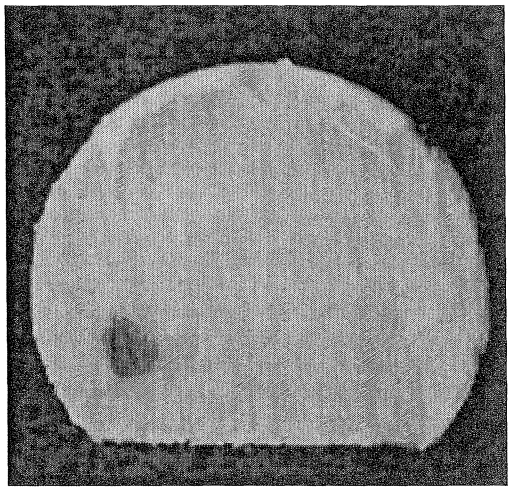
***Note**: Images can also be deleted from the CompactFlash Memory card through Windows Explorer as you would any other files…*

To review photographs already taken while still in the camera (see above)

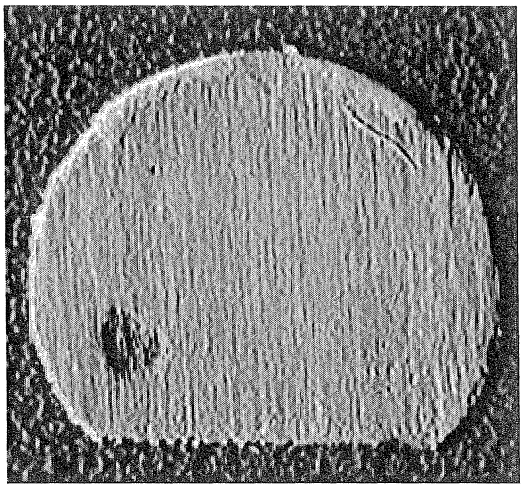
Useful also to check the number of the last photograph.
Switch to play, the last image taken will appear on the screen. To check back further, press (◀). After checking, switch back to Automatic and refocus before continuing photographing.

Embossing Spiral Grain Images.

Embossing and sharpening the images improves the grain features for Spiral Grain measurements.



Un-enhanced image from camera.



Embossed and sharpened image.

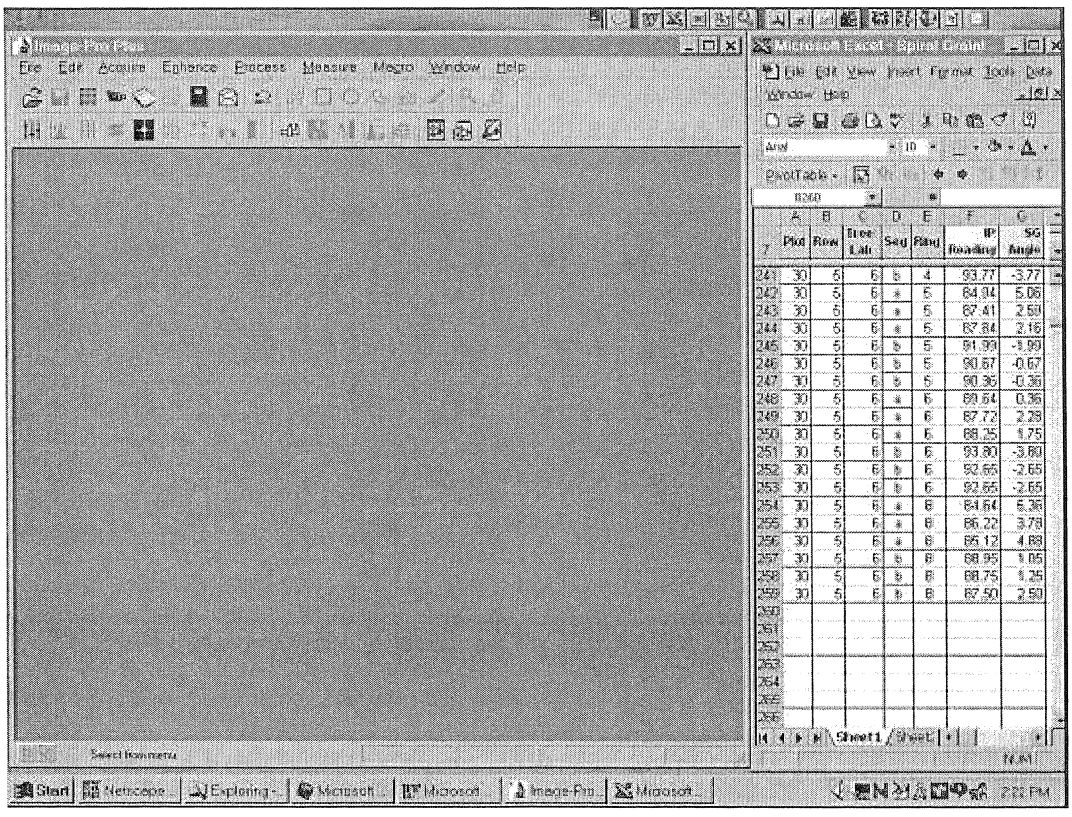
- Go to Programs, Microsoft Photo Editor, file, open, 'f' drive....through to SPIRAL GRAIN PICTURES. Click on appropriate tree and photo file contents will show up. Eg. DSCN0019(57)
- Double click to open photo. If image is too light – click image – Balance – move needles marginally to create improved effect-OK.
- Go to *Effects* on the Menu Bar and click *Emboss* (setting is needle at approx. 13 and light position left). Press *enter* for quick transaction. Return to *effects* and click *Sharpen*, (setting on 1-3), and press *enter*. Image should be greatly improved.
- File – Save as eg. A2B2.
- Close ONLY photo image – back to file, open and repeat until all samples are embossed for that tree.
- After adjusting last photo – close down and go to file open. (This saves having to relocate the file and next tree No.).
- Open Window Explorer, (which normally between trees you leave minimized for quick access and go to view refresh between trees). Negotiate to SPIRAL GRAIN PICTURES – click on tree No. that has just been embossed and check that all Renamed embossed photos are present. Delete all original photos eg. DSCN0019, as these are not required anymore.
- Highlight the folder, which is the tree no. – File – Rename - ensuring, after clicking on tree no. to add EMB on the end, that it is not highlighted. (Highlighted area will be deleted otherwise). Minimize for future access and return to next tree No. for embossing.

Opening an Excel File:

- Open an *Excel* spreadsheet as you would normally,
- On the Menu Bar, select *File* and go to *New,* select the *Spiral Grain* template from the active window and double-click to open it.
- Enter the appropriate project details at the top of the Excel SpiralGrain worksheet.
- On the menu bar, select *File* and go to *Save As* and name the file and save into the appropriate project directory in which you will be working.
- Now reduce the size of the *Excel* sheet onto the right hand side of the screen to approximately 9cm wide by 22cm high. (This so we can have both the *Excel* and *ImagePro* programs open and visible simultaneously on the desktop – see next section).

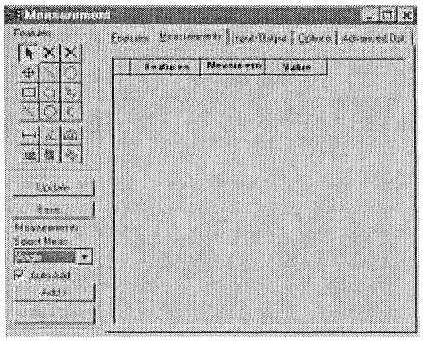
Opening ImageProV4.1:

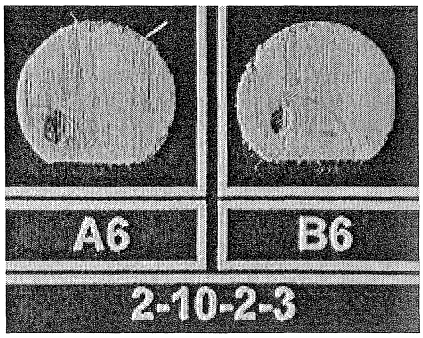
- Ensure the *ImagePro Protection Key (Dongel)* is inserted into the parallel port at the back of the computer tower. You will only be able to run ImagePro in "Demo Mode" without the *Protection Key.*
- Double-click the "*ImageProV4.1*" icon located on the desktop
- Resize the *ImagePro* window to fit into the remainder of the desktop so we now have both the *Excel* and *ImagePro* programs open and visible simultaneously on the desktop.



- Open a previously saved image of the rings that you will measure the Spiral Grain angles on by clicking on *File* and *Open* from the *ImagePro* menu bar.

- Navigate to the appropriate directory of the saved images and open the correct image e.g. A2B2 signifies segment A & B rings 2. A reduced image will open and may need to be magnified.
- On the *ImagePro* toolbar, click on the *Magnify* button to activate it.
- Now click on the previously opened image with the *Magnify* tool. This will enlarge the image into the reduced window.
- Maximise the image window by clicking on the maximise button on the top right of the image window.
- Now arrange the image so that you can see the segment properly within the window.
- On the *ImagePro* toolbar, select the *"Manual Measurements"* button. This will open up a *Measurement* Window . Slide the *Measurement* window to the top right of the screen so that you can see as much of the image as possible.





- In the *Measurement* window select the M*easurements* tab.
- Click on the *Angle Measurement* button, and take the *cross-hair*, +, cursor onto the A2 image and select the top end of a fibre line to be measured. Holding a left click on the mouse, drag a line to follow the angle of that fibre to the bottom of it (from top to bottom). This will create a line named L1 on the image.
- On the baseline of the A2 sample, slightly to the left of the base of the L1 line, hold a left click on the mouse and drag a line from left to right along the samples baseline. This creates a line named L2.
- An angle has now been produced which will be named AN1. In the *Measurement* window there is now an angle recorded in the *Value* column against the AN1 feature e.g. 82.18615.

	Features	Measurem	Value
1	AN1	Angle	82.18615

- If you are measuring 3 angles to get an average, then, create another 2 angles on the A segment in the same manner, being particular when you draw the baseline that you go over the same baseline as created in the first angle measure (notice that the *cross-hair* cursor changes colour when you are directly on another line). This is to ensure that the same reference (the Baseline) is identical for each of the 3 angles measured.
- Repeat another 3 angle measurements in the B segment on the open image – you may need to manipulate the image position in the window to have a clear view of the B segment.

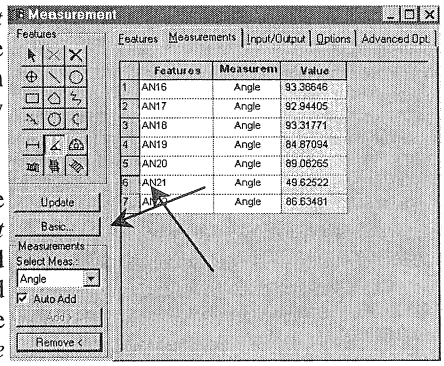
Note: *Always try and start the baseline measure slightly to the left of the vertical line and proceed to drag it 3 – 5 cm horizontally to the right. Otherwise some angles over 100 degs may be incorrectly obtained.*

- You should now have 6 angles measured, 3 for the A and 3 for the B ring segment.
- Slide the *Measurement* window over to the top left of the screen so you can see the *Excel* sheet properly.

Altering/Deleting Incorrect Lines or Angles.

If you are not satisfied with a line or angle, it is possible to alter or delete them on the image and/or in the *Measurement* window.

- To **alter** a lines position or angle on the image, go to the *Measurement* window and select the Arrow button or *Select features.* On the image, select the line with a left mouse click and a *Hand* cursor will appear and you will notice the line has been selected. If you go to either end of the line the Hand cursor will change to an *Arrowed Cross-hair* cursor . Hold a left click on the mouse and drag the line to the desired position. The angle will automatically be updated in the *Measurement* window.
- To **delete** an angle measurement in the *Measurement* window that has already been done, left click with the mouse on the selected line number e.g. 6 and then click on the *Remove* button. This removes the data from the window but not the lines on the actual image.



- To **delete** a particular line or angle on the image, go to the *Measurement* window and select the Arrow button or *Select features.* On the image, select the line or angle to be deleted with a left mouse click and a *Hand* cursor will appear and you will notice the line has been selected. In the *Measurement* window, click on the Black Cross or *Delete selected features.* This will only delete one line at a time.
- To **delete** all the line and angle features on an image and start measuring from the first line, go to the M*easurement* window and select the Red Cross or *Delete All features.*

Copying Measured Angles into Excel from the *Measurement* window:

All the appropriate sample ID's (Plot, Row, Tree/Lab Seg and ring) should have been entered into the proper cells in the *Excel* worksheet. You need this info for each angle measured for a pivot table to work properly.

- In the *ImagePro Measurement* window click on the first angle value for AN1 to select it.
- On the keyboard, do *Ctrl C* to copy this value.
- Mouse click into the appropriate cell in the *IP Reading* column in the *Excel* worksheet then on the keyboard do *Ctrl V* to paste the copied angle value into the cell. Advance to the next cell down in the *IP Reading* column.
- Mouse click back onto the 2nd angle value in the *Measurement* window and *Ctrl C* to copy again, then mouse click in the Excel sheet and *Ctrl V* to paste. Continue until you have copied and pasted all 6 of the angle values into the Excel sheet.

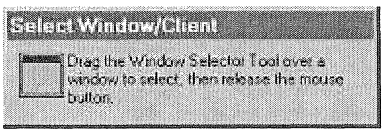
Notice that the SG Angle in the right column appear either as positive or negative numbers which reflect the slope of the SG angle from 90 degrees. If the vertical angle line slopes to the left, the SG angle will be negative.

- Save the *Excel* sheet regularly by doing *Alt, F and S* on the keyboard or Save from the *Excel Menu Bar.*

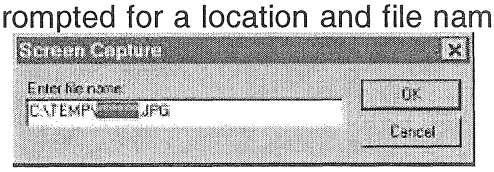
Saving the Image with the Angle Measurements.

Once an image has been overlayed with the grain angle measurement lines and all angle data has been transferred to the *Excel* worksheet, the ring segment image can now be saved into an appropriate project directory. This is accomplished by:

- Pressing the *F7* key on the keyboard.
- A *Select Window/Client* window is activated from which you drag the window selector tool over the ring segment window, then release the mouse button. Ensure that you only select the ring segment window by closing the *Measurement* window first.

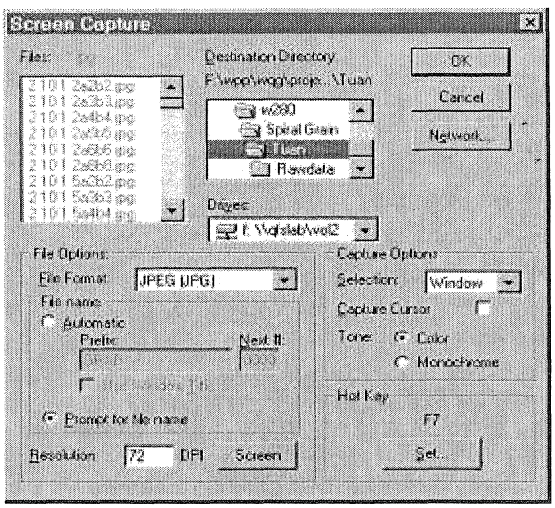


- You are then prompted for a location and file name in which to save the new image, e.g.



- Type in the appropriate file name (eg 2 10-1-2-A2B2) in the highlighted area and click the *OK* button – the image will have a horizontal line scroll down it and will be now saved

- To change the *Screen Capture* save location:
  - In *ImagePro*, click on *File*
  - Scroll down to *Screen Capture* and click (this will open the *Screen Capture* window – see below)
  - Navigate to the required "destination directory",



e.g. F:\wpp\wqg\projects\W280\Spiral Grain\Tuan

- Click *OK* (in top right corner – NOT THE SET BUTTON)
- **Keep each of the tree's images open in *ImagePro* until all ring segments have been measured.**
- Using Windows Explorer – (click on *View, Refresh* if *Explore*r has been previously opened) check, under the appropriate Project work folder/file, that all the images have been correctly saved.
- If any images are missing, return the images open in *ImagePro* and resave the missing one/s.
- Return to the *File, Open* window of *ImagePro,* select the folder corresponding to the tree you have just completed (and checked), you may need to go up one level first, and DELETE that folder using the delete button on the keyboard.

MAKE CERTAIN THAT YOU ARE DELETING THE CORRECT FOLDER.

Appendix 5 SAS code for calculating within-site and across-site least squares means for taxa, and testing significance of taxon × site interactions

```
/************************************
******  WITHIN-SITE LSMEANS  *********
************************************/

libname FINAL 'c:\windows\desktop\working\phdanlys\FINAL';

data TOTAL; set FINAL.TOTAL;

/**** re-scaling variables *****/

T=TAXON;
S=SITE;
R=REP;
F=FEMALE;
M=MALE;
PROT= SQRT(((SPGN+SPGS)/2)**2); * mean bark window spiral angle;
UBVOL= ((BAUB*(HT*1000))/2)/(1000);

/*NOTE: the program below puts its results into a set of txt files in \pheno folder
        you have to open them in excel*/

PROC SORT;
BY SITE;

PROC GLM;
BY SITE;
CLASS S T R;
MODEL

HT DBHOB DBHUB BAOB BAUB OBVOL UBVOL STR
GRAV DENS JUVDENS MATDENS EWD JUVEWD MATEWD LWD JUVLWD MATLWD LWP JUVLWP MATLWP
SLOPE DEV DWWI PROT SGMEAN SGSD

= T R T*R;
LSMEANS T / OUT=CH3TMEANSWS;
DATA CH3TMEANSWS; SET CH3TMEANSWS; FILE
'c:\windows\desktop\working\phdanlys\FINAL\pheno\CH3TMEANSWS.TXT';
PUT _NAME_ T S LSMEAN STDERR;
RUN;
```

```
/************************************************
******* ACROSS-SITE LSMEANS CHAPTER 3 TRAITS *******
************************************************/

libname FINAL 'c:\windows\desktop\working\phdanlys\FINAL';

data TOTAL; set FINAL.TOTAL;

T=TAXON;
S=SITE;
R=REP;
F=FEMALE;
M=MALE;
PROT= SQRT(((SPGN+SPGS)/2)**2); * mean bark window spiral angle;
UBVOL= ((BAUB*(HT*1000))/2)/(1000);

PROC GLM;
CLASS T S R;
MODEL

HT DBHOB DBHUB BAOB BAUB OBVOL UBVOL STR
GRAV DENS JUVDENS MATDENS EWD JUVEWD MATEWD LWD JUVLWD MATLWD LWP JUVLWP MATLWP
SLOPE DEV DWWI PROT SGMEAN SGSD

= S T R(S) S*T T*R(S);
random R(S) T*R(S) / test;
LSMEANS T / tdiff OUT=CH3TMEANS ;
DATA CH3TMEANS; SET CH3TMEANS; FILE
'c:\windows\desktop\working\phdanlys\FINAL\pheno\CH3TMEANS.TXT';
PUT _NAME_ T LSMEAN STDERR;
RUN;
```

Appendix 6 SAS code for performing linear contrasts of hybrid on mid-parent and hybrid on better parent

```
/*************************************************************************
TESTING WHETHER F1 AND F2 MEAN PERFORMANCE IS SIGNIFICANTLY DIFFERENT FROM
THE PURE SPECIES MID-PARENT, AT EACH SITE, USING LINEAR CONTRASTS
*************************************************************************/

libname FINAL 'c:\windows\desktop\working\phdanlys\FINAL';

data TOTAL; set FINAL.TOTAL;

T=TAXON;
S=SITE;
R=REP;
F=FEMALE;
M=MALE;
PROT= SQRT(((SPGN+SPGS)/2)**2); * mean bark window spiral angle;
UBVOL= ((BAUB*(HT*1000))/2)/(1000);


******* TRAITS IN WHICH F2 WAS MEASURED *******;

PROC GLM;

CLASS S T R;
MODEL

HT DBHOB BAOB OBVOL STR PROT GRAV

= S T R(S) S*T T*R(S);
random R(S) T*R(S);

contrast 'tuan F1 vs midparent' T  -0.5 -0.5 1 0
                              S*T -0.5 -0.5 1 0 0 0 0 0;

contrast 'beerwah F1 vs midparent' T -0.5 -0.5 1 0
                                 S*T 0 0 0 0 -0.5 -0.5 1 0;

contrast 'tuan F2 vs midparent' T -0.5 -0.5 0 1
                              S*T -0.5 -0.5 0 1 0 0 0 0;

contrast 'beerwah F2 vs midparent' T -0.5 -0.5 0 1
                                 S*T 0 0 0 0 -0.5 -0.5 0 1;


LSMEANS T / tdiff OUT=CH3TMEANS ;

RUN;
```

```
******* TRAITS IN WHICH F2 WAS NOT MEASURED *******;

libname FINAL 'c:\windows\desktop\working\phdanlys\FINAL';

data TOTAL; set FINAL.TOTAL;

T=TAXON;
S=SITE;
R=REP;
F=FEMALE;
M=MALE;
PROT= SQRT(((SPGN+SPGS)/2)**2); * mean bark window spiral angle;
UBVOL= ((BAUB*(HT*1000))/2)/(1000);

PROC GLM;

CLASS S T R;
MODEL

UBVOL DWWI DBHUB BAUB SLOPE DEV DENS JUVDENS MATDENS LWP EWD LWD

= S T R(S) S*T T*R(S);
random R(S) T*R(S);

contrast 'tuan F1 vs midparent' T  -0.5 -0.5 1
                              S*T -0.5 -0.5 1 0 0 0;

contrast 'beerwah F1 vs midparent' T -0.5 -0.5 1
                                  S*T 0 0 0 -0.5 -0.5 1;

LSMEANS T / tdiff OUT=CH3TMEANS ;

RUN;



/*************************************************************************
TESTING WHETHER F1 AND F2 MEAN PERFORMANCE IS SIGNIFICANTLY DIFFERENT FROM
THE PURE SPECIES BETTER PARENT, AT EACH SITE, USING LINEAR CONTRASTS
*************************************************************************/

libname FINAL 'c:\windows\desktop\working\phdanlys\FINAL';

data TOTAL; set FINAL.TOTAL;

T=TAXON;
S=SITE;
R=REP;
F=FEMALE;
M=MALE;
PROT= SQRT(((SPGN+SPGS)/2)**2); * mean bark window spiral angle;
UBVOL= ((BAUB*(HT*1000))/2)/(1000);



******* TRAITS IN WHICH F2 WAS MEASURED *******;
```

```
PROC GLM;

CLASS S T R;
MODEL

HT DBHOB BAOB OBVOL STR PROT GRAV

= S T R(S) S*T T*R(S);
random R(S) T*R(S);

contrast 'tuan F1 vs Pee' T  -1 0 1 0
                         S*T -1 0 1 0 0 0 0 0;

contrast 'tuan F1 vs Pch' T  0 -1 0 1
                         S*T 0 -1 0 1 0 0 0 0;

contrast 'tuan F2 vs Pee' T  -1 0 0 1
                         S*T -1 0 0 1 0 0 0 0;

contrast 'tuan F2 vs Pch' T 0 -1 0 1
                         S*T 0 -1 0 1 0 0 0 0;

contrast 'tuan F1 vs F2'  T 0 0 1 -1
                         S*T 0 0 1 -1 0 0 0 0;


contrast 'beerwah F1 vs Pee' T  -1 0 1 0
                            S*T 0 0 0 0 -1 0 1 0;

contrast 'beerwah F1 vs Pch' T  0 -1 0 1
                            S*T 0 0 0 0 0 -1 0 1;

contrast 'beerwah F2 vs Pee' T  -1 0 0 1
                            S*T 0 0 0 0 -1 0 0 1;

contrast 'beerwah F2 vs Pch' T 0 -1 0 1
                            S*T 0 0 0 0 0 -1 0 1;

contrast 'beerwah F1 vs F2'  T 0 0 1 -1
                            S*T 0 0 0 0 0 0 1 -1;


LSMEANS T / tdiff OUT=CH3TMEANS ;

RUN;
```

```
******* TRAITS IN WHICH F2 WAS NOT MEASURED *******;

libname FINAL 'c:\windows\desktop\working\phdanlys\FINAL';

data TOTAL; set FINAL.TOTAL;

T=TAXON;
S=SITE;
R=REP;
F=FEMALE;
M=MALE;
PROT= SQRT(((SPGN+SPGS)/2)**2);
PROT_=PROT;                * mean bark window spiral angle;
UBVOL= ((BAUB*(HT*1000))/2)/(1000);
UBVOL_=UBVOL/10000;

PROC GLM;
CLASS S T R;
MODEL

UBVOL DWWI DBHUB BAUB SLOPE DEV DENS JUVDENS MATDENS LWP EWD LWD

= S T R(S) S*T T*R(S);
random R(S) T*R(S);


contrast 'tuan F1 vs Pee' T  -1 0 1
                         S*T  -1 0 1 0 0 0;

contrast 'tuan F1 vs Pch' T  0 -1 1
                         S*T  0 -1 1 0 0 0;

contrast 'beerwah F1 vs Pee' T  -1 0 1
                            S*T  0 0 0 -1 0 1;

contrast 'beerwah F1 vs Pch' T  0 -1 1
                            S*T  0 0 0 0 -1 1;

LSMEANS T / tdiff OUT=CH3TMEANS ;

RUN;
```

Appendix 7 SAS code for REML analysis of variance in PEE, PCH, F_1 and F_2: single-site analysis, Chapter 3, 4 and 5 traits

PATH: D:\ACRSITE\PHENO\RAW TRAITS WS ANALYSIS.SAS

```
/*************************************************************************
********** SINGLE-SITE ANALYSIS OF VARIANCE - CH 3 AND 4 TRAITS*************
*************************************************************************/

libname FINAL 'D:\FINAL';

data TOTAL; set FINAL.TOTAL;

T=TAXON;
S=SITE;
R=REP;
F=FEMALE;
M=MALE;
PROT= SQRT(((SPGN+SPGS)/2)**2); * mean bark window spiral angle;
UBVOL= ((BAUB*(HT*1000))/2)/(1000);

proc sort;
by taxon;

/*************ANALYSIS OF WHOLE TREE TRAITS************/

****** SLASH PINE **************;

PROC VARCOMP METHOD=REML; OPTIONS NODATE PAGESIZE=MAX LINESIZE=MAX;
BY S;
WHERE T=1;
CLASS R F M;
MODEL
HT DBHOB DBHUB BAOB BAUB OBVOL UBVOL STR
GRAV DENS JUVDENS MATDENS EWD JUVEWD MATEWD LWD JUVLWD MATLWD LWP JUVLWP MATLWP
SLOPE DEV DWWI PROT

= R F M R*F R*M F*M;
RUN;


****** CARIBBEAN PINE **********;

PROC VARCOMP METHOD=REML; OPTIONS NODATE PAGESIZE=MAX LINESIZE=MAX;
BY S;
WHERE T=2;
CLASS R F M;
MODEL
HT DBHOB DBHUB BAOB BAUB OBVOL UBVOL STR
GRAV DENS JUVDENS MATDENS EWD JUVEWD MATEWD LWD JUVLWD MATLWD LWP JUVLWP MATLWP
SLOPE DEV DWWI PROT

= R F M R*F R*M F*M;
RUN;
```

```
****** F1 HYBRID ***************;

PROC VARCOMP METHOD=REML; OPTIONS NODATE PAGESIZE=MAX LINESIZE=MAX;
BY S;
WHERE T=3;
CLASS R F M;
MODEL
HT DBHOB DBHUB BAOB BAUB OBVOL UBVOL STR
GRAV DENS JUVDENS MATDENS EWD JUVEWD MATEWD LWD JUVLWD MATLWD LWP JUVLWP MATLWP
SLOPE DEV DWWI PROT SGMEAN SGSD

= R F M R*F R*M F*M;
RUN;


****** F2 HYBRID ***************

** NOTE: F2 HYBRID DATA USED ONLY IN CHAPTER 3, NOT IN CHAPTER 4 *****

PROC VARCOMP METHOD=REML; OPTIONS NODATE PAGESIZE=MAX LINESIZE=MAX;
BY S;
WHERE T=4;
CLASS R F M;
MODEL
HT DBHOB DBHUB BAOB BAUB OBVOL UBVOL STR
GRAV DENS JUVDENS MATDENS EWD JUVEWD MATEWD LWD JUVLWD MATLWD LWP JUVLWP MATLWP
SLOPE DEV DWWI PROT

= R F M R*F R*M F*M;
RUN;



/*****************************************************************************
************ SINGLE-SITE ANALYSIS OF VARIANCE - CH 5 TRAITS  *****************
*****************************************************************************/

****** SLASH PINE **************;

PROC VARCOMP METHOD=REML; OPTIONS NODATE PAGESIZE=MAX LINESIZE=MAX;
BY S;
WHERE T=1;
CLASS R F M;
MODEL
CMBA88 CMBA89 CMBA90 CMBA91 CMBA92 CMBA93 CMBA94 CMBA95 CMBA96 CMBA97 CMBA98
CUMRD88 CUMRD89 CUMRD90 CUMRD91 CUMRD92 CUMRD93 CUMRD94 CUMRD95 CUMRD96 CUMRD97 CUMRD98
RD88 RD89 RD90 RD91 RD92 RD93 RD94 RD95 RD96 RD97 RD98
cumrd1 cumrd2 cumrd3 cumrd4 cumrd5 cumrd6 cumrd7 cumrd8 cumrd9 cumrd10 cumrd11
rd1 rd2 rd3 rd4 rd5 rd6 rd7 rd8 rd9 rd10 rd11
PILN1 PILN2 PILS1 PILS2 PILNTH PILSTH PILMN
HT DBHOB OBVOL STR DENS SLOPE DEV
JUVDENS MATDENS LWP EWD LWD DWWI

= R F M R*F R*M F*M;
RUN;
```

```
****** CARIBBEAN PINE **********;

PROC VARCOMP METHOD=REML; OPTIONS NODATE PAGESIZE=MAX LINESIZE=MAX;
BY S;
WHERE T=2;
CLASS R F M;
MODEL
CMBA88 CMBA89 CMBA90 CMBA91 CMBA92 CMBA93 CMBA94 CMBA95 CMBA96 CMBA97 CMBA98
CUMRD88 CUMRD89 CUMRD90 CUMRD91 CUMRD92 CUMRD93 CUMRD94 CUMRD95 CUMRD96 CUMRD97 CUMRD98
RD88 RD89 RD90 RD91 RD92 RD93 RD94 RD95 RD96 RD97 RD98
cumrd1 cumrd2 cumrd3 cumrd4 cumrd5 cumrd6 cumrd7 cumrd8 cumrd9 cumrd10 cumrd11
rd1 rd2 rd3 rd4 rd5 rd6 rd7 rd8 rd9 rd10 rd11
PILN1 PILN2 PILS1 PILS2 PILNTH PILSTH PILMN
HT DBHOB OBVOL STR DENS SLOPE DEV
JUVDENS MATDENS LWP EWD LWD DWWI

= R F M R*F R*M F*M;
RUN;

****** F1 HYBRID ***************;

PROC VARCOMP METHOD=REML; OPTIONS NODATE PAGESIZE=MAX LINESIZE=MAX;
BY S;
WHERE T=3;
CLASS R F M;
MODEL
CMBA88 CMBA89 CMBA90 CMBA91 CMBA92 CMBA93 CMBA94 CMBA95 CMBA96 CMBA97 CMBA98
CUMRD88 CUMRD89 CUMRD90 CUMRD91 CUMRD92 CUMRD93 CUMRD94 CUMRD95 CUMRD96 CUMRD97 CUMRD98
RD88 RD89 RD90 RD91 RD92 RD93 RD94 RD95 RD96 RD97 RD98
cumrd1 cumrd2 cumrd3 cumrd4 cumrd5 cumrd6 cumrd7 cumrd8 cumrd9 cumrd10 cumrd11
rd1 rd2 rd3 rd4 rd5 rd6 rd7 rd8 rd9 rd10 rd11
SG90 SG91 SG92 SG93 SG94 SG96
PILN1 PILN2 PILS1 PILS2 PILNTH PILSTH PILMN
SGMEAN SGSD HT DBHOB OBVOL STR DENS SLOPE DEV
JUVDENS MATDENS LWP EWD LWD DWWI

= R F M R*F R*M F*M;
RUN;
```

Appendix 8 SAS code for REML analysis of variance in PEE, PCH, F_1 and F_2: pooled across-site analysis of unstandardised data, Chapter 3

PATH: D:\ACRSITE\PHENO\RAW TRAITS AS ANALYSIS.SAS

```
/*****************************************************************************
******* ACROSS-SITE ANALYSIS OF VARIANCE IN UNSTANDARDISED DATA ******************
*** - TO BE USED ONLY TO CALCULATE PHENOTYPIC VARIANCES, FOR USE IN CHAPTER 3 *****
*****************************************************************************/

libname FINAL 'D:\FINAL';

data TOTAL; set FINAL.TOTAL;

T=TAXON;
S=SITE;
R=REP;
F=FEMALE;
M=MALE;
PROT= SQRT(((SPGN+SPGS)/2)**2); * mean bark window spiral angle;
UBVOL= ((BAUB*(HT*1000))/2)/(1000);

PROC SORT;
BY T;

PROC VARCOMP METHOD=REML; OPTIONS NODATE PAGESIZE=MAX LINESIZE=MAX;
BY T;
CLASS S R F M;
MODEL
HT DBHOB DBHUB BAOB BAUB OBVOL UBVOL STR
GRAV DENS JUVDENS MATDENS EWD JUVEWD MATEWD LWD JUVLWD MATLWD LWP JUVLWP MATLWP
SLOPE DEV DWWI PROT SGMEAN SGSD

= S R(S) F F*S F*R(S) M M*S M*R(S) F*M F*M*S;
RUN;


/* note: traits SGMEAN (mean of internal spiral grain measurements) and SGSD (standard
deviation of internal spiral grain measurements) not measured in PEE or PCH, only in F1
hybrid.  SAS only fits the model to these traits in the hybrid */
```

Appendix 9 SAS code for least squares and REML analysis of variance in PEE, PCH and F_1: pooled across-site analysis of standardised data, Chapter 4

PATH: D:\ACRSITE\ACROSS-SITE\ACROSS-SITE CODE 1

```
/*********************************************************************
******** ACROSS-SITE ANALYSIS, STANDARDISED DATA, CH 3/4 TRAITS *****
*********************************************************************/

libname FINAL 'D:\FINAL';

data TOTAL; set FINAL.TOTAL;

T=TAXON;
S=SITE;
R=REP;
F=FEMALE;
M=MALE;
PROT= SQRT(((SPGN+SPGS)/2)**2); * mean bark window spiral angle;
UBVOL= ((BAUB*(HT*1000))/2)/(1000);

/* STANDARDISING DATA TO REMOVE HETEROGENEITY OF VARIANCES BETWEEN SITES */

** Note: all standardised variables are denoted VARNAME_S

if taxon =1 and site =1 then DENS_S=(DENS/9.42551)*100;
else if taxon =1 and site =2 then DENS_S=(DENS/9.27948)*100;
else if taxon =2 and site =1 then DENS_S=(DENS/8.1455)*100;
else if taxon =2 and site =2 then DENS_S=(DENS/13.79203)*100;
else if taxon =3 and site =1 then DENS_S=(DENS/7.95651)*100;
else if taxon =3 and site =2 then DENS_S=(DENS/11.38236)*100;

if taxon =1 and site =1 then BAUB_S=(BAUB/16.5129)*100;
else if taxon =1 and site =2 then BAUB_S=(BAUB/11.42707)*100;
else if taxon =2 and site =1 then BAUB_S=(BAUB/22.19278)*100;
else if taxon =2 and site =2 then BAUB_S=(BAUB/25.37078)*100;
else if taxon =3 and site =1 then BAUB_S=(BAUB/40.69877)*100;
else if taxon =3 and site =2 then BAUB_S=(BAUB/31.90042)*100;

if taxon =1 and site =1 then DWWI_S=(DWWI/2.46694)*100;
else if taxon =1 and site =2 then DWWI_S=(DWWI/1.91933)*100;
else if taxon =2 and site =1 then DWWI_S=(DWWI/2.69211)*100;
else if taxon =2 and site =2 then DWWI_S=(DWWI/3.76321)*100;
else if taxon =3 and site =1 then DWWI_S=(DWWI/5.0373)*100;
else if taxon =3 and site =2 then DWWI_S=(DWWI/5.30626)*100;

/* similar standardisation code for all traits analysed in the statistical models below
..................
..................                                          */

if taxon =1 and site =1 then PROT_S=(PROT/1.39685)*100;
else if taxon =1 and site =2 then PROT_S=(PROT/1.34743)*100;
else if taxon =2 and site =1 then PROT_S=(PROT/1.77571)*100;
else if taxon =2 and site =2 then PROT_S=(PROT/1.63819)*100;
else if taxon =3 and site =1 then PROT_S=(PROT/1.68042)*100;
else if taxon =3 and site =2 then PROT_S=(PROT/1.55707)*100;
```

```
/*********** OBTAINING TYPE III EMS COEFFICIENTS  ***************
 ***************** ACROSS-SITE USING PROC GLM ********************/

PROC SORT; BY T;

PROC GLM;
BY T;
CLASS S R F M;
model
HT_S DBHOB_S DBHUB_S BAOB_S BAUB_S OBVOL_S UBVOL_S STR_S
GRAV_S DENS_S JUVDENS_S MATDENS_S EWD_S JUVEWD_S MATEWD_S
LWD_S JUVLWD_S MATLWD_S LWP_S JUVLWP_S MATLWP_S
SLOPE_S DEV_S DWWI_S PROT_S SGMEAN_S SGSD_S

= S R(S) F F*S F*R(S) M M*S M*R(S) F*M F*M*S;
RANDOM S R(S) F F*S F*R(S) M M*S M*R(S) F*M F*M*S;
RUN;


/****************** ESTIMATING VARIANCE COMPONENTS *********************
****************** ACROSS-SITE USING PROC VARCOMP **********************/

PROC VARCOMP METHOD=REML; OPTIONS NODATE PAGESIZE=MAX LINESIZE=MAX;
BY T;
CLASS S R F M;
MODEL
HT_S DBHOB_S DBHUB_S BAOB_S BAUB_S OBVOL_S UBVOL_S STR_S
GRAV_S DENS_S JUVDENS_S MATDENS_S EWD_S JUVEWD_S MATEWD_S
LWD_S JUVLWD_S MATLWD_S LWP_S JUVLWP_S MATLWP_S
SLOPE_S DEV_S DWWI_S PROT_S SGMEAN_S SGSD_S

 = S R(S) F F*S F*R(S) M M*S M*R(S) F*M F*M*S;
RUN;
```

Appendix 10 Sample SAS input code for genetic correlation analysis: estimating genetic correlations among Chapter 4 traits, PEE only

PATH: D:\ACRSITE\CORRELS\CH3PARENTTRAITS&CORRELATIONSCH3ONLY

```
/****** GENETIC CORRELATION ANALYSIS ******/

* note: all genetic correlations estimated on a pooled-site basis only

libname FINAL 'D:\FINAL';

data TOTAL; set FINAL.TOTAL;

T=TAXON;
S=SITE;
R=REP;
F=FEMALE;
M=MALE;
PROT= SQRT(((SPGN+SPGS)/2)**2); * mean bark window spiral angle;
UBVOL= ((BAUB*(HT*1000))/2)/(1000);

/* STANDARDISING DATA TO REMOVE HETEROGENEITY OF VARIANCES BETWEEN SITES */

** Note: all standardised variables are denoted VARNAME_S

if taxon =1 and site =1 then DENS_S=(DENS/9.42551)*100;
else if taxon =1 and site =2 then DENS_S=(DENS/9.27948)*100;
else if taxon =2 and site =1 then DENS_S=(DENS/8.1455)*100;
else if taxon =2 and site =2 then DENS_S=(DENS/13.79203)*100;
else if taxon =3 and site =1 then DENS_S=(DENS/7.95651)*100;
else if taxon =3 and site =2 then DENS_S=(DENS/11.38236)*100;

if taxon =1 and site =1 then BAUB_S=(BAUB/16.5129)*100;
else if taxon =1 and site =2 then BAUB_S=(BAUB/11.42707)*100;
else if taxon =2 and site =1 then BAUB_S=(BAUB/22.19278)*100;
else if taxon =2 and site =2 then BAUB_S=(BAUB/25.37078)*100;
else if taxon =3 and site =1 then BAUB_S=(BAUB/40.69877)*100;
else if taxon =3 and site =2 then BAUB_S=(BAUB/31.90042)*100;

if taxon =1 and site =1 then DWWI_S=(DWWI/2.46694)*100;
else if taxon =1 and site =2 then DWWI_S=(DWWI/1.91933)*100;
else if taxon =2 and site =1 then DWWI_S=(DWWI/2.69211)*100;
else if taxon =2 and site =2 then DWWI_S=(DWWI/3.76321)*100;
else if taxon =3 and site =1 then DWWI_S=(DWWI/5.0373)*100;
else if taxon =3 and site =2 then DWWI_S=(DWWI/5.30626)*100;

/* list of traits abbreviated
.................
.................                                    */

if taxon =1 and site =1 then PROT_S=(PROT/1.39685)*100;
else if taxon =1 and site =2 then PROT_S=(PROT/1.34743)*100;
else if taxon =2 and site =1 then PROT_S=(PROT/1.77571)*100;
else if taxon =2 and site =2 then PROT_S=(PROT/1.63819)*100;
else if taxon =3 and site =1 then PROT_S=(PROT/1.68042)*100;
else if taxon =3 and site =2 then PROT_S=(PROT/1.55707)*100;
```

```
/********** CREATING SUMMED TRAIT COMBINATIONS *************/

DBHOB_S__HT_S = DBHOB_S+HT_S;
DBHOB_S__BAUB_S = DBHOB_S+BAUB_S;
DBHOB_S__OBVOL_S = DBHOB_S+OBVOL_S;
DBHOB_S__UBVOL_S = DBHOB_S+UBVOL_S;

/*   list of traits abbreviated
.....
.....
.....  */

DWWI_S__PROT_S = DWWI_S+PROT_S;
DWWI_S__PILS_S = DWWI_S+PILS_S;
PROT_S__PILS_S = PROT_S+PILS_S;


/******* ANALYSIS OF TRAITS AND SUMMED TRAIT COMBINATIONS USING PROC VARCOMP *****/


********* ANALYSIS OF TRAITS ***********;

PROC VARCOMP METHOD=REML; OPTIONS NODATE PAGESIZE=MAX LINESIZE=MAX;
WHERE T=1;
CLASS S R F M;
MODEL
DBHOB_S HT_S BAUB_S OBVOL_S UBVOL_S STR_S GRAV_S DENS_S JUVDENS_S MATDENS_S
EWD_S JUVEWD_S MATEWD_S LWD_S JUVLWD_S MATLWD_S LWP_S JUVLWP_S MATLWP_S
SLOPE_S DEV_S DWWI_S PROT_S PILS_S SGAV_S SGSD_S

 = S R(S) F F*S F*R(S) M M*S M*R(S) F*M F*M*S;
RUN;


********* ANALYSIS OF SUMMED TRAITS ***********;

PROC VARCOMP METHOD=REML; OPTIONS NODATE PAGESIZE=MAX LINESIZE=MAX;
WHERE T=1;
CLASS S R F M;
MODEL

DBHOB_S__HT_S
DBHOB_S__BAUB_S
DBHOB_S__OBVOL_S
DBHOB_S__UBVOL_S

/*   list abbreviated
.....
.....
.....  */

DWWI_S__PROT_S
DWWI_S__PILS_S
PROT_S__PILS_S


 = S R(S) F F*S F*R(S) M M*S M*R(S) F*M F*M*S;
```

```
RUN;

/* note: covariance between each pair of traits was calculated by subtracting the
variance due to each trait from the variance due to the sum of the two traits, and
dividing by two (see Section 4.2).  This calculation was carried out using Microsoft
Excel, and was used to calculate both the genetic and phenotypic covariances.  The
genetic and phenotypic correlations are calculated from the estimated variances of the
traits and covariances among them */
```

Appendix 11 Variance components and genetic parameters estimated from single-site REML analysis of variance, Chapter 3/4 traits

taxon	site	trait	Var(R)	Var(F)	Var(M)	Var(R*F)	Var(R*M)	Var(F*M)	Var(Error)	var(Var)F	var(Var(M))	cov(Var(F), Var(M))	var(Var(F*M))	var(add)	var(dom)	var(phen)	h^2b	se(h^2b)	d^2b	se(d^2b)	H^2b
1	1	DBHOB	0.09661	0.75751	0.94283	0	0	0.30636	3.79632	0.325384	0.472377	0.0021065	0.06140227	3.40068	1.22544	5.80302	0.59	0.31	0.21	0.17	0.80
1	2	DBHOB	0.2632	0.49113	0.25129	0	0.19916	0.17137	2.25271	0.124628	0.046032	0.0003804	0.01296338	1.48484	0.68548	3.36566	0.44	0.25	0.20	0.14	0.64
2	1	DBHOB	0.92431	0	0.89072	0.45241	0	0.53056	4.68858	0	0.483855	0	0.10764886	1.78144	2.12224	6.56227	0.27	0.21	0.32	0.20	0.59
2	2	DBHOB	0.24341	0.32581	0.19652	0.26374	0	0.23998	4.61062	0.089618	0.040369	0.0010927	0.0410691	1.04466	0.95992	5.63667	0.19	0.13	0.17	0.14	0.36
3	1	DBHOB	0.07483	0.11705	0	0	0.66513	0	7.00158	0.027757	0	0	0	0.2341	0	7.78376	0.03	0.04	0.00	0.00	0.03
3	2	DBHOB	0.008009	0.11276	0	0	0.84751	0.82264	6.44531	0.051094	0	0	0.13390822	0.22552	3.29056	8.22822	0.03	0.05	0.40	0.18	0.43
1	1	BAUB	0.51658	4.18772	3.90261	0	0.19132	1.46979	16.5129	9.45906	8.439422	0.0388495	1.32129006	16.18066	5.87916	26.26434	0.62	0.32	0.22	0.18	0.84
1	2	BAUB	0.7811	2.08172	1.28217	0	0	0.53224	11.42707	2.257997	0.996305	0.0069197	0.25212765	6.72778	2.12896	15.3232	0.44	0.24	0.14	0.13	0.58
2	1	BAUB	3.87541	0	7.09164	1.39695	0	1.67366	22.19278	0	25.28589	0	1.97056244	14.18328	6.69464	32.35503	0.44	0.31	0.21	0.17	0.65
2	2	BAUB	1.80528	1.00654	1.47309	0	0	0.62008	25.37078	0.989214	1.664324	0.0297683	0.90877475	4.95926	2.48032	28.47049	0.17	0.12	0.09	0.13	0.26
3	1	BAUB	0.93162	2.23343	0	0	5.04745	0	40.69877	2.868496	0	0	0	4.46686	0	47.97965	0.09	0.07	0.00	0.00	0.09
3	2	BAUB	1.94307	0.74517	1.34638	1.14634	4.64018	3.70324	31.90042	1.71245	2.75349	0.36312	4.0597	4.1831	14.81296	43.48173	0.10	0.10	0.34	0.19	0.44
1	1	HT	5.8625	19.33007	2.79486	0	3.96235	2.55814	68.06259	183.6293	12.53741	0.3364787	13.3813104	44.24986	10.23256	96.70801	0.46	0.29	0.11	0.15	0.56
1	2	HT	11.53458	44.88631	3.63572	3.65315	1.81683	0	69.3244	861.548	9.990003	0.002313	0	97.04406	0	123.3164	0.79	0.48	0.00	0.00	0.79
2	1	HT	33.42853	6.10056	24.7401	14.53989	0	5.76295	81.36377	51.18658	309.9791	-0.094902	26.9859151	61.68132	23.0518	132.5073	0.47	0.29	0.17	0.16	0.64
2	2	HT	21.12183	2.00096	19.97044	0	0	1.69478	125.9929	8.142416	200.3566	0.4654996	17.3755247	43.9428	6.77912	149.6591	0.29	0.19	0.05	0.11	0.34
3	1	HT	3.21525	7.91563	11.90789	0	6.21286	0	121.9822	30.53285	57.47703	-0.899416	0	39.64704	0	148.0186	0.27	0.13	0.00	0.00	0.27
3	2	HT	9.64853	21.63799	19.75064	0	6.80846	30.32557	147.2554	214.1106	196.8414	4.0524039	154.773949	82.77726	121.3023	225.778	0.37	0.18	0.54	0.22	0.90
1	1	OBVOL	0.56606	4.61904	4.11571	0	0.11353	1.93102	18.13367	11.61177	9.619339	0.0583498	1.73290803	17.4695	7.72408	28.91297	0.60	0.32	0.27	0.18	0.87
1	2	OBVOL	2.32361	5.54689	1.46596	0.41232	1.06097	0.72789	15.30994	14.2482	1.53651	0.01226	0.42943	14.0257	2.91156	24.52397	0.57	0.32	0.12	0.11	0.69
2	1	OBVOL	9.86673	0	10.05764	3.04382	0	4.71591	47.1398	0	58.22163	0	9.92940383	20.11528	18.86364	64.95717	0.31	0.23	0.29	0.19	0.60
2	2	OBVOL	4.16831	3.10956	3.64193	2.54142	0	2.15141	53.77525	8.724981	9.717788	0.1249077	4.75697219	13.50298	8.60564	65.21957	0.21	0.13	0.13	0.13	0.34
3	1	OBVOL	1.69966	0.96797	0.03532	0	5.27861	0	57.49307	1.910109	1.887368	-0.222716	0	2.00658	0	63.77497	0.03	0.06	0.00	0.00	0.03
3	2	OBVOL	1.59161	2.06155	0.20707	0	6.60208	9.42383	73.59483	8.715076	6.427652	1.4949172	22.5057991	4.53724	37.69532	91.88936	0.05	0.09	0.41	0.21	0.46
1	1	UBVOL	0.003895	0.027	0.01857	0	0.001043	0.00956	0.09291	0.000385	0.000206	1.605E-06	0.00004699	0.09114	0.038241	0.149083	0.61	0.33	0.26	0.18	0.87
1	2	UBVOL	0.007124	0.02443	0.009461	0.0014	0	0.001909	0.07795	0.000276	5E-05	2.471E-07	8.8473E-06	0.067782	0.007637	0.11515	0.59	0.31	0.07	0.10	0.65
2	1	UBVOL	0.03782	0	0.05913	0.0127	0	0.009606	0.16123	0	0.001697	0	0.00009534	0.11826	0.038425	0.242666	0.49	0.34	0.16	0.16	0.65
2	2	UBVOL	0.023	0.008436	0.01959	0	0	0.006173	0.23368	7.61E-05	0.000247	2.417E-06	0.00008102	0.056052	0.024692	0.267879	0.21	0.14	0.09	0.13	0.30
3	1	UBVOL	0.009281	0.01027	0	0	0.03531	0	0.28365	9.08E-05	0	0	0	0.02054	0	0.32923	0.06	0.06	0.00	0.00	0.06
3	2	UBVOL	0.02862	0.009971	0.01595	0.002593	0.03812	0.04087	0.31586	0.000199	0.000316	4.996E-05	0.0004566	0.051842	0.16348	0.423364	0.12	0.12	0.39	0.20	0.51
1	1	STR	1.35636	1.9865	3.64227	0	2.62328	0	73.47189	5.612603	13.58256	0.0011056	0	11.25754	0	81.72394	0.14	0.11	0.00	0.00	0.14
1	2	STR	2.21329	3.48743	0.84758	3.89407	0.52608	0	74.45663	10.64488	1.91069	0.0119646	0	8.67002	0	83.21379	0.10	0.09	0.00	0.00	0.10
2	1	STR	13.91243	0.42912	3.05362	0	3.74466	0	88.36735	2.748953	13.07276	-0.101521	0	6.96548	0	95.59475	0.07	0.08	0.00	0.00	0.07
2	2	STR	6.89735	1.68314	3.22567	2.124	0	0	129.1917	6.757999	11.52775	0.0410356	0	9.81762	0	136.2245	0.07	0.06	0.00	0.00	0.07
3	1	STR	11.82228	0	0.007602	0	3.9647	0	102.4693	0	3.892359	0	0	0.015204	0	106.4416	0.00	0.04	0.00	0.00	0.00
3	2	STR	1.30338	3.22539	0	0	1.70326	11.42649	90.33592	14.24318	0	0	23.9352386	6.45078	45.70596	106.6911	0.06	0.07	0.43	0.18	0.49
1	1	GRAV	0.19422	1.12411	3.05231	0	0	0.10177	4.86022	0.634604	4.065669	0.0004667	0.05822224	8.35284	0.40708	9.13841	0.91	0.47	0.04	0.11	0.96
1	2	GRAV	0.36225	0.98523	3.9457	0	0.14652	0	5.03406	0.461778	6.553234	0.0031763	0	9.86186	0	10.11151	0.98	0.52	0.00	0.00	0.98
2	1	GRAV	0.25303	0.26041	0.91895	0.15888	0.03369	0.19767	5.08734	0.08084	0.47083	0.0027539	0.07648	2.35872	0.79068	6.65694	0.35	0.22	0.12	0.17	0.47
2	2	GRAV	0.13376	1.06542	0.79604	0	0	0	7.09643	0.561532	0.335039	-0.000412	0	3.72292	0	8.95789	0.42	0.21	0.00	0.00	0.42
3	1	GRAV	0.22828	1.32543	1.41204	0.16947	0.16117	0.12589	3.75274	0.47255	0.50537	-0.0229	0.03934	5.47494	0.50356	6.94674	0.79	0.28	0.07	0.11	0.86
3	2	GRAV	0.0693	1.42013	1.46616	0	0.12924	0.07899	5.62165	0.482904	0.511235	-0.016235	0.03369966	5.77258	0.31596	8.71617	0.66	0.23	0.04	0.08	0.70
1	1	DENS	2.81306	1.09001	4.54899	0	0.34179	0.17262	9.42551	0.728983	9.451895	0.0012389	0.21660087	11.278	0.69048	15.57892	0.72	0.41	0.04	0.12	0.77
1	2	DENS	3.02045	1.10799	5.32718	0.30499	0	0.12947	9.27948	0.70752	12.14592	0.0111904	0.10299469	12.87034	0.51788	16.14911	0.80	0.44	0.03	0.08	0.83
2	1	DENS	2.7701	0.55298	2.42846	0.35667	0	0.08451	8.1455	0.276081	2.798871	0.0027491	0.14481436	5.96288	0.33804	11.56812	0.52	0.30	0.03	0.13	0.54
2	2	DENS	1.79266	1.80109	1.63049	0	0	0	13.79203	1.66043	1.392897	-0.004423	0	6.86316	0	17.22361	0.40	0.20	0.00	0.00	0.40
3	1	DENS	4.47705	1.87882	1.58102	0	0.3816	0.02162	7.95651	0.9696	0.757125	-0.02511	0.12057003	6.91968	0.08648	11.81957	0.59	0.22	0.01	0.12	0.59
3	2	DENS	4.4625	2.08283	1.76002	0	0.40182	0	11.38236	1.136712	0.816063	-0.026423	0	7.6857	0	15.62703	0.49	0.18	0.00	0.00	0.49

taxon	site	trait	Var(R)	Var(F)	Var(M)	Var(R*F)	Var(R*M)	Var(F*M)	Var(Error)	var(Var)F	var(Var(M))	cov(Var(F), Var(M))	var(Var(F*M))	var(add)	var(dom)	var(phen)	h^2b	se(h^2b)	d^2b	se(d^2b)	H^2b
1	1	JUVDENS	2.89961	0.70518	4.44102	0	0.57682	0.19635	8.31548	0.356645	9.078949	0.0004536	0.17549629	10.2924	0.7854	14.23485	0.72	0.43	0.06	0.12	0.78
1	2	JUVDENS	2.3119	0.82126	5.88364	0.20629	0	0.21642	8.38041	0.424866	14.71613	0.0081291	0.10113773	13.4098	0.86568	15.50802	0.86	0.50	0.06	0.08	0.92
2	1	JUVDENS	2.6297	0.15799	1.91705	0.23811	0	0	7.88028	0.063636	1.784471	0.0007413	0	4.15008	0	10.19343	0.41	0.27	0.00	0.00	0.41
2	2	JUVDENS	1.51632	1.69745	1.25276	0	0	0	13.09866	1.478066	0.872108	-0.004677	0	5.90042	0	16.04887	0.37	0.19	0.00	0.00	0.37
3	1	JUVDENS	4.37072	1.49535	1.19586	0	0.25884	0	6.55024	0.627395	0.437909	-0.041754	0	5.38242	0	9.50029	0.57	0.21	0.00	0.00	0.57
3	2	JUVDENS	4.1465	2.20242	1.13804	0	0.55703	0.11305	10.12755	1.224488	0.423273	-0.004589	0.10924259	6.68092	0.4522	14.13809	0.47	0.18	0.03	0.09	0.50
1	1	MATDENS	1.37548	1.65236	5.00604	0	0.40035	0.73785	14.52535	1.820702	12.30528	0.0133339	0.70647476	13.3168	2.9514	22.32195	0.60	0.34	0.13	0.15	0.73
1	2	MATDENS	4.64674	1.93416	5.50759	0.32042	0.01872	0	15.38699	2.013812	13.34771	0.0161277	0	14.8835	0	23.16788	0.64	0.34	0.00	0.00	0.64
2	1	MATDENS	2.3471	1.44762	3.48955	0.39489	0.0293	0.53012	11.58005	1.42862	6.00918	0.0091425	0.42456	9.87434	2.12048	17.47153	0.57	0.31	0.12	0.15	0.69
2	2	MATDENS	2.56139	2.41497	3.33716	1.50591	0	0	19.74768	3.381306	5.406455	-0.009476	0	11.50426	0	27.00572	0.43	0.22	0.00	0.00	0.43
3	1	MATDENS	4.16321	2.57509	2.01246	0.12456	0.79741	0	12.7232	1.823393	1.331524	0.0216867	0	9.1751	0	18.23272	0.50	0.20	0.00	0.00	0.50
3	2	MATDENS	4.81858	2.23591	3.19515	0.01375	0.57591	0	18.5333	1.560155	2.596948	-0.112702	0	10.86212	0	24.55402	0.44	0.16	0.00	0.00	0.44
1	1	EWD	2.8006	0.5238	1.93223	0.01763	0.19065	0.06934	5.27395	0.17906	1.7691	0.0029386	0.06316	4.91206	0.27736	8.0076	0.61	0.35	0.03	0.13	0.65
1	2	EWD	3.97297	0.07739	1.96021	0.29359	0	0.15638	4.52538	0.019437	1.705991	0.0009267	0.03323505	4.0752	0.62552	7.01295	0.58	0.37	0.09	0.10	0.67
2	1	EWD	2.82039	0.6073	2.0766	0.26913	0	0.1431	5.87908	0.27016	2.019626	0.0005371	0.09136375	5.3678	0.5724	8.97521	0.60	0.34	0.06	0.13	0.66
2	2	EWD	2.29563	1.45806	1.0423	0	0	0	8.08553	1.019733	0.556301	-0.000823	0	5.00072	0	10.58589	0.47	0.24	0.00	0.00	0.47
3	1	EWD	4.52364	1.53873	0.85155	0	0.01324	0	4.92962	0.603559	0.232377	-0.049411	0	4.78056	0	7.33314	0.65	0.23	0.00	0.00	0.65
3	2	EWD	5.67017	1.73292	0.8577	0.13961	0.08772	0	6.82238	0.739868	0.210608	-0.02755	0	5.18124	0	9.64033	0.54	0.20	0.00	0.00	0.54
1	1	JUVEWD	2.7296	0.56584	1.67395	0	0.4112	0	5.58574	0.196069	1.402471	0.0021638	0	4.47958	0	8.23673	0.54	0.31	0.00	0.00	0.54
1	2	JUVEWD	2.92471	0.12384	2.27662	0.25364	0	0.21072	4.26144	0.028205	2.277538	0.0009406	0.03596158	4.80092	0.84288	7.12626	0.67	0.43	0.12	0.11	0.79
2	1	JUVEWD	2.74818	0.4897	2.01286	0.15005	0	0.12822	6.21026	0.192692	1.917302	0.0004403	0.0997086	5.00512	0.51288	8.99109	0.56	0.32	0.06	0.14	0.61
2	2	JUVEWD	2.15789	1.51277	0.8723	0.03404	0	0	8.7062	1.110373	0.416181	-0.00117	0	4.77014	0	11.12531	0.43	0.22	0.00	0.00	0.43
3	1	JUVEWD	4.41154	1.43079	0.67886	0	0.20567	0.02278	4.31202	0.528807	0.176855	-0.047444	0.03625894	4.2193	0.09112	6.65012	0.63	0.24	0.01	0.11	0.65
3	2	JUVEWD	4.83473	1.98494	0.57611	0.07044	0.20786	0	6.04694	0.897501	0.11101	-0.010673	0	5.1221	0	8.88629	0.58	0.22	0.00	0.00	0.58
1	1	MATEWD	2.09221	0.40864	2.44852	0	0.05146	0.23159	8.50602	0.174194	2.927671	0.004668	0.18789428	5.71432	0.92636	11.64623	0.49	0.30	0.08	0.15	0.57
1	2	MATEWD	7.54881	0	1.40234	0.31075	0.17766	0.26444	9.02276	0	1.054412	0	0.10955418	2.80468	1.05776	11.17795	0.25	0.18	0.09	0.12	0.35
2	1	MATEWD	2.54291	1.10259	2.57762	0.26239	0.31899	0.37209	7.38785	0.77464	3.30289	0.0030104	0.18596	7.36042	1.48836	12.02153	0.61	0.34	0.12	0.14	0.74
2	2	MATEWD	2.8507	2.37935	2.03487	0.35844	0	0	10.79549	2.705486	1.968936	-0.002327	0	8.82844	0	15.56815	0.57	0.28	0.00	0.00	0.57
3	1	MATEWD	4.1761	1.69496	1.17651	0	0.008825	0	7.83773	0.78006	0.44955	-0.057573	0	5.74294	0	10.71803	0.54	0.20	0.00	0.00	0.54
3	2	MATEWD	7.80525	1.55463	1.77675	0.25812	0	0	11.34715	0.744925	0.836881	-0.082187	0	6.66276	0	14.93665	0.45	0.16	0.00	0.00	0.45
1	1	LWD	2.31627	1.86505	4.97235	0	0	0	14.00507	1.940517	11.28717	-0.006441	0	13.6748	0	20.84247	0.66	0.35	0.00	0.00	0.66
1	2	LWD	2.21357	2.65684	5.13316	0	0	0	12.7205	3.3267	11.48188	0.0208231	0	15.58	0	20.5105	0.76	0.38	0.00	0.00	0.76
2	1	LWD	1.13431	2.87881	4.56775	1.87246	0	0	38.95689	6.954358	12.22864	0.1091916	0	14.89312	0	48.27591	0.31	0.18	0.00	0.00	0.31
2	2	LWD	0.9162	9.06458	9.47946	0.84333	1.15349	0.59577	54.77177	41.63948	45.486	-0.08981	3.47659	37.08808	2.38308	75.9084	0.49	0.25	0.03	0.10	0.52
3	1	LWD	4.97498	2.23771	2.85668	0.15016	0.94395	0.19019	16.26818	1.98273	2.58178	0.21516	0.65148	10.18878	0.76076	22.64687	0.45	0.20	0.03	0.14	0.48
3	2	LWD	2.94528	3.04254	3.55998	0	0.5612	0	23.36294	2.678402	3.327878	0.0550805	0	13.20504	0	30.52666	0.43	0.16	0.00	0.00	0.43
1	1	JUVLWD	2.26211	1.98659	4.86049	0	0	0	14.36845	2.180174	10.86325	-0.011725	0	13.69416	0	21.21553	0.65	0.34	0.00	0.00	0.65
1	2	JUVLWD	1.97851	2.82926	4.79774	0	0.01167	0	12.56399	3.727763	10.07713	0.0171071	0	15.254	0	20.20266	0.76	0.37	0.00	0.00	0.76
2	1	JUVLWD	1.30874	4.11142	3.66688	0.17021	0	0	45.74313	11.21868	9.198097	0.132239	0	15.5566	0	53.69164	0.29	0.17	0.00	0.00	0.29
2	2	JUVLWD	3.16056	14.92917	13.20519	1.11838	2.27229	0.63227	72.6076	107.6819	87.93539	-0.2039	5.87161	56.26872	2.52908	104.7649	0.54	0.27	0.02	0.09	0.56
3	1	JUVLWD	4.57481	1.27079	2.7412	0	1.03494	0	17.15901	0.813334	2.337493	0.0055608	0	8.02398	0	22.20594	0.36	0.16	0.00	0.00	0.36
3	2	JUVLWD	2.74487	2.93705	3.52326	0	0	0.21263	25.69301	2.715534	3.374954	0.118954	0.67332627	12.92062	0.85052	32.36595	0.40	0.16	0.03	0.10	0.43
1	1	MATLWD	2.12203	1.68861	5.39693	0	0	0	16.53591	1.740053	13.43189	-0.003164	0	14.17108	0	23.62145	0.60	0.33	0.00	0.00	0.60
1	2	MATLWD	2.7518	2.21858	6.78673	0	0.01826	0	17.3479	2.555216	20.15146	0.0309391	0	18.01062	0	26.37147	0.68	0.36	0.00	0.00	0.68
2	1	MATLWD	1.8937	1.16459	3.87724	1.82726	2.91613	0	45.52346	2.806248	11.99518	0.003196	0	10.08366	0	55.30868	0.18	0.14	0.00	0.00	0.18
2	2	MATLWD	1.49581	2.09503	6.16787	2.4325	1.44382	0	36.60263	3.536887	19.31097	-0.041192	0	16.5258	0	48.74185	0.34	0.20	0.00	0.00	0.34
3	1	MATLWD	4.9419	3.54862	2.70326	0	0.95445	1.56547	20.25859	5.057318	3.250324	0.6011787	1.8810393	12.50376	6.26188	29.03039	0.43	0.21	0.22	0.19	0.65
3	2	MATLWD	3.97993	3.69456	3.75748	0	1.86977	0.05625	27.1316	4.061432	4.254651	0.1268484	0.67519803	14.90408	0.225	36.50966	0.41	0.16	0.01	0.09	0.41

taxon	site	trait	Var(R)	Var(F)	Var(M)	Var(R*F)	Var(R*M)	Var(F*M)	Var(Error)	var(Var)F	var(Var(M))	cov(Var(F), Var(M))	var(Var(F*M))	var(add)	var(dom)	var(phen)	h^2b	se(h^2b)	d^2b	se(d^2b)	H^2b
1	1	LWP	0	3.97548	4.23679	0	0.76068	1.22575	28.70966	9.536047	11.16231	0.0303452	2.55727478	16.42454	4.903	38.90836	0.42	0.23	0.13	0.16	0.55
1	2	LWP	0.95773	2.95618	8.10779	1.17145	2.51036	1.02155	29.11405	5.70204	32.71967	0.06431	1.38894	22.12794	4.0862	44.88138	0.49	0.28	0.09	0.11	0.58
2	1	LWP	2.35077	1.14585	0.53483	0.54097	0.46192	0.50804	31.53837	1.89204	0.94744	0.06127	2.31879	3.36136	2.03216	34.72998	0.10	0.10	0.06	0.18	0.16
2	2	LWP	0.64662	1.36733	0.38836	0.54367	0.90717	1.52892	18.27116	1.62502	0.47901	0.01966	0.97729	3.51138	6.11568	23.00661	0.15	0.13	0.27	0.17	0.42
3	1	LWP	0	3.11898	4.47373	0	1.82911	0.13161	20.06271	3.004066	5.937847	0.3834026	0.84522306	15.18542	0.52644	29.61614	0.51	0.21	0.02	0.12	0.53
3	2	LWP	0.38446	0.94813	2.43285	0.67859	1.18663	0.09485	19.21266	0.49735	1.8619	0.08556	0.36121	6.76196	0.3794	24.55371	0.28	0.13	0.02	0.10	0.29
1	1	JUVLWP	0.53356	3.96908	5.79035	0	1.53335	0	34.50435	9.199457	18.89181	-0.070162	0	19.51886	0	45.79713	0.43	0.23	0.00	0.00	0.43
1	2	JUVLWP	3.1307	3.40821	8.76428	0.69549	2.70999	0	31.4505	6.514182	36.73241	0.0156881	0	24.34498	0	47.02847	0.52	0.28	0.00	0.00	0.52
2	1	JUVLWP	0.79778	3.49244	0	1.75975	1.18034	0	53.85134	10.4919	0	0	0	6.98488	0	60.28387	0.12	0.11	0.00	0.00	0.12
2	2	JUVLWP	0.37281	1.36682	0	1.49663	2.2264	1.19015	26.2575	1.936387	0	0	1.16931004	2.73364	4.7606	32.5375	0.08	0.09	0.15	0.13	0.23
3	1	JUVLWP	0.36296	2.78861	4.29496	0	1.3713	0.39863	18.1113	2.46608	5.284432	0.2179004	0.7568508	14.16714	1.59452	26.9648	0.53	0.21	0.06	0.13	0.58
3	2	JUVLWP	0	1.18389	2.22232	1.47002	1.81767	0	17.92646	0.624212	1.584025	0.0248791	0	6.81242	0	24.62036	0.28	0.12	0.00	0.00	0.28
1	1	MATLWP	3.13958	4.07239	2.39896	0	0	4.45367	58.73158	15.83883	8.735607	0.3319534	14.0672587	12.9427	17.81468	69.6566	0.19	0.14	0.26	0.22	0.44
1	2	MATLWP	1.97229	2.87638	9.10802	2.47314	1.1995	2.65678	59.8334	8.84863	46.22882	0.25315	6.53233	23.9688	10.62712	78.14722	0.31	0.19	0.14	0.13	0.44
2	1	MATLWP	2.77868	0.55499	0.9197	3.32552	2.8662	2.89464	44.92304	3.3001	3.70836	0.1713	8.32649	2.94938	11.57856	55.48409	0.05	0.10	0.21	0.21	0.26
2	2	MATLWP	1.5528	1.97759	3.10592	1.3131	0	0.74423	34.86232	3.284193	5.936795	0.0092162	1.58969159	10.16702	2.97692	42.00316	0.24	0.14	0.07	0.12	0.31
3	1	MATLWP	0	3.82077	4.87092	0	3.04172	0	55.60082	6.914277	10.55653	0.6687521	0	17.38338	0	67.33423	0.26	0.13	0.00	0.00	0.26
3	2	MATLWP	2.67894	1.46453	3.81229	0	0	1.37963	46.58413	2.102932	5.93196	0.6235643	3.22925533	10.55364	5.51852	53.24058	0.20	0.11	0.10	0.14	0.30
1	1	SLOPE	0.56903	4.2858	3.0465	0	0	1.45704	19.20347	10.00052	5.655671	0.0369698	1.50836964	14.6646	5.82816	27.99281	0.52	0.28	0.21	0.18	0.73
1	2	SLOPE	0.8425	2.21893	3.21323	2.04118	1.30193	0.30043	18.86299	3.20919	5.58225	0.01558	0.4262	10.86432	1.20172	27.93869	0.39	0.21	0.04	0.09	0.43
2	1	SLOPE	0.003228	4.08049	1.88313	1.06598	0	0.87757	16.60876	9.182264	2.409074	0.0169595	0.87635933	11.92724	3.51028	24.51593	0.49	0.28	0.14	0.15	0.63
2	2	SLOPE	1.4724	4.7595	6.53903	0.9475	0	0.15381	28.12809	11.52635	19.90908	0.0076134	0.82318231	22.59706	0.61524	40.52793	0.56	0.28	0.02	0.09	0.57
3	1	SLOPE	0.09387	2.72572	3.78077	0	0.51055	0.28388	18.53118	2.438185	4.111909	0.206108	0.79657445	13.01298	1.13552	25.8321	0.50	0.20	0.04	0.14	0.55
3	2	SLOPE	0.28252	1.96699	4.61626	0	0.20106	0.30553	23.28197	1.363011	5.187326	-0.014686	0.56432074	13.1665	1.22212	30.37181	0.43	0.17	0.04	0.10	0.47
1	1	DEV	0.298	2.29791	1.12154	0.04916	0	0	7.1956	2.457508	0.670918	-0.001279	0	6.8389	0	10.66421	0.64	0.33	0.00	0.00	0.64
1	2	DEV	2.13386	4.72078	2.27002	0	0.23252	0	11.9233	9.728125	2.516722	0.0148588	0	13.9816	0	19.14662	0.73	0.37	0.00	0.00	0.73
2	1	DEV	0	0.60486	0.25387	0.18911	0.08803	0	4.89108	0.2298	0.060468	0.0008978	0	1.71746	0	6.02695	0.28	0.18	0.00	0.00	0.28
2	2	DEV	0	1.92621	1.68307	0	0.38714	0.54814	11.47254	1.969283	1.631641	-0.000903	0.25327257	7.21856	2.19256	16.0171	0.45	0.24	0.14	0.13	0.59
3	1	DEV	0	1.0493	1.1071	0	0.57224	0.156	7.1224	0.398851	0.446569	0.0555385	0.13657258	4.3128	0.624	10.00704	0.43	0.20	0.06	0.15	0.49
3	2	DEV	0.78279	2.63389	2.31865	0	0	0.02947	13.56428	1.690915	1.372443	0.0739264	0.16313363	9.90508	0.11788	18.54629	0.53	0.19	0.01	0.09	0.54
1	1	DWWI	0.09924	0.63333	0.89685	0	0.16317	0.17171	2.46694	0.209682	0.408114	0.0009273	0.02454517	3.06036	0.68684	4.332	0.71	0.36	0.16	0.14	0.87
1	2	DWWI	0.24549	0.2865	0.2705	0.009204	0	0.05455	1.91933	0.043809	0.039441	6.838E-05	0.00560886	1.114	0.2182	2.540084	0.44	0.23	0.09	0.12	0.52
2	1	DWWI	0.58955	0	0.41007	0.195	0	0.19513	2.69211	0	0.104765	0	0.02702307	0.82014	0.78052	3.49231	0.23	0.19	0.22	0.19	0.46
2	2	DWWI	0.42959	0.03091	0.15993	0	0	0.13646	3.76321	0.006224	0.025237	0.0007544	0.02333207	0.38168	0.54584	4.09051	0.09	0.09	0.13	0.15	0.23
3	1	DWWI	0.02934	0.40987	0	0.007139	0.46416	0	5.0373	0.071577	0	0	0	0.81974	0	5.918469	0.14	0.09	0.00	0.00	0.14
3	2	DWWI	0.62414	0.2074	0.12133	0.07005	0.38521	0.48055	5.30626	0.05078	0.03756	0.0043602	0.08214	0.65746	1.9222	6.5708	0.10	0.09	0.29	0.17	0.39
1	1	PROT	0.52811	0.1246	0.05055	0	0.02505	0.02456	1.39685	0.01064	0.003616	0.0001567	0.00450665	0.3503	0.09824	1.62161	0.22	0.15	0.06	0.17	0.28
1	2	PROT	0.20588	0.02895	0	0.005959	0	0	1.34743	0.001107	0	0	0	0.0579	0	1.382339	0.04	0.05	0.00	0.00	0.04
2	1	PROT	0.12368	0.42092	0.21029	0	0.08218	0.22796	1.77571	0.101693	0.037663	0.0007002	0.0210214	1.26242	0.91184	2.71706	0.46	0.28	0.34	0.21	0.80
2	2	PROT	0.17004	0.03957	0.01243	0	0.09067	0.03523	1.63819	0.002225	0.001354	7.692E-05	0.00337508	0.104	0.14092	1.81609	0.06	0.07	0.08	0.13	0.13
3	1	PROT	0.27144	0.02153	0.05761	0.05677	0	0.10579	1.68042	0.003446	0.004581	0.0007398	0.00986147	0.15828	0.42316	1.92212	0.08	0.10	0.22	0.21	0.30
3	2	PROT	0.29191	0.04056	0.09209	0	0.10714	0.04365	1.55707	0.001855	0.004671	-7.25E-05	0.00312544	0.2653	0.1746	1.84051	0.14	0.09	0.09	0.12	0.24
3	1	SGMEAN	6.61525	7.60541	10.21428	0	0	1.35032	82.23455	25.1653	36.30052	-0.840692	15.401487	35.63938	5.40128	101.4046	0.35	0.15	0.05	0.15	0.40
3	2	SGMEAN	5.3972	10.07896	7.24388	0	1.56533	11.29541	65.78457	48.493	35.97967	3.0334048	35.5302988	34.64568	45.18164	95.96815	0.36	0.20	0.47	0.25	0.83
3	1	SGSD	2.9988	0.1427	1.72855	1.26089	0	0	17.8164	0.229663	1.074312	-0.015868	0	3.7425	0	20.94854	0.18	0.11	0.00	0.00	0.18
3	2	SGSD	0.17455	1.21436	1.28747	0.87717	0	0.36452	14.5331	0.857844	0.907013	-0.157461	0.50875718	5.00366	1.45808	18.27662	0.27	0.13	0.08	0.16	0.35

Appendix 12 Variance components and genetic parameters estimated from across-site REML analysis of variance, Chapter 3/4 traits

taxon	trait	Var(S)	Var(R(S))	Var(F)	Var(S*F)	Var(R*F(S))	Var(M)	Var(S*M)	Var(R*M(S))	Var(F*M)	Var(S*F*M)	Var(Err)	Var(Var(F))	Var(Var(M))	cov(Var(F),Var(M))	Var(Var(FM))	var(add)	var(dom)	var(phen)	h^2_i	se(h^2_i)	d^2	se(d^2)	H^2_i
1	DBHOB	59432.40	340.729	798.376	0	0	535.128	27.100	220.520	0	245.278	3721.300	293279.33	156159.02	21.99	0	2667.007	0	5547.702	0.4807	0.1865	0	0	0.4807
2	DBHOB	0.00	221.504	58.281	0	167.330	141.363	85.348	0	38.107	143.828	2155.500	4820.23	21966.71	90.56	7343.44	399.288	152.426	2789.757	0.1431	0.1115	0.0546	0.1229	0.1978
3	DBHOB	370.56	8.135	0.602	32.229	0	23.601	0	155.234	61.121	16.645	1529.400	1203.89	1120.15	44.07	2926.76	48.406	244.485	1818.832	0.0266	0.0538	0.1344	0.1190	0.1610
1	BAUB	934.48	44.236	163.767	0	0	122.662	0	0	20.956	11.830	767.202	12439.64	7307.71	11.30	657.88	572.859	83.822	1086.417	0.5273	0.1931	0.0772	0.0944	0.6044
2	BAUB	72.02	48.386	4.378	0.543	9.544	47.033	32.704	0	2.731	20.386	419.871	87.46	2130.65	3.63	224.19	102.822	10.926	537.189	0.1914	0.1631	0.0203	0.1115	0.2117
3	BAUB	123.94	13.840	7.307	3.649	4.938	10.683	0	36.632	11.971	4.893	291.483	88.96	89.84	10.14	137.52	35.979	47.885	371.557	0.0968	0.0741	0.1289	0.1262	0.2257
1	HT	302.10	20.045	67.475	2.946	2.539	8.297	0	4.030	2.054	0	147.332	2024.86	43.08	0.37	9.73	151.546	8.215	234.673	0.6458	0.2657	0.0350	0.0532	0.6808
2	HT	1301.30	27.816	3.281	1.706	7.898	18.620	6.221	0	0.289	3.667	97.656	16.06	219.46	0.16	9.40	43.802	1.157	139.339	0.3144	0.1903	0.0083	0.0880	0.3227
3	HT	0.00	3.296	7.245	0.677	0	8.836	0	3.387	3.751	4.111	73.569	21.33	25.55	0.23	11.19	32.162	15.006	101.576	0.3166	0.1181	0.1477	0.1317	0.4644
1	OBVOL	708.43	67.911	199.492	0	2.445	87.954	1.127	27.133	20.884	16.180	621.218	17758.58	4115.28	8.42	487.90	574.892	83.534	976.432	0.5888	0.2172	0.0856	0.0905	0.6743
2	OBVOL	2.76	26.388	4.959	0	11.282	19.793	7.677	0	1.702	12.006	196.640	32.50	305.39	0.53	51.03	49.503	6.807	254.059	0.1948	0.1334	0.0268	0.1125	0.2216
3	OBVOL	1.57	3.935	1.398	3.240	0	3.149	0	11.105	5.590	0.433	154.484	14.25	11.85	1.33	26.09	9.095	22.359	179.400	0.0507	0.0592	0.1246	0.1139	0.1753
1	UBVOL	847.65	92.570	374.885	0	0	186.282	0	0	47.194	0	1215.100	62582.93	17117.64	36.89	1248.96	1122.334	188.776	1823.461	0.6155	0.2168	0.1035	0.0775	0.7190
2	UBVOL	253.01	83.239	5.610	0	15.647	78.181	48.973	0	2.283	23.084	509.672	86.91	5221.57	0.96	294.72	167.581	9.133	683.449	0.2452	0.1923	0.0134	0.1005	0.2586
3	UBVOL	11.77	22.057	7.994	5.093	0	15.038	0	34.908	16.933	0.414	338.172	110.80	141.80	14.27	175.51	46.064	67.730	418.552	0.1101	0.0776	0.1618	0.1266	0.2719
1	STR	3.46	3.571	5.709	0	3.030	2.587	1.123	2.536	0	0	135.652	20.94	9.84	-0.02	0	16.593	0	150.637	0.1102	0.0705	0	0	0.1102
2	STR	98.50	10.068	1.189	0	0	3.496	0	0	0	0	93.391	1.79	7.74	-0.01	0	9.369	0	98.075	0.0955	0.0603	0	0	0.0955
3	STR	2.05	5.421	1.993	0	0	0.057	0	2.388	0	8.120	105.837	4.27	2.53	-0.62	0	4.100	0	118.395	0.0346	0.0395	0	0	0.0346
1	GRAV	0.00	113.750	420.510	6.732	0	1356.000	76.032	26.525	9.207	0	2030.100	79872.25	806073.61	161.56	1526.37	3553.020	36.830	3925.106	0.9052	0.2663	0.0094	0.0398	0.9146
2	GRAV	14815.90	57.232	155.140	13.402	16.340	193.711	60.061	0	20.150	0	1654.400	13735.40	24462.70	28.35	1175.15	697.702	80.601	2113.204	0.3302	0.1579	0.0381	0.0649	0.3683
3	GRAV	43795.50	81.335	601.289	73.607	13.647	660.614	12.539	73.763	3.541	43.512	2165.400	88980.60	94761.20	-2874.50	3550.60	2523.806	14.163	3647.912	0.6918	0.1572	0.0039	0.0653	0.6957
1	DENS	0.00	321.704	130.082	0	0	548.675	24.338	0	0	12.215	1101.400	8122.17	131778.58	19.62	0	1357.514	0	1816.710	0.7472	0.2607	0	0	0.7472
2	DENS	14127.10	223.233	93.821	0	15.539	120.709	101.071	0	8.871	0	930.984	4472.67	14563.81	1.21	360.61	429.059	35.482	1270.993	0.3376	0.1882	0.0279	0.0598	0.3655
3	DENS	7370.80	493.799	205.271	11.014	0	171.949	0	41.786	13.587	0	1026.000	10516.34	7023.10	-245.40	460.45	754.440	54.348	1469.608	0.5134	0.1353	0.0370	0.0584	0.5503
1	JUVDENS	60.84	370.401	112.854	0	0	725.903	28.862	2.205	0	24.904	1238.700	6524.66	228783.40	14.54	0	1677.514	0	2133.428	0.7863	0.2791	0	0	0.7863
2	JUVDENS	13154.60	222.138	75.002	0	2.012	87.077	100.437	0	1.642	0	976.363	2915.36	10010.07	6.39	317.55	324.157	6.569	1242.532	0.2609	0.1661	0.0053	0.0574	0.2662
3	JUVDENS	13906.40	653.139	263.973	12.058	0	153.072	22.117	56.808	12.866	0	1201.600	16794.64	6830.26	-402.89	583.33	834.091	51.465	1722.494	0.4842	0.1364	0.0299	0.0561	0.5141
1	MATDENS	54.96	145.821	82.046	0	0	229.451	7.101	6.156	2.019	7.692	677.395	3247.18	23353.39	9.93	305.96	622.995	8.076	1011.859	0.6157	0.2262	0.0080	0.0691	0.6237
2	MATDENS	6664.30	109.517	80.413	1.420	33.685	111.336	60.829	0	5.403	3.481	660.452	3331.90	9458.79	0.62	290.31	383.499	21.611	957.020	0.4007	0.1960	0.0226	0.0712	0.4233
3	MATDENS	3522.70	188.365	89.313	9.775	3.521	101.424	0	25.855	4.504	0	641.078	2203.97	2421.57	-55.31	153.37	381.474	18.016	875.470	0.4357	0.1234	0.0206	0.0566	0.4563
1	EWD	1157.60	1569.300	75.816	26.685	82.775	806.940	37.449	0	0	54.611	2103.600	6466.34	291733.09	94.05	0	1765.512	0	3187.876	0.5538	0.2510	0	0	0.5538
2	EWD	9992.00	536.674	213.058	0	20.269	254.772	115.105	0	19.050	0	1428.600	21543.44	45284.01	-7.39	941.37	935.660	76.199	2050.853	0.4562	0.2007	0.0372	0.0598	0.4934
3	EWD	11378.30	1478.400	465.967	27.021	0	235.784	1.817	19.233	22.208	0	1687.900	51491.12	14197.94	-1965.14	1204.67	1403.501	88.833	2459.931	0.5705	0.1479	0.0361	0.0564	0.6067
1	JUVEWD	7378.40	1324.200	109.282	8.619	73.049	812.039	112.545	0	0	53.445	2172.100	8816.20	324847.17	82.71	0	1842.642	0	3341.079	0.5515	0.2551	0	0	0.5515
2	JUVEWD	8932.90	454.230	176.330	0	14.517	159.679	151.109	0	19.663	0	1331.400	15067.92	28263.13	4.72	842.90	672.018	78.652	1852.698	0.3627	0.1925	0.0425	0.0627	0.4052
3	JUVEWD	14907.50	1746.900	614.771	36.029	0	187.943	37.875	85.337	42.128	0	1904.400	89075.66	13007.54	-2737.12	1902.37	1605.427	168.514	2908.484	0.5520	0.1585	0.0579	0.0600	0.6099
1	MATEWD	987.67	674.006	16.994	5.950	11.084	246.259	0	13.080	0	31.704	1149.500	598.38	27349.69	16.22	0	526.505	0	1474.570	0.3571	0.1883	0	0	0.3571
2	MATEWD	8729.30	337.942	197.122	8.722	33.085	262.090	60.837	0	12.587	0	1134.900	19002.84	38009.54	-19.24	561.14	918.424	50.347	1709.343	0.5373	0.2089	0.0295	0.0554	0.5668
3	MATEWD	6374.30	636.879	174.481	9.678	0	158.458	0	0	0.396	0	1049.700	7554.14	5899.38	-432.48	322.75	665.876	1.584	1392.713	0.4781	0.1250	0.0011	0.0516	0.4793
1	LWD	2299.10	129.641	130.429	3.760	0	289.789	0	0	0	0	754.931	7932.68	35396.31	13.60	0	840.437	0	1178.910	0.7129	0.2295	0	0	0.7129
2	LWD	172.04	4.983	20.577	5.204	6.322	8.597	22.900	1.124	0	0	214.894	277.86	275.68	0.41	0	58.347	0	279.617	0.2087	0.1576	0	0	0.2087
3	LWD	2498.80	108.132	69.036	1.089	0	86.895	0	18.745	11.061	0	497.570	1358.32	1812.64	83.54	141.29	311.861	44.242	684.395	0.4557	0.1338	0.0646	0.0695	0.5203

taxon	trait	Var(S)	Var(R(S))	Var(F)	Var(S*F)	Var(R*F(S))	Var(M)	Var(S*M)	Var(R*M(S))	Var(F*M)	Var(S*F*M)	Var(Err)	Var(Var(F))	Var(Var(M))	cov(Var(F),Var(M))	Var(Var(FM))	var(add)	var(dom)	var(phen)	h^2_i	se(h^2_i)	d^2	se(d^2)	H^2_i
1	JUVLWD	2705.50	119.520	141.079	2.192	0	273.525	0.258	0	0	0	753.832	9077.76	31725.47	5.84	0	829.210	0	1170.887	0.7082	0.2253	0	0	0.7082
2	JUVLWD	348.80	6.167	21.925	2.964	1.129	8.774	13.058	1.967	0	0	172.158	259.99	148.01	0.20	0	61.398	0	221.975	0.2766	0.1627	0	0	0.2766
3	JUVLWD	3034.50	87.549	49.107	0.016	0	73.980	0	9.759	0.171	0	468.655	664.87	1235.59	28.18	68.18	246.174	0.685	601.688	0.4091	0.1197	0.0011	0.0549	0.4103
1	MATLWD	64.29	86.064	62.046	6.762	0	214.218	0	0	0	0	587.483	2088.98	19395.36	8.30	0	552.527	0	870.509	0.6347	0.2321	0	0	0.6347
2	MATLWD	2184.20	10.367	10.439	0.881	14.308	14.074	19.203	12.242	1.078	0	250.144	93.49	370.51	0.86	23.44	49.026	4.312	322.370	0.1521	0.1279	0.0134	0.0601	0.1655
3	MATLWD	683.27	80.053	67.533	3.631	0	59.930	0	23.848	15.440	0	418.221	1351.52	986.11	83.17	139.01	254.926	61.758	588.602	0.4331	0.1370	0.1049	0.0801	0.5380
1	LWP	66.37	7.684	37.399	3.396	3.438	69.511	6.522	20.549	2.542	10.243	350.048	799.09	2546.20	2.24	128.37	213.820	10.168	503.648	0.4245	0.1854	0.0202	0.0900	0.4447
2	LWP	1191.70	20.726	17.169	10.071	12.368	11.079	0	17.749	1.720	25.164	452.100	449.69	151.69	3.66	281.78	56.496	6.880	547.419	0.1032	0.0873	0.0126	0.1227	0.1158
3	LWP	25.01	2.513	36.016	7.421	9.870	62.065	17.857	41.878	0	6.307	513.107	473.52	1333.19	22.67	0	196.162	0	694.520	0.2824	0.1104	0	0	0.2824
1	JUVLWP	0.00	20.222	34.262	0	1.954	63.629	6.687	21.677	0.377	0	307.088	565.29	2083.50	-0.33	31.34	195.783	1.509	435.676	0.4494	0.1865	0.0035	0.0514	0.4528
2	JUVLWP	615.24	4.423	11.691	4.659	15.736	0	0	20.567	0	8.559	301.534	167.86	0.00	0.00	0	23.383	0	362.747	0.0645	0.0699	0	0	0.0645
3	JUVLWP	52.21	1.416	56.519	0	18.320	69.285	25.599	52.679	0	0	568.692	814.18	1743.17	17.46	0	251.609	0	791.095	0.3181	0.1118	0	0	0.3181
1	MATLWP	9.72	7.870	10.267	0	0.804	17.956	0	0	0.104	8.550	172.912	66.43	168.25	0.47	31.07	56.447	0.414	210.593	0.2680	0.1280	0.0020	0.1059	0.2700
2	MATLWP	226.75	14.166	8.576	2.499	11.527	7.643	9.302	0	7.258	0.647	266.949	98.26	135.11	1.76	68.67	32.437	29.033	314.401	0.1032	0.0950	0.0923	0.1054	0.1955
3	MATLWP	12.30	7.030	0.847	6.914	0	11.834	4.218	3.946	0.651	3.855	201.116	26.56	74.07	6.99	42.62	25.361	2.603	233.381	0.1087	0.0899	0.0112	0.1119	0.1198
1	SLOPE	43.10	25.859	82.143	5.273	15.394	92.602	0	5.537	0.541	12.968	556.395	3468.40	3988.75	1.79	247.17	349.489	2.164	770.853	0.4534	0.1765	0.0028	0.0816	0.4562
2	SLOPE	0.00	9.906	96.806	0.656	22.823	64.081	11.102	0	2.604	11.423	457.782	4372.46	2345.65	1.40	182.44	321.774	10.417	667.277	0.4822	0.1901	0.0156	0.0810	0.4978
3	SLOPE	0.00	3.761	28.837	21.300	0	83.379	9.257	9.656	13.376	0	470.341	534.95	1839.43	9.68	134.95	224.432	53.505	636.146	0.3528	0.1309	0.0841	0.0730	0.4369
1	DEV	597.78	115.377	384.437	0	0	189.773	0	0	11.453	0	1063.900	63115.59	16427.26	45.74	476.13	1148.420	45.811	1649.563	0.6962	0.2251	0.0278	0.0529	0.7240
2	DEV	737.21	0.000	174.131	26.988	22.614	68.642	57.506	24.201	0	0	1385.200	16742.26	5941.19	-4.24	0	485.546	0	1759.282	0.2760	0.1512	0	0	0.2760
3	DEV	981.69	21.632	179.738	0	0	179.070	0	44.984	16.875	0	1001.400	7738.22	7757.43	540.47	498.83	717.618	67.498	1422.068	0.5046	0.1385	0.0475	0.0628	0.5521
1	DWWI	2608.40	473.777	935.863	0	0	1069.100	0	34.275	81.218	43.729	4818.300	402401.70	518513.08	393.77	19358.89	4009.926	324.872	6982.485	0.5743	0.1988	0.0465	0.0797	0.6208
2	DWWI	1455.40	507.608	6.706	0	74.822	129.994	198.369	0	47.219	126.998	3125.800	1774.52	38654.16	167.92	11347.43	273.401	188.876	3709.908	0.0737	0.1067	0.0509	0.1149	0.1246
3	DWWI	6.66	138.578	61.683	53.004	11.465	29.047	0	151.124	87.011	0	1941.500	4925.86	1725.18	340.68	3398.21	181.458	348.043	2334.834	0.0777	0.0719	0.1491	0.0999	0.2268
1	PROT	2803.60	1780.700	82.216	269.723	0	0	24.541	1.747	177.349	0	7340.400	56991.18	0.00	0.00	26615.31	164.431	709.396	7895.976	0.0208	0.0602	0.0898	0.0826	0.1107
2	PROT	367.37	544.900	475.236	230.984	0	329.331	0	295.445	0	310.584	5959.300	194976.00	75146.59	62.79	0	1609.136	0	7600.881	0.2117	0.1249	0	0	0.2117
3	PROT	285.17	1121.800	174.184	0	0	284.676	27.499	145.346	279.674	0	6351.500	24600.44	47601.23	1185.59	32863.96	917.720	1118.696	7262.879	0.1264	0.0721	0.1540	0.0998	0.2804
3	SGMEAN	76.47	11.471	18.799	0	0	17.410	0	0.671	8.870	2.957	137.953	113.10	101.73	0.94	39.08	72.418	35.482	186.660	0.3880	0.1320	0.1901	0.1340	0.5781
3	SGSD	173.71	51.211	10.206	22.142	40.657	54.721	6.450	0	9.339	0	623.340	437.29	1098.61	-43.97	256.85	129.854	37.354	766.854	0.1693	0.0937	0.0487	0.0836	0.2180

Genetic correlations among wood and growth traits in PEE (*Pinus elliottii* var. *elliottii*)

	DBHOB	HT	BAUB	OBVOL	UBVOL	STR	GRAV	DENS	JUV-DENS	MAT-DENS	EWD	JUV-EWD	MAT-EWD	LWD	JUV-LWD	MAT-LWD	LWP	JUV-LWP	MAT-LWP	SLOPE	DEV	DWI	PROT	PILS	
DBHOB		0.72	1.00	0.98	0.99	1.01	-0.07	-0.04	-0.07	-0.04	-0.02	-0.09	0.07	-0.12	-0.17	-0.06	0.04	0.05	-0.09	-0.35	-0.14	0.90	-0.33	-0.03	DBHOB
HT	0.55		0.78	0.85	0.89	0.73	0.19	0.21	0.20	0.19	0.04	0.03	-0.01	0.10	0.11	0.06	0.49	0.44	0.40	-0.09	0.23	0.74	0.20	-0.11	HT
BAUB	0.86	0.52		0.98	0.98	0.97	-0.01	0.00	-0.04	-0.01	0.02	-0.04	0.07	-0.06	-0.12	-0.02	0.09	0.06	0.00	-0.31	-0.05	0.92	0.17	-0.07	BAUB
OBVOL	0.96	0.73	0.86		1.00	0.97	0.01	0.04	0.02	0.04	0.00	-0.05	0.08	-0.05	-0.09	-0.02	0.18	0.17	0.08	-0.27	-0.03	0.90	-0.10	-0.06	OBVOL
UBVOL	0.86	0.70	0.95	0.92		0.94	0.02	0.03	0.00	0.03	0.03	-0.02	0.07	-0.05	-0.09	-0.02	0.16	0.13	0.10	-0.27	0.00	0.90	0.16	-0.06	UBVOL
STR	0.22	0.17	0.22	0.23	0.22		0.14	0.25	0.19	0.29	0.37	0.25	0.62	0.08	0.04	0.14	0.27	0.25	0.23	-0.01	-0.11	0.99	-0.36	-0.28	STR
GRAV	-0.11	0.17	-0.06	-0.03	-0.03	0.10		1.00	1.00	0.93	0.89	0.86	0.88	0.90	0.95	0.81	0.82	0.84	0.68	0.60	0.77	0.35	-0.04	-0.88	GRAV
DENS	-0.08	0.17	-0.04	-0.01	-0.01	0.07	0.89		0.98	0.97	0.91	0.88	0.93	0.91	0.95	0.83	0.82	0.80	0.71	0.66	0.75	0.38	0.02	-0.93	DENS
JUVDENS	-0.12	0.16	-0.08	-0.04	-0.05	0.06	0.88	0.96		0.91	0.91	0.90	0.88	0.86	0.92	0.76	0.84	0.84	0.68	0.57	0.71	0.33	0.27	-0.88	JUVDENS
MATDENS	-0.09	0.16	-0.07	-0.01	-0.03	0.04	0.77	0.90	0.79		0.84	0.79	0.93	0.92	0.93	0.86	0.78	0.69	0.78	0.80	0.74	0.38	-0.23	-1.00	MATDENS
EWD	-0.03	0.07	0.01	0.00	0.02	0.05	0.62	0.78	0.79	0.65		1.00	0.98	0.73	0.76	0.67	0.65	0.63	0.58	0.45	0.42	0.35	0.53	-0.74	EWD
JUVEWD	-0.08	0.03	-0.04	-0.05	-0.02	0.04	0.60	0.76	0.80	0.62	0.95		0.96	0.71	0.74	0.64	0.58	0.58	0.49	0.36	0.41	0.27	0.81	-0.67	JUVEWD
MATEWD	0.03	0.09	0.04	0.06	0.06	0.04	0.49	0.64	0.59	0.65	0.84	0.66		0.74	0.74	0.69	0.72	0.65	0.74	0.65	0.41	0.44	0.08	-0.94	MATEWD
LWD	-0.20	0.07	-0.15	-0.13	-0.14	-0.03	0.67	0.79	0.75	0.75	0.59	0.58	0.46		0.98	0.98	0.61	0.58	0.52	0.65	0.90	0.28	-0.45	-0.91	LWD
JUVLWD	-0.23	0.07	-0.20	-0.16	-0.17	-0.01	0.69	0.79	0.79	0.69	0.60	0.60	0.44	0.96		0.93	0.72	0.70	0.59	0.67	0.89	0.23	-0.30	-0.94	JUVLWD
MATLWD	-0.17	0.07	-0.11	-0.11	-0.11	-0.04	0.58	0.71	0.64	0.74	0.52	0.49	0.46	0.93	0.81		0.46	0.43	0.39	0.59	0.87	0.30	-0.54	-0.88	MATLWD
LWP	0.01	0.27	0.05	0.09	0.08	0.11	0.72	0.67	0.65	0.64	0.25	0.26	0.21	0.24	0.26	0.19		0.95	0.91	0.64	0.61	0.40	0.19	-0.89	LWP
JUVLWP	0.00	0.27	0.05	0.09	0.08	0.10	0.68	0.61	0.66	0.49	0.24	0.21	0.23	0.21	0.25	0.21	0.90		0.76	0.46	0.62	0.36	0.30	-0.85	JUVLWP
MATLWP	-0.04	0.15	-0.03	0.03	0.01	0.07	0.51	0.53	0.43	0.67	0.16	0.24	0.11	0.18	0.19	0.11	0.80	0.50		0.80	0.46	0.30	-0.09	-0.96	MATLWP
SLOPE	-0.22	0.05	-0.22	-0.16	-0.20	-0.02	0.54	0.63	0.48	0.77	0.28	0.24	0.37	0.56	0.51	0.56	0.55	0.40	0.61		0.55	-0.03	-0.66	-0.90	SLOPE
DEV	-0.17	0.13	-0.14	-0.10	-0.12	-0.05	0.59	0.55	0.53	0.46	0.19	0.18	0.09	0.80	0.79	0.73	0.24	0.27	0.09	0.39		0.22	-0.61	-0.79	DEV
DWI	0.78	0.52	0.94	0.80	0.91	0.23	0.23	0.29	0.24	0.25	0.26	0.21	0.25	0.10	0.06	0.12	0.28	0.25	0.17	0.00	0.02		0.17	-0.34	DWI
PROT	0.02	0.01	0.07	0.02	0.07	0.01	-0.02	0.00	0.03	-0.03	0.05	0.05	0.03	-0.01	0.00	0.00	0.01	0.06	-0.02	-0.04	-0.02	0.02		0.36	PROT
PILS	0.04	-0.13	0.06	0.00	0.03	-0.10	-0.71	-0.69	-0.64	-0.70	-0.44	-0.40	-0.45	-0.57	-0.56	-0.56	-0.57	-0.53	-0.50	-0.60	-0.45	-0.16	0.02		PILS

Genetic correlations among wood and growth traits in PCH (*Pinus caribaea* var. *hondurensis*)

	DBHOB	HT	BAUB	OBVOL	UBVOL	STR	GRAV	DENS	JUV-DENS	MAT-DENS	EWD	JUV-EWD	MAT-EWD	LWD	JUV-LWD	MAT-LWD	LWP	JUV-LWP	MAT-LWP	SLOPE	DEV	DWWI	PROT	PILS	
DBHOB		0.63	0.89	0.98	0.82	0.06	-0.57	-0.68	-0.68	-0.60	-0.92	-0.96	-0.80	0.30	0.32	0.20	-0.46	-0.95	0.05	-0.18	0.57	1.00	-0.70	0.57	DBHOB
HT	0.60		0.90	0.81	0.96	-0.16	-0.37	-0.48	-0.48	-0.37	-0.66	-0.65	-0.56	0.20	0.38	0.04	0.30	-0.28	0.47	0.09	0.38	1.35	-0.60	-0.22	HT
BAUB	0.80	0.52		0.89	0.99	0.15	-0.72	-0.91	-0.93	-0.82	-0.91	-0.94	-0.82	-0.14	-0.04	-0.36	-0.61	-0.73	-0.43	-0.43	0.16	0.93	-0.11	0.66	BAUB
OBVOL	0.95	0.71	0.78		0.89	0.25	-0.61	-0.75	-0.76	-0.62	-0.96	-0.99	-0.81	0.16	0.23	-0.03	-0.23	-0.75	0.17	-0.19	0.45	1.16	-0.68	0.26	OBVOL
UBVOL	0.80	0.67	0.97	0.84		0.14	-0.66	-0.84	-0.83	-0.72	-0.89	-0.91	-0.78	-0.07	0.05	-0.25	-0.50	-0.65	-0.11	-0.31	0.23	1.09	-0.19	0.38	UBVOL
STR	0.09	0.03	0.17	0.09	0.16		-0.04	-0.20	-0.25	-0.23	0.01	-0.04	-0.07	-0.51	-0.46	-0.45	-0.23	0.43	-0.58	-0.23	-0.61	0.08	-0.69	0.43	STR
GRAV	-0.27	-0.08	-0.29	-0.24	-0.25	-0.05		1.02	1.01	1.00	0.97	0.98	0.97	0.49	0.46	0.67	0.68	0.52	0.65	0.85	-0.05	-0.44	-0.39	-0.91	GRAV
DENS	-0.22	0.00	-0.27	-0.18	-0.23	-0.10	0.88		0.98	1.00	0.93	0.93	0.96	0.54	0.48	0.62	0.95	0.77	0.93	0.85	0.02	-0.66	-0.41	-0.93	DENS
JUVDENS	-0.22	-0.05	-0.28	-0.19	-0.25	-0.10	0.86	0.95		0.96	0.88	0.89	0.91	0.61	0.54	0.61	0.92	0.76	0.88	0.82	0.10	-0.66	-0.50	-0.89	JUVDENS
MATDENS	-0.22	0.06	-0.28	-0.17	-0.22	-0.12	0.81	0.93	0.81		0.91	0.91	0.94	0.54	0.48	0.65	0.96	0.73	0.96	0.88	0.02	-0.55	-0.34	-0.96	MATDENS
EWD	-0.20	-0.05	-0.24	-0.18	-0.21	-0.07	0.78	0.92	0.88	0.84		1.00	1.01	0.16	0.10	0.30	0.71	0.76	0.57	0.67	-0.38	-0.87	-0.14	-0.83	EWD
JUVEWD	-0.21	-0.08	-0.26	-0.19	-0.23	-0.08	0.76	0.89	0.92	0.77	0.96		1.01	0.17	0.13	0.28	0.68	0.83	0.51	0.68	-0.37	-0.82	-0.22	-0.84	JUVEWD
MATEWD	-0.21	0.01	-0.24	-0.17	-0.20	-0.07	0.73	0.88	0.76	0.91	0.93	0.82		0.22	0.18	0.43	0.74	0.69	0.67	0.72	-0.34	-0.74	-0.10	-0.86	MATEWD
LWD	-0.13	0.12	-0.23	-0.09	-0.17	-0.12	0.72	0.75	0.75	0.70	0.53	0.56	0.50		1.01	0.89	0.65	0.11	0.99	0.72	0.86	0.31	-0.68	-0.50	LWD
JUVLWD	-0.13	0.11	-0.23	-0.10	-0.18	-0.12	0.67	0.68	0.73	0.61	0.47	0.53	0.42	0.95		0.90	0.63	-0.01	0.92	0.65	0.89	0.41	-0.61	-0.46	JUVLWD
MATLWD	-0.09	0.17	-0.19	-0.04	-0.12	-0.10	0.62	0.70	0.64	0.73	0.55	0.53	0.57	0.83	0.72		0.60	0.12	0.82	0.84	0.64	0.13	-0.60	-0.59	MATLWD
LWP	-0.12	0.04	-0.07	-0.09	-0.04	0.00	0.39	0.34	0.31	0.36	0.21	0.20	0.23	0.09	0.06	0.07		0.79	1.05	0.92	0.23	-0.31	-0.98	-1.01	LWP
JUVLWP	-0.08	-0.01	-0.03	-0.07	-0.02	0.05	0.23	0.19	0.20	0.15	0.16	0.13	0.15	-0.14	-0.16	-0.06	0.85		0.77	0.48	-0.22	-0.78	-0.52	-0.71	JUVLWP
MATLWP	-0.15	0.04	-0.14	-0.13	-0.11	-0.08	0.42	0.37	0.31	0.47	0.18	0.20	0.24	0.33	0.31	0.18	0.72	0.25		1.00	0.57	0.21	-0.98	-1.11	MATLWP
SLOPE	-0.16	0.17	-0.21	-0.09	-0.14	-0.06	0.63	0.71	0.56	0.81	0.56	0.49	0.68	0.61	0.56	0.65	0.39	0.17	0.49		0.29	0.05	-0.55	-0.95	SLOPE
DEV	-0.10	0.17	-0.16	-0.04	-0.10	-0.09	0.58	0.54	0.56	0.51	0.25	0.27	0.23	0.85	0.83	0.70	0.21	0.04	0.33	0.51		0.49	-0.53	-0.02	DEV
DWWI	0.79	0.58	0.92	0.79	0.92	0.15	0.00	0.06	0.04	0.03	0.06	0.05	0.05	0.04	0.02	0.07	0.06	0.05	0.01	0.02	0.03		-0.71	0.40	DWWI
PROT	0.02	-0.07	0.06	0.01	0.05	-0.15	-0.10	-0.07	-0.06	-0.07	-0.04	-0.02	-0.06	-0.05	-0.08	-0.03	-0.05	0.00	-0.06	-0.12	-0.07	-0.02		0.34	PROT
PILS	0.14	-0.19	0.22	0.02	0.10	0.03	-0.73	-0.70	-0.61	-0.73	-0.61	-0.56	-0.66	-0.53	-0.49	-0.55	-0.36	-0.22	-0.38	-0.70	-0.39	-0.01	0.08		PILS

Genetic (top triangle) and phenotypic correlations among wood and growth traits in F_1 (*Pinus elliottii* var. *elliottii* x *Pinus caribaea* var. *hondurensis* F_1 hybrid), across-site analysis

	DBHOB	HT	BAUB	OBVOL	UBVOL	STR	GRAV	DENS	JUV-DENS	MAT-DENS	EWD	JUV-EWD	MAT-EWD	LWD	JUV-LWD	MAT-LWD	LWP	JUV-LWP	MAT-LWP	SLOPE	DEV	DWWI	PROT	PILS	SGAV	SGSD	
DBHOB		-0.32	0.59	0.50	0.48	0.19	-0.72	-0.71	-0.59	-0.85	-0.18	-0.06	-0.37	-1.09	-0.91	-1.22	-0.66	-0.93	-0.02	-0.63	-1.36	-0.20	0.84	0.93	0.66	0.76	DBHOB
HT	0.63		0.36	0.78	0.89	0.26	0.21	0.19	0.16	0.24	0.08	0.05	0.19	-0.05	0.07	-0.18	0.44	0.36	0.81	0.20	0.04	0.35	-0.32	-0.18	-0.18	-0.10	HT
BAUB	0.81	0.56		0.59	0.73	-0.46	-0.38	-0.33	-0.31	-0.38	-0.11	-0.06	-0.23	-0.69	-0.54	-0.83	-0.24	-0.46	0.25	-0.65	-0.48	0.74	0.78	0.25	0.52	0.35	BAUB
OBVOL	0.96	0.76	0.86		1.05	0.21	-0.32	-0.25	-0.25	-0.24	-0.07	-0.04	-0.05	-0.70	-0.54	-0.86	-0.10	-0.26	0.72	-0.35	-0.64	0.30	0.26	0.38	0.32	0.55	OBVOL
UBVOL	0.81	0.71	0.95	0.92		0.15	-0.16	-0.19	-0.19	-0.18	-0.04	-0.02	-0.08	-0.55	-0.41	-0.67	0.10	-0.20	0.68	-0.35	-0.45	0.63	0.57	0.08	0.41	0.27	UBVOL
STR	0.19	0.14	0.18	0.17	0.18		0.48	0.50	0.52	0.38	0.47	0.54	0.35	0.37	0.34	0.21	0.57	0.42	0.55	0.03	0.37	-0.31	-0.16	-0.16	0.32	0.93	STR
GRAV	-0.18	0.05	-0.12	-0.15	-0.11	0.00		0.96	0.94	0.95	0.87	0.84	0.90	0.84	0.82	0.84	0.43	0.41	0.40	0.76	0.58	0.52	-0.03	-0.93	-0.19	-0.18	GRAV
DENS	-0.12	0.09	-0.07	-0.07	-0.07	-0.01	0.84		0.99	0.99	0.91	0.87	0.93	0.90	0.88	0.88	0.48	0.46	0.50	0.78	0.61	0.52	-0.12	-0.97	-0.21	-0.09	DENS
JUVDENS	-0.16	0.04	-0.11	-0.12	-0.10	-0.02	0.81	0.95		0.96	0.91	0.89	0.91	0.86	0.87	0.82	0.49	0.49	0.48	0.73	0.58	0.58	-0.18	-0.94	-0.18	-0.06	JUVDENS
MATDENS	-0.13	0.10	-0.10	-0.07	-0.08	-0.02	0.76	0.91	0.79		0.87	0.82	0.92	0.91	0.89	0.90	0.52	0.48	0.58	0.86	0.62	0.41	0.01	-1.03	-0.17	0.00	MATDENS
EWD	-0.07	0.06	-0.03	-0.03	-0.02	-0.01	0.68	0.88	0.87	0.77		0.99	0.97	0.71	0.68	0.70	0.15	0.13	0.23	0.60	0.26	0.73	0.06	-0.85	0.07	0.03	EWD
JUVEWD	-0.09	0.02	-0.05	-0.06	-0.04	0.00	0.66	0.85	0.89	0.69	0.96		0.94	0.66	0.63	0.65	0.11	0.10	0.17	0.54	0.20	0.78	0.07	-0.83	0.09	0.09	JUVEWD
MATEWD	-0.07	0.10	-0.05	-0.01	-0.03	-0.02	0.62	0.82	0.72	0.84	0.91	0.78		0.77	0.73	0.77	0.23	0.19	0.34	0.72	0.34	0.63	0.05	-0.93	0.05	0.06	MATEWD
LWD	-0.22	0.00	-0.18	-0.19	-0.20	-0.02	0.66	0.79	0.74	0.74	0.63	0.60	0.58		0.98	0.98	0.38	0.37	0.30	0.72	0.82	0.07	-0.12	-0.80	-0.25	-0.10	LWD
JUVLWD	-0.27	-0.01	-0.22	-0.23	-0.23	-0.02	0.64	0.75	0.76	0.65	0.58	0.58	0.50	0.95		0.92	0.44	0.43	0.36	0.72	0.84	0.20	-0.22	-0.79	-0.29	-0.14	JUVLWD
MATLWD	-0.15	0.00	-0.12	-0.13	-0.14	-0.03	0.58	0.72	0.64	0.73	0.61	0.55	0.62	0.90	0.74		0.29	0.30	0.20	0.72	0.75	-0.10	0.01	-0.84	-0.14	-0.08	MATLWD
LWP	-0.05	0.15	0.01	0.02	0.04	-0.01	0.53	0.51	0.49	0.51	0.20	0.20	0.20	0.15	0.19	0.05		1.01	1.04	0.58	0.59	0.10	-0.53	-0.70	-0.65	-0.11	LWP
JUVLWP	-0.07	0.11	-0.02	-0.01	0.01	-0.02	0.48	0.46	0.51	0.38	0.21	0.20	0.20	0.11	0.14	0.09	0.88		1.03	0.60	0.57	-0.15	-0.63	-0.66	-0.60	-0.14	JUVLWP
MATLWP	-0.12	0.09	-0.03	-0.03	0.00	-0.02	0.39	0.39	0.30	0.52	0.11	0.14	0.14	0.12	0.16	-0.04	0.82	0.49		0.60	0.45	0.54	-0.15	-1.00	-0.56	-0.25	MATLWP
SLOPE	-0.17	0.12	-0.13	-0.09	-0.10	-0.01	0.56	0.66	0.50	0.78	0.45	0.36	0.58	0.54	0.47	0.52	0.52	0.38	0.52		0.54	0.00	-0.48	-0.98	-0.62	-0.26	SLOPE
DEV	-0.20	0.05	-0.16	-0.16	-0.16	0.00	0.58	0.57	0.54	0.51	0.25	0.23	0.21	0.81	0.82	0.68	0.34	0.30	0.21	0.39		-0.15	-0.28	-0.51	-0.42	-0.32	DEV
DWWI	0.80	0.56	0.93	0.81	0.89	0.17	0.12	0.22	0.16	0.19	0.23	0.19	0.20	0.06	0.00	0.11	0.16	0.11	0.10	0.06	0.00		0.92	-0.30	0.54	0.27	DWWI
PROT	0.05	0.04	0.05	0.04	0.04	-0.03	-0.03	-0.02	-0.02	-0.03	0.00	0.01	-0.01	-0.01	-0.01	0.00	-0.05	-0.05	-0.04	-0.07	-0.04	0.06		0.14	0.90	0.75	PROT
PILS	0.08	-0.18	0.08	0.03	0.03	-0.02	-0.73	-0.68	-0.61	-0.71	-0.53	-0.49	-0.56	-0.57	-0.52	-0.54	-0.46	-0.39	-0.44	-0.64	-0.45	-0.10	0.08		-0.08	-0.06	PILS
SGAV	0.07	-0.03	0.11	0.06	0.08	-0.01	-0.08	-0.03	-0.03	-0.04	0.04	0.05	0.02	-0.02	-0.02	0.00	-0.13	-0.15	-0.07	-0.12	-0.08	0.10	0.38	-0.09		0.86	SGAV
SGSD	-0.02	-0.06	-0.04	-0.02	-0.04	0.03	-0.04	-0.01	-0.01	0.01	0.00	0.02	-0.01	-0.01	-0.01	-0.01	0.00	-0.03	0.04	-0.01	-0.05	-0.03	0.07	-0.08	0.31		SGSD

GRAV

ONE	(PEE Tuan - F_1 Tuan)		TWO	(PEE Tuan - F_1 Beerwah)		THREE	(PEE Beerwah - F_1 Tuan)		FOUR	(PEE Beerwah - F_1 Beerwah)		FIVE	(PCH Tuan - F_1 Tuan)		SIX	(PCH Tuan - F_1 Beerwah)		SEVEN	(PCH Beerwah - F_1 Tuan)		EIGHT	(PCH Beerwah - F_1 Beerwa	
LOCATION	5854.70953		LOCATION	0		LOCATION	3494.62483		LOCATION	0		LOCATION	0		LOCATION	0		LOCATION	0		LOCATION	0		
BLOCK(LOC)	540.617089		BLOCK(LOC)	230.072482		BLOCK(LOC)	717.810381		BLOCK(LOC)	479.14405		BLOCK(LOC)	614.500934		BLOCK(LOC)	276.431005		BLOCK(LOC)	406.226285		BLOCK(LOC)	160.584385	
GCA	3433.91571		GCA	2610.48716		GCA	3239.67697		GCA	9354.24199		GCA	2493.07277		GCA	2036.25104		GCA	2025.60018		GCA	1659.44707	
SCA	200.671019		SCA	153.030893		SCA	0		SCA	0		SCA	315.381639		SCA	208.567434		SCA	21.891142		SCA	34.244285	
LOCxGCA	305.353806		LOCxGCA	336.752105		LOCxGCA	709.977971		LOCxGCA	201.915564		LOCxGCA	383.560516		LOCxGCA	107.776998		LOCxGCA	679.917097		LOCxGCA	495.626628	
ERROR	10467.1348		ERROR	10151.3921		ERROR	10583.0932		ERROR	10256.3488		ERROR	10597.8796		ERROR	10255.3306		ERROR	10437.6587		ERROR	10142.9639	
LOCATION	LOCATION	82881076.6	LOCATION	LOCATION	0	LOCATION	LOCATION	33015783	LOCATION	LOCATION	0	LOCATION	LOCATION	0	LOCATION	LOCATION	0	LOCATION	LOCATION	0	LOCATION	LOCATION	0
LOCATION	BLOCK(LOC)	-15322.094	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	-16217.615	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0
LOCATION	GCA	-107354.43	LOCATION	GCA	0	LOCATION	GCA	-95102.529	LOCATION	GCA	0	LOCATION	GCA	0	LOCATION	GCA	0	LOCATION	GCA	0	LOCATION	GCA	0
LOCATION	SCA	3752.30873	LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	0
LOCATION	LOCxGCA	-20030.215	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	-41497.595	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0
LOCATION	ERROR	1658.95741	LOCATION	ERROR	0	LOCATION	ERROR	3011.28317	LOCATION	ERROR	0	LOCATION	ERROR	0	LOCATION	ERROR	0	LOCATION	ERROR	0	LOCATION	ERROR	0
BLOCK(LOC)	BLOCK(LOC)	107240.173	BLOCK(LOC)	BLOCK(LOC)	29550.9532	BLOCK(LOC)	BLOCK(LOC)	133014.244	BLOCK(LOC)	BLOCK(LOC)	60558.1566	BLOCK(LOC)	BLOCK(LOC)	131912.989	BLOCK(LOC)	BLOCK(LOC)	36227.8739	BLOCK(LOC)	BLOCK(LOC)	61053.1618	BLOCK(LOC)	BLOCK(LOC)	16712.9648
BLOCK(LOC)	GCA	-0.1826419	BLOCK(LOC)	GCA	-15.596143	BLOCK(LOC)	GCA	36.0769381	BLOCK(LOC)	GCA	-2551.1929	BLOCK(LOC)	GCA	4.92180763	BLOCK(LOC)	GCA	-1127.6868	BLOCK(LOC)	GCA	18.8766559	BLOCK(LOC)	GCA	-0.6404595
BLOCK(LOC)	SCA	1614.1501	BLOCK(LOC)	SCA	879.740063	BLOCK(LOC)	SCA	0	BLOCK(LOC)	SCA	0	BLOCK(LOC)	SCA	1655.71744	BLOCK(LOC)	SCA	970.565025	BLOCK(LOC)	SCA	1071.49179	BLOCK(LOC)	SCA	673.485915
BLOCK(LOC)	LOCxGCA	5.1931807	BLOCK(LOC)	LOCxGCA	1.61735819	BLOCK(LOC)	LOCxGCA	294.05369	BLOCK(LOC)	LOCxGCA	132.744232	BLOCK(LOC)	LOCxGCA	-0.1245935	BLOCK(LOC)	LOCxGCA	-227.8157	BLOCK(LOC)	LOCxGCA	31.1234959	BLOCK(LOC)	LOCxGCA	-0.1694604
BLOCK(LOC)	ERROR	-11441.099	BLOCK(LOC)	ERROR	-7804.0138	BLOCK(LOC)	ERROR	-8831.9246	BLOCK(LOC)	ERROR	-6919.9271	BLOCK(LOC)	ERROR	-11855.748	BLOCK(LOC)	ERROR	-7955.7388	BLOCK(LOC)	ERROR	-9548.7793	BLOCK(LOC)	ERROR	-8960.6573
GCA	GCA	1537044.2	GCA	GCA	$36765.746	GCA	GCA	1645644.51	GCA	GCA	6347741.93	GCA	GCA	983932.916	GCA	GCA	533020.266	GCA	GCA	954925.475	GCA	GCA	$20286.689
GCA	SCA	-1033.6093	GCA	SCA	-1185.8011	GCA	SCA	0	GCA	SCA	0	GCA	SCA	-1884.5182	GCA	SCA	-363.71279	GCA	SCA	-1112.6666	GCA	SCA	-898.31391
GCA	LOCxGCA	-82828.943	GCA	LOCxGCA	-67761.1	GCA	LOCxGCA	-168141.1	GCA	LOCxGCA	-38590.006	GCA	LOCxGCA	-103047.07	GCA	LOCxGCA	-32736.307	GCA	LOCxGCA	-207405.64	GCA	LOCxGCA	-82030.2
GCA	ERROR	-136.77257	GCA	ERROR	593.430155	GCA	ERROR	-1399.0339	GCA	ERROR	567.649951	GCA	ERROR	-68.686902	GCA	ERROR	820.902219	GCA	ERROR	-749.12918	GCA	ERROR	-7.2619876
SCA	SCA	130264.705	SCA	SCA	77552.516	SCA	SCA	0	SCA	SCA	0	SCA	SCA	148373.669	SCA	SCA	84994.6195	SCA	SCA	68251.8862	SCA	SCA	47895.5711
SCA	LOCxGCA	-27320.808	SCA	LOCxGCA	-16918.753	SCA	LOCxGCA	0	SCA	LOCxGCA	0	SCA	LOCxGCA	-30826.585	SCA	LOCxGCA	-17876.541	SCA	LOCxGCA	-14285.75	SCA	LOCxGCA	-10315.845
SCA	ERROR	-68117.065	SCA	ERROR	-38704.082	SCA	ERROR	0	SCA	ERROR	0	SCA	ERROR	-70520.227	SCA	ERROR	-39718.237	SCA	ERROR	-44058.727	SCA	ERROR	-28922.707
LOCxGCA	LOCxGCA	110386.451	LOCxGCA	LOCxGCA	91677.5706	LOCxGCA	LOCxGCA	222031.172	LOCxGCA	LOCxGCA	42910.6446	LOCxGCA	LOCxGCA	141009.748	LOCxGCA	LOCxGCA	42271.5908	LOCxGCA	LOCxGCA	289053.495	LOCxGCA	LOCxGCA	113174.467
LOCxGCA	ERROR	-31.565202	LOCxGCA	ERROR	-40.846962	LOCxGCA	ERROR	-11374.43	LOCxGCA	ERROR	-6795.3374	LOCxGCA	ERROR	-49.912336	LOCxGCA	ERROR	-55.306271	LOCxGCA	ERROR	-1202.3441	LOCxGCA	ERROR	-2.9455542
ERROR	ERROR	462978.444	ERROR	ERROR	331615.42	ERROR	ERROR	366309.74	ERROR	ERROR	277371.822	ERROR	ERROR	477416.742	ERROR	ERROR	339535.53	ERROR	ERROR	377133.414	ERROR	ERROR	284500.336
0.91833865	0.00827964	0.09099251	0.88573981	0.01126723	0.10614719	0.82024313	0.01616305	0.12713398	0.97887063	0.00050854	0.02255075	0.86865737	0.01779101	0.13338296	0.9497775	0.00924986	0.09617621	0.69715628	0.03738991	0.19336471	0.77001871	0.02662952	0.16318555
rph	var(rph)	se(rph)	rph	var(rph)	se(rph)	rph	var(rph)	se(rph)	rph	var(rph)	se(rph)	rph	var(rph)	se(rph)	rph	var(rph)	se(rph)	rph	var(rph)	se(rph)	rph	var(rph)	se(rph)

DEHOB

ONE	(PEE Tuan - F_1 Tuan)		TWO	(PEE Tuan - F_1 Beerwah)		THREE	(PEE Beerwah - F_1 Tuan)		FOUR	(PEE Beerwah - F_1 Beerwah)		FIVE	(PCH Tuan - F_1 Tuan)		SIX	(PCH Tuan - F_1 Beerwah)		SEVEN	(PCH Beerwah - F_1 Tuan)		EIGHT	(PCH Beerwah - F_1 Beerwa	
LOCATION	6251.3356		LOCATION	4098.02242		LOCATION	0		LOCATION	0		LOCATION	0		LOCATION	0		LOCATION	0		LOCATION	0		
BLOCK(LOC)	188.763619		BLOCK(LOC)	140.390073		BLOCK(LOC)	798.745101		BLOCK(LOC)	641.95556		BLOCK(LOC)	1081.20989		BLOCK(LOC)	7586.01287		BLOCK(LOC)	405.085298		BLOCK(LOC)	6136.62422	
GCA	394.088759		GCA	138.356188		GCA	314.778843		GCA	437.108961		GCA	290.925241		GCA	440.925669		GCA	211.516989		GCA	428.514804	
SCA	0		SCA	959.637828		SCA	152.062989		SCA	880.073997		SCA	165.278856		SCA	1094.23005		SCA	23.049213		SCA	788.810654	
LOCxGCA	523.72082		LOCxGCA	775.170591		LOCxGCA	440.043675		LOCxGCA	330.321807		LOCxGCA	84.548559		LOCxGCA	0		LOCxGCA	150.084069		LOCxGCA	0	
ERROR	10739.5453		ERROR	10826.1291		ERROR	10946.645		ERROR	11037.5906		ERROR	11192.0273		ERROR	11148.1512		ERROR	10806.7981		ERROR	10906.2621	
LOCATION	LOCATION	143819698	LOCATION	LOCATION	38289458	LOCATION	LOCATION	0	LOCATION	LOCATION	0	LOCATION	LOCATION	0	LOCATION	LOCATION	0	LOCATION	LOCATION	0	LOCATION	LOCATION	0
LOCATION	BLOCK(LOC)	-4859.173	LOCATION	BLOCK(LOC)	-2530.667	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0
LOCATION	GCA	10432.005	LOCATION	GCA	27201.4737	LOCATION	GCA	0	LOCATION	GCA	0	LOCATION	GCA	0	LOCATION	GCA	0	LOCATION	GCA	0	LOCATION	GCA	0
LOCATION	SCA	0	LOCATION	SCA	5967.01615	LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	0
LOCATION	LOCxGCA	-27439.273	LOCATION	LOCxGCA	-56194.017	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0
LOCATION	ERROR	3368.80678	LOCATION	ERROR	895.43275	LOCATION	ERROR	0	LOCATION	ERROR	0	LOCATION	ERROR	0	LOCATION	ERROR	0	LOCATION	ERROR	0	LOCATION	ERROR	0
BLOCK(LOC)	BLOCK(LOC)	33702.8687	BLOCK(LOC)	BLOCK(LOC)	20871.9307	BLOCK(LOC)	BLOCK(LOC)	150830.389	BLOCK(LOC)	BLOCK(LOC)	92612.8209	BLOCK(LOC)	BLOCK(LOC)	304657.759	BLOCK(LOC)	BLOCK(LOC)	7772204.73	BLOCK(LOC)	BLOCK(LOC)	58929.433	BLOCK(LOC)	BLOCK(LOC)	435101.83
BLOCK(LOC)	GCA	11.0513822	BLOCK(LOC)	GCA	-2.3957701	BLOCK(LOC)	GCA	6.91133978	BLOCK(LOC)	GCA	0.02873949	BLOCK(LOC)	GCA	1.52334017	BLOCK(LOC)	GCA	-2195.923	BLOCK(LOC)	GCA	5.61962989	BLOCK(LOC)	GCA	-1772.8316
BLOCK(LOC)	SCA	0	BLOCK(LOC)	SCA	1011.98529	BLOCK(LOC)	SCA	1154.65003	BLOCK(LOC)	SCA	805.791511	BLOCK(LOC)	SCA	1803.60765	BLOCK(LOC)	SCA	39.3726587	BLOCK(LOC)	SCA	1116.12842	BLOCK(LOC)	SCA	157.853671
BLOCK(LOC)	LOCxGCA	316.326122	BLOCK(LOC)	LOCxGCA	-7.2646547	BLOCK(LOC)	LOCxGCA	21.7600054	BLOCK(LOC)	LOCxGCA	0.02408555	BLOCK(LOC)	LOCxGCA	-4.9995505	BLOCK(LOC)	LOCxGCA	0	BLOCK(LOC)	LOCxGCA	15.7573398	BLOCK(LOC)	LOCxGCA	0
BLOCK(LOC)	ERROR	-10303.334	BLOCK(LOC)	ERROR	-8633.9833	BLOCK(LOC)	ERROR	-10663.373	BLOCK(LOC)	ERROR	-8052.0189	BLOCK(LOC)	ERROR	-12809.42	BLOCK(LOC)	ERROR	-9132.1166	BLOCK(LOC)	ERROR	-9754.5683	BLOCK(LOC)	ERROR	-7577.3233
GCA	GCA	157811.52	GCA	GCA	201225.711	GCA	GCA	122725.634	GCA	GCA	142326.614	GCA	GCA	58124.584	GCA	GCA	65353.7998	GCA	GCA	43778.5981	GCA	GCA	52470.8351
GCA	SCA	0	GCA	SCA	-557.80626	GCA	SCA	-449.75167	GCA	SCA	-1134.7925	GCA	SCA	-684.36193	GCA	SCA	-29481.46	GCA	SCA	-218.1192	GCA	SCA	-17852.418
GCA	LOCxGCA	-94332.342	GCA	LOCxGCA	-175627.45	GCA	LOCxGCA	-73213.186	GCA	LOCxGCA	-73300.822	GCA	LOCxGCA	-28052.135	GCA	LOCxGCA	0	GCA	LOCxGCA	-23893.905	GCA	LOCxGCA	0
GCA	ERROR	-502.55773	GCA	ERROR	103.467986	GCA	ERROR	-304.55695	GCA	ERROR	-5.4009857	GCA	ERROR	26.7775964	GCA	ERROR	393.459878	GCA	ERROR	-232.28936	GCA	ERROR	-3.5046117
SCA	SCA	0	SCA	SCA	202147.011	SCA	SCA	85044.2224	SCA	SCA	156733.005	SCA	SCA	130730.7	SCA	SCA	197398.617	SCA	SCA	68257.7737	SCA	SCA	119386.386
SCA	LOCxGCA	0	SCA	LOCxGCA	-43295.7	SCA	LOCxGCA	-16659.223	SCA	LOCxGCA	-32044.144	SCA	LOCxGCA	-24351.29	SCA	LOCxGCA	0	SCA	LOCxGCA	-12566.459	SCA	LOCxGCA	0
SCA	ERROR	0	SCA	ERROR	-43949.246	SCA	ERROR	-46818.805	SCA	ERROR	-33533.737	SCA	ERROR	-75816.112	SCA	ERROR	-47216.219	SCA	ERROR	-45521	SCA	ERROR	-32727.7
LOCxGCA	LOCxGCA	141204.566	LOCxGCA	LOCxGCA	287595.127	LOCxGCA	LOCxGCA	113441.789	LOCxGCA	LOCxGCA	113574.984	LOCxGCA	LOCxGCA	45281.4939	LOCxGCA	LOCxGCA	0	LOCxGCA	LOCxGCA	37703.6255	LOCxGCA	LOCxGCA	0
LOCxGCA	ERROR	-13445.712	LOCxGCA	ERROR	312.20843	LOCxGCA	ERROR	-938.01829	LOCxGCA	ERROR	-5.6214981	LOCxGCA	ERROR	13.5787379	LOCxGCA	ERROR	0	LOCxGCA	ERROR	-704.66569	LOCxGCA	ERROR	0
ERROR	ERROR	429449.246	ERROR	ERROR	374039.969	ERROR	ERROR	403972.785	ERROR	ERROR	333024.479	ERROR	ERROR	522062.717	ERROR	ERROR	390803.81	ERROR	ERROR	393930.047	ERROR	ERROR	324982.922
0.42937965	0.14677954	0.38311818	0.15145278	0.23567588	0.48546439	0.41702365	0.17031236	0.41268918	0.56957445	0.16835811	0.41031465	0.77482168	0.28316376	0.53213133	1	0	0	0.5849457	0.2450731	0.49504858	1	0	0
rph	var(rph)	se(rph)	rph	var(rph)	se(rph)	rph	var(rph)	se(rph)	rph	var(rph)	se(rph)	rph	var(rph)	se(rph)	rph	var(rph)	se(rph)	rph	var(rph)	se(rph)	rph	var(rph)	se(rph)

HT

ONE	(PEE Tuan - F_1 Tuan)		TWO	(PEE Tuan - F_1 Beerwah)		THREE	(PEE Beerwah - F_1 Tuan)		FOUR	(PEE Beerwah - F_1 Beerwah)		FIVE	(PCH Tuan - F_1 Tuan)		SIX	(PCH Tuan - F_1 Beerwah)		SEVEN	(PCH Beerwah - F_1 Tuan)		EIGHT	(PCH Beerwah - F_1 Beerwa	
LOCATION	0		LOCATION	0		LOCATION	0		LOCATION	0		LOCATION	0		LOCATION	0		LOCATION	0		LOCATION	7764.56907	
BLOCK(LOC)	23139.0817		BLOCK(LOC)	780.223021		BLOCK(LOC)	1271.56716		BLOCK(LOC)	1202.22336		BLOCK(LOC)	2185.36289		BLOCK(LOC)	2032.63649		BLOCK(LOC)	1090.3312		BLOCK(LOC)	1153.73702	
GCA	1307.09754		GCA	1257.27901		GCA	0		GCA	1392.75595		GCA	993.151174		GCA	1392.90624		GCA	477.576637		GCA	962.830426	
SCA	0		SCA	1293.79018		SCA	0		SCA	828.242062		SCA	134.928437		SCA	1396.28515		SCA	44.977903		SCA	1078.98342	
LOCxGCA	0		LOCxGCA	369.978752		LOCxGCA	17340.7763		LOCxGCA	901.603778		LOCxGCA	216.107748		LOCxGCA	287.120354		LOCxGCA	366.479091		LOCxGCA	383.489544	
ERROR	10500.8765		ERROR	10438.5801		ERROR	10535.89		ERROR	10636.819		ERROR	10946.7907		ERROR	10773.8312		ERROR	10227.9545		ERROR	10254.8675	
LOCATION	LOCATION	0	LOCATION	LOCATION	0	LOCATION	LOCATION	0	LOCATION	LOCATION	0	LOCATION	LOCATION	0	LOCATION	LOCATION	0	LOCATION	LOCATION	0	LOCATION	LOCATION	131467112
LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	-21690.453
LOCATION	GCA	0	LOCATION	GCA	0	LOCATION	GCA	0	LOCATION	GCA	0	LOCATION	GCA	0	LOCATION	GCA	0	LOCATION	GCA	0	LOCATION	GCA	-412.43928
LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	5151.53698
LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	-28192.65
LOCATION	ERROR	0	LOCATION	ERROR	0	LOCATION	ERROR	0	LOCATION	ERROR	0	LOCATION	ERROR	0	LOCATION	ERROR	0	LOCATION	ERROR	0	LOCATION	ERROR	697.977778
BLOCK(LOC)	BLOCK(LOC)	84623264.6	BLOCK(LOC)	BLOCK(LOC)	140868.191	BLOCK(LOC)	BLOCK(LOC)	314578.091	BLOCK(LOC)	BLOCK(LOC)	237127.361	BLOCK(LOC)	BLOCK(LOC)	1009596.45	BLOCK(LOC)	BLOCK(LOC)	704281.659	BLOCK(LOC)	BLOCK(LOC)	239853.538	BLOCK(LOC)	BLOCK(LOC)	218904.522
BLOCK(LOC)	GCA	-9457.5907	BLOCK(LOC)	GCA	-11.430938	BLOCK(LOC)	GCA	0	BLOCK(LOC)	GCA	0.05948379	BLOCK(LOC)	GCA	2.44822836	BLOCK(LOC)	GCA	-10.841886	BLOCK(LOC)	GCA	8.62055667	BLOCK(LOC)	GCA	0.07017576
BLOCK(LOC)	SCA	0	BLOCK(LOC)	SCA	959.098956	BLOCK(LOC)	SCA	0	BLOCK(LOC)	SCA	749.803754	BLOCK(LOC)	SCA	1748.01751	BLOCK(LOC)	SCA	1036.51011	BLOCK(LOC)	SCA	1006.00778	BLOCK(LOC)	SCA	696.639744
BLOCK(LOC)	LOCxGCA	0	BLOCK(LOC)	LOCxGCA	-2.3671818	BLOCK(LOC)	LOCxGCA	-4144.2643	BLOCK(LOC)	LOCxGCA	-0.044909	BLOCK(LOC)	LOCxGCA	-3.6157349	BLOCK(LOC)	LOCxGCA	-3.3943162	BLOCK(LOC)	LOCxGCA	19.2000991	BLOCK(LOC)	LOCxGCA	0.03649531
BLOCK(LOC)	ERROR	-9468.4497	BLOCK(LOC)	ERROR	-8192.8642	BLOCK(LOC)	ERROR	-8648.1097	BLOCK(LOC)	ERROR	-7494.0008	BLOCK(LOC)	ERROR	-12444.606	BLOCK(LOC)	ERROR	-8998.3499	BLOCK(LOC)	ERROR	-8808.4438	BLOCK(LOC)	ERROR	-6962.6109
GCA	GCA	229630.56	GCA	GCA	446401.674	GCA	GCA	0	GCA	GCA	696896.032	GCA	GCA	236128.143	GCA	GCA	475735.769	GCA	GCA	126929.927	GCA	GCA	311755.074
GCA	SCA	0	GCA	SCA	-2794.7526	GCA	SCA	0	GCA	SCA	-1961.9915	GCA	SCA	-1198.811	GCA	SCA	-3166.0003	GCA	SCA	-457.39192	GCA	SCA	-1837.1695
GCA	LOCxGCA	0	GCA	LOCxGCA	-126869.27	GCA	LOCxGCA	0	GCA	LOCxGCA	-24579.81	GCA	LOCxGCA	-52304.488	GCA	LOCxGCA	-112309.84	GCA	LOCxGCA	-58020.676	GCA	LOCxGCA	-102090.12
GCA	ERROR	-10525.833	GCA	ERROR	484.9691	GCA	ERROR	0	GCA	ERROR	-5.3159631	GCA	ERROR	59.4393767	GCA	ERROR	599.38143	GCA	ERROR	-352.59565	GCA	ERROR	-4.3288117
SCA	SCA	0	SCA	SCA	255813.405	SCA	SCA	0	SCA	SCA	144978.545	SCA	SCA	123722.071	SCA	SCA	286622.738	SCA	SCA	64454.4437	SCA	SCA	177232.19
SCA	LOCxGCA	0	SCA	LOCxGCA	-54064.408	SCA	LOCxGCA	0	SCA	LOCxGCA	-31918.643	SCA	LOCxGCA	-24310.899	SCA	LOCxGCA	-60338.053	SCA	LOCxGCA	-12570.688	SCA	LOCxGCA	-37222.542
SCA	ERROR	0	SCA	ERROR	-41031.179	SCA	ERROR	0	SCA	ERROR	-31063.452	SCA	ERROR	-73223.38	SCA	ERROR	-44765.389	SCA	ERROR	-40676.439	SCA	ERROR	-28662.452
LOCxGCA	LOCxGCA	0	LOCxGCA	LOCxGCA	184893.441	LOCxGCA	LOCxGCA	19149946	LOCxGCA	LOCxGCA	354703.887	LOCxGCA	LOCxGCA	75529.959	LOCxGCA	LOCxGCA	164300.935	LOCxGCA	LOCxGCA	87045.902	LOCxGCA	LOCxGCA	150419.584
LOCxGCA	ERROR	0	LOCxGCA	ERROR	54.9701312	LOCxGCA	ERROR	-13352.644	LOCxGCA	ERROR	-5.817922	LOCxGCA	ERROR	36.0526793	LOCxGCA	ERROR	16.5611959	LOCxGCA	ERROR	-849.07745	LOCxGCA	ERROR	-4.0163678
ERROR	ERROR	403759.122	ERROR	ERROR	347460.803	ERROR	ERROR	345793.657	ERROR	ERROR	308829.78	ERROR	ERROR	502574.571	ERROR	ERROR	374660.396	ERROR	ERROR	352760.816	ERROR	ERROR	286929.129
1	0	0	0.77263666	0.06723108	0.25929957	0	#DIV/0!	#DIV/0!	0.60703469	0.06754626	0.25990046	0.8212891	0.05049645	0.22471414	0.82909773	0.056214	0.23709492	0.56581174	0.11271791	0.33573468	0.7151572	0.07934528	0.28168295

UBVOL

ONE	(PEE Tuan - F. Tuan)	
LOCATION	748.600663	
BLOCK(LOC)	402.270524	
GCA	502.745604	
SCA	101.755484	
LOCxGCA	565.218894	
ERROR	10884.0637	
LOCATION	LOCATION	2139593.89
LOCATION	BLOCK(LOC)	-11111.565
LOCATION	GCA	11742.4172
LOCATION	SCA	3467.73328
LOCATION	LOCxGCA	-34339.446
LOCATION	ERROR	1896.82386
BLOCK(LOC)	BLOCK(LOC)	77783.8577
BLOCK(LOC)	GCA	0.92563923
BLOCK(LOC)	SCA	1870.96609
BLOCK(LOC)	LOCxGCA	3.14512022
BLOCK(LOC)	ERROR	-13194.704
GCA	GCA	210363.381
GCA	SCA	-1052.9725
GCA	LOCxGCA	-116988.48
GCA	ERROR	-31.630874
SCA	SCA	133587.243
SCA	LOCxGCA	-26510.73
SCA	ERROR	-78821.459
LOCxGCA	LOCxGCA	178934.024
LOCxGCA	ERROR	-11.879764
ERROR	ERROR	519941.751
0.47075123	0.13753977	0.37086355

TWO	(PEE Tuan - F. Beerwah)	
LOCATION	0	
BLOCK(LOC)	752.012681	
GCA	578.364992	
SCA	1001.38985	
LOCxGCA	614.528165	
ERROR	10845.6435	
LOCATION	LOCATION	0
LOCATION	BLOCK(LOC)	0
LOCATION	GCA	0
LOCATION	SCA	0
LOCATION	LOCxGCA	0
LOCATION	ERROR	0
BLOCK(LOC)	BLOCK(LOC)	138271.628
BLOCK(LOC)	GCA	1097.00051
BLOCK(LOC)	SCA	1558.02615
BLOCK(LOC)	LOCxGCA	-3131.3616
BLOCK(LOC)	ERROR	-9702.3102
GCA	GCA	287211.497
GCA	SCA	-2388.3146
GCA	LOCxGCA	-160927.31
GCA	ERROR	306.722627
SCA	SCA	222874.784
SCA	LOCxGCA	-45916.285
SCA	ERROR	-48770.287
LOCxGCA	LOCxGCA	243226.467
LOCxGCA	ERROR	345.464659
ERROR	ERROR	395575.886
0.48484224	0.150238	0.38760547

THREE	(PEE Beerwah - F. Tuan)	
LOCATION	8691.58856	
BLOCK(LOC)	705.75671	
GCA	487.54954	
SCA	0	
LOCxGCA	533.150921	
ERROR	10645.8684	
LOCATION	LOCATION	161454187
LOCATION	BLOCK(LOC)	-16060.684
LOCATION	GCA	8651.25661
LOCATION	SCA	0
LOCATION	LOCxGCA	-26889.568
LOCATION	ERROR	2886.36796
BLOCK(LOC)	BLOCK(LOC)	131773
BLOCK(LOC)	GCA	19.8740845
BLOCK(LOC)	SCA	0
BLOCK(LOC)	LOCxGCA	277.460678
BLOCK(LOC)	ERROR	-10158.778
GCA	GCA	177810.988
GCA	SCA	0
GCA	LOCxGCA	-93878.853
GCA	ERROR	-751.38111
SCA	SCA	0
SCA	LOCxGCA	0
SCA	ERROR	0
LOCxGCA	LOCxGCA	138841.562
LOCxGCA	ERROR	-11086.7
ERROR	ERROR	378877.372
0.47766172	0.12193684	0.34919456

FOUR	(PEE Beerwah - F. Beerwah)	
LOCATION	3373.3079	
BLOCK(LOC)	959.20716	
GCA	726.720297	
SCA	636.020177	
LOCxGCA	479.623472	
ERROR	10766.1086	
LOCATION	LOCATION	27293623.2
LOCATION	BLOCK(LOC)	-17125.641
LOCATION	GCA	5565.9094
LOCATION	SCA	3761.49551
LOCATION	LOCxGCA	-29539.937
LOCATION	ERROR	861.075667
BLOCK(LOC)	BLOCK(LOC)	171081.751
BLOCK(LOC)	GCA	0.56213959
BLOCK(LOC)	SCA	863.102721
BLOCK(LOC)	LOCxGCA	2.5124361
BLOCK(LOC)	ERROR	-8731.9303
GCA	GCA	247967.568
GCA	SCA	-1294.1068
GCA	LOCxGCA	-104793.81
GCA	ERROR	13.9342924
SCA	SCA	129418.123
SCA	LOCxGCA	-27197.93
SCA	ERROR	-36083.435
LOCxGCA	LOCxGCA	155732.929
LOCxGCA	ERROR	18.8094732
ERROR	ERROR	337802.962
0.60241559	0.10026474	0.31664609

FIVE	(PCH Tuan - F. Tuan)	
LOCATION	4886.95937	
BLOCK(LOC)	1358.60506	
GCA	579.23803	
SCA	0	
LOCxGCA	221.716872	
ERROR	11117.2636	
LOCATION	LOCATION	54647764.8
LOCATION	BLOCK(LOC)	-64910.774
LOCATION	GCA	1358.02472
LOCATION	SCA	0
LOCATION	LOCxGCA	-13429.145
LOCATION	ERROR	4044.00777
BLOCK(LOC)	BLOCK(LOC)	454012.998
BLOCK(LOC)	GCA	20.5534596
BLOCK(LOC)	SCA	0
BLOCK(LOC)	LOCxGCA	381.514252
BLOCK(LOC)	ERROR	-12891.965
GCA	GCA	133249.382
GCA	SCA	0
GCA	LOCxGCA	-49851.267
GCA	ERROR	-668.834
SCA	SCA	0
SCA	LOCxGCA	0
SCA	ERROR	0
LOCxGCA	LOCxGCA	70332.8955
LOCxGCA	ERROR	-16011.278
ERROR	ERROR	493979.361
0.72318432	0.10436572	0.32305683

SIX	(PCH Tuan - F. Beerwah)	
LOCATION	1176.08493	
BLOCK(LOC)	1517.06604	
GCA	999.928458	
SCA	716.294017	
LOCxGCA	0	
ERROR	11049.8377	
LOCATION	LOCATION	4490645.22
LOCATION	BLOCK(LOC)	-52243.316
LOCATION	GCA	-13774.834
LOCATION	SCA	-1579.251
LOCATION	LOCxGCA	0
LOCATION	ERROR	1110.86297
BLOCK(LOC)	BLOCK(LOC)	430266.794
BLOCK(LOC)	GCA	-9.7316107
BLOCK(LOC)	SCA	1178.16654
BLOCK(LOC)	LOCxGCA	0
BLOCK(LOC)	ERROR	-10376.702
GCA	GCA	172719.152
GCA	SCA	-25413.672
GCA	LOCxGCA	0
GCA	ERROR	577.943274
SCA	SCA	152166.136
SCA	LOCxGCA	0
SCA	ERROR	-51113.183
LOCxGCA	LOCxGCA	0
LOCxGCA	ERROR	0
ERROR	ERROR	414441.686
1	0	0

SEVEN	(PCH Beerwah - F. Tuan)	
LOCATION	2192.92532	
BLOCK(LOC)	724.962554	
GCA	260.109254	
SCA	0	
LOCxGCA	181.479321	
ERROR	10579.3345	
LOCATION	LOCATION	11338937.1
LOCATION	BLOCK(LOC)	-16445.643
LOCATION	GCA	2850.40891
LOCATION	SCA	0
LOCATION	LOCxGCA	-8547.3397
LOCATION	ERROR	2572.83337
BLOCK(LOC)	BLOCK(LOC)	135151.983
BLOCK(LOC)	GCA	12.0680525
BLOCK(LOC)	SCA	0
BLOCK(LOC)	LOCxGCA	246.710276
BLOCK(LOC)	ERROR	-9796.3501
GCA	GCA	55397.6699
GCA	SCA	0
GCA	LOCxGCA	-29868.333
GCA	ERROR	-455.23262
SCA	SCA	0
SCA	LOCxGCA	0
SCA	ERROR	0
LOCxGCA	LOCxGCA	44138.5133
LOCxGCA	ERROR	-9945.2602
ERROR	ERROR	370439.949
0.58903076	0.2006727	0.44796507

EIGHT	(PCH Beerwah - F. Beerwa	
LOCATION	24.954759	
BLOCK(LOC)	984.503236	
GCA	607.387052	
SCA	635.650036	
LOCxGCA	0	
ERROR	10686.6135	
LOCATION	LOCATION	96586.647
LOCATION	BLOCK(LOC)	-17633.442
LOCATION	GCA	-6127.0712
LOCATION	SCA	-1195.9104
LOCATION	LOCxGCA	0
LOCATION	ERROR	842.542088
BLOCK(LOC)	BLOCK(LOC)	176331.015
BLOCK(LOC)	GCA	1.71933395
BLOCK(LOC)	SCA	841.121413
BLOCK(LOC)	LOCxGCA	0
BLOCK(LOC)	ERROR	-8435.4372
GCA	GCA	78429.16
GCA	SCA	-16818.21
GCA	LOCxGCA	0
GCA	ERROR	9.40704155
SCA	SCA	106881.446
SCA	LOCxGCA	0
SCA	ERROR	-35019.73
LOCxGCA	LOCxGCA	0
LOCxGCA	ERROR	0
ERROR	ERROR	330437.183
1	0	0

STR

ONE	(PEE Tuan - F. Tuan)	
LOCATION	1574.91686	
BLOCK(LOC)	737.308433	
GCA	0	
SCA	0	
LOCxGCA	149.980822	
ERROR	10339.8484	
LOCATION	LOCATION	6155880.24
LOCATION	BLOCK(LOC)	-23304.348
LOCATION	GCA	0
LOCATION	SCA	0
LOCATION	LOCxGCA	-3496.3035
LOCATION	ERROR	2834.46761
BLOCK(LOC)	BLOCK(LOC)	162887.901
BLOCK(LOC)	GCA	0
BLOCK(LOC)	SCA	0
BLOCK(LOC)	LOCxGCA	269.519609
BLOCK(LOC)	ERROR	-9537.6739
GCA	GCA	0
GCA	SCA	0
GCA	LOCxGCA	0
GCA	ERROR	0
SCA	SCA	0
SCA	LOCxGCA	0
SCA	ERROR	0
LOCxGCA	LOCxGCA	13985.7023
LOCxGCA	ERROR	-11390.552
ERROR	ERROR	394813.223
0	#DIV/0!	#DIV/0!

TWO	(PEE Tuan - F. Beerwah)	
LOCATION	1590.48196	
BLOCK(LOC)	180.963236	
GCA	0	
SCA	769.46909	
LOCxGCA	287.704056	
ERROR	10203.8915	
LOCATION	LOCATION	6015215.6
LOCATION	BLOCK(LOC)	-2830.6478
LOCATION	GCA	0
LOCATION	SCA	4046.67749
LOCATION	LOCxGCA	-8724.6057
LOCATION	ERROR	783.244359
BLOCK(LOC)	BLOCK(LOC)	23332.9089
BLOCK(LOC)	GCA	0
BLOCK(LOC)	SCA	849.786618
BLOCK(LOC)	LOCxGCA	-4.6763146
BLOCK(LOC)	ERROR	-7493.152
GCA	GCA	0
GCA	SCA	0
GCA	LOCxGCA	0
GCA	ERROR	0
SCA	SCA	151748.284
SCA	LOCxGCA	-30905.301
SCA	ERROR	-37499.868
LOCxGCA	LOCxGCA	37903.1718
LOCxGCA	ERROR	213.029156
ERROR	ERROR	326456.258
0	#DIV/0!	#DIV/0!

THREE	(PEE Beerwah - F. Tuan)	
LOCATION	487.403632	
BLOCK(LOC)	734.520119	
GCA	2.487856	
SCA	0	
LOCxGCA	145.442344	
ERROR	10411.9922	
LOCATION	LOCATION	830859.779
LOCATION	BLOCK(LOC)	-16058.953
LOCATION	GCA	2892.45588
LOCATION	SCA	0
LOCATION	LOCxGCA	-5709.5479
LOCATION	ERROR	2061.92394
BLOCK(LOC)	BLOCK(LOC)	132040.254
BLOCK(LOC)	GCA	0.10985071
BLOCK(LOC)	SCA	0
BLOCK(LOC)	LOCxGCA	197.042257
BLOCK(LOC)	ERROR	-8344.1912
GCA	GCA	17570.0173
GCA	SCA	0
GCA	LOCxGCA	-17426.595
GCA	ERROR	-4.6352899
SCA	SCA	0
SCA	LOCxGCA	0
SCA	ERROR	0
LOCxGCA	LOCxGCA	28641.3658
LOCxGCA	ERROR	-8074.4846
ERROR	ERROR	335358.076
0.01681777	0.80282089	0.89600273

FOUR	(PEE Beerwah - F. Beerwah)	
LOCATION	493.737089	
BLOCK(LOC)	253.182569	
GCA	0	
SCA	629.377324	
LOCxGCA	280.263715	
ERROR	10332.2101	
LOCATION	LOCATION	794526.399
LOCATION	BLOCK(LOC)	-2793.6056
LOCATION	GCA	0
LOCATION	SCA	2818.11344
LOCATION	LOCxGCA	-7063.822
LOCATION	ERROR	680.711583
BLOCK(LOC)	BLOCK(LOC)	27934.5936
BLOCK(LOC)	GCA	0
BLOCK(LOC)	SCA	672.922135
BLOCK(LOC)	LOCxGCA	-0.063232
BLOCK(LOC)	ERROR	-6837.0193
GCA	GCA	0
GCA	SCA	0
GCA	LOCxGCA	0
GCA	ERROR	0
SCA	SCA	108706.68
SCA	LOCxGCA	-21834.455
SCA	ERROR	-28718.774
LOCxGCA	LOCxGCA	30377.9861
LOCxGCA	ERROR	8.73560747
ERROR	ERROR	288082.422
0	#DIV/0!	#DIV/0!

FIVE	(PCH Tuan - F. Tuan)	
LOCATION	170.967171	
BLOCK(LOC)	1399.17952	
GCA	17.432547	
SCA	0	
LOCxGCA	60.925035	
ERROR	10364.7217	
LOCATION	LOCATION	369432.388
LOCATION	BLOCK(LOC)	-65026.244
LOCATION	GCA	2298.33615
LOCATION	SCA	0
LOCATION	LOCxGCA	-4610.6666
LOCATION	ERROR	2793.20767
BLOCK(LOC)	BLOCK(LOC)	454961.501
BLOCK(LOC)	GCA	0.8890468
BLOCK(LOC)	SCA	0
BLOCK(LOC)	LOCxGCA	257.087068
BLOCK(LOC)	ERROR	-9640.6412
GCA	GCA	15167.0736
GCA	SCA	0
GCA	LOCxGCA	-14252.211
GCA	ERROR	-29.983658
SCA	SCA	0
SCA	LOCxGCA	0
SCA	ERROR	0
LOCxGCA	LOCxGCA	23197.0124
LOCxGCA	ERROR	-11196.071
ERROR	ERROR	397100.129
0.22247428	2.48342523	1.57588871

SIX	(PCH Tuan - F. Beerwah)	
LOCATION	272.447946	
BLOCK(LOC)	694.588501	
GCA	348.804518	
SCA	493.828034	
LOCxGCA	0	
ERROR	10300.6586	
LOCATION	LOCATION	370236.876
LOCATION	BLOCK(LOC)	-14194.363
LOCATION	GCA	-2731.9217
LOCATION	SCA	-1142.976
LOCATION	LOCxGCA	0
LOCATION	ERROR	835.317619
BLOCK(LOC)	BLOCK(LOC)	116914.094
BLOCK(LOC)	GCA	-6.9571674
BLOCK(LOC)	SCA	854.751424
BLOCK(LOC)	LOCxGCA	0
BLOCK(LOC)	ERROR	-7749.9626
GCA	GCA	37075.5138
GCA	SCA	-14721.886
GCA	LOCxGCA	0
GCA	ERROR	316.385748
SCA	SCA	97777.2518
SCA	LOCxGCA	0
SCA	ERROR	-38153.579
LOCxGCA	LOCxGCA	0
LOCxGCA	ERROR	0
ERROR	ERROR	333046.366
1	0	0

SEVEN	(PCH Beerwah - F. Tuan)	
LOCATION	6511.17302	
BLOCK(LOC)	825.512006	
GCA	4.327251	
SCA	0	
LOCxGCA	89.745755	
ERROR	10239.8929	
LOCATION	LOCATION	88815352.2
LOCATION	BLOCK(LOC)	-18944.335
LOCATION	GCA	2050.65267
LOCATION	SCA	0
LOCATION	LOCxGCA	-4043.4377
LOCATION	ERROR	1921.23687
BLOCK(LOC)	BLOCK(LOC)	155823.14
BLOCK(LOC)	GCA	0.14493859
BLOCK(LOC)	SCA	0
BLOCK(LOC)	LOCxGCA	182.59404
BLOCK(LOC)	ERROR	-8018.0639
GCA	GCA	12621.2478
GCA	SCA	0
GCA	LOCxGCA	-12410.25
GCA	ERROR	-5.9149123
SCA	SCA	0
SCA	LOCxGCA	0
SCA	ERROR	0
LOCxGCA	LOCxGCA	20305.9074
LOCxGCA	ERROR	-7516.8206
ERROR	ERROR	323063.601
0.04599886	1.42591794	1.19411806

EIGHT	(PCH Beerwah - F. Beerwa	
LOCATION	6600.22813	
BLOCK(LOC)	327.952998	
GCA	289.623727	
SCA	465.34691	
LOCxGCA	0	
ERROR	10250.0802	
LOCATION	LOCATION	89600524
LOCATION	BLOCK(LOC)	-3660.0218
LOCATION	GCA	-2005.5272
LOCATION	SCA	-909.76636
LOCATION	LOCxGCA	0
LOCATION	ERROR	670.472991
BLOCK(LOC)	BLOCK(LOC)	36598.302
BLOCK(LOC)	GCA	0.04842043
BLOCK(LOC)	SCA	657.450274
BLOCK(LOC)	LOCxGCA	0
BLOCK(LOC)	ERROR	-6712.7836
GCA	GCA	27224.5994
GCA	SCA	-10828.72
GCA	LOCxGCA	0
GCA	ERROR	4.82751121
SCA	SCA	74612.0586
SCA	LOCxGCA	0
SCA	ERROR	-28110.537
LOCxGCA	LOCxGCA	0
LOCxGCA	ERROR	0
ERROR	ERROR	282762.145
1	0	0

DENS

ONE	(PEE Tuan - F. Tuan)	
LOCATION	1124.41915	
BLOCK(LOC)	4364.48944	
GCA	2374.21908	
SCA	21.305185	
LOCxGCA	40.939646	
ERROR	10388.042	
LOCATION	LOCATION	8026529.53
LOCATION	BLOCK(LOC)	-508867.82
LOCATION	GCA	-50596.423
LOCATION	SCA	2662.98526
LOCATION	LOCxGCA	-6387.8514
LOCATION	ERROR	1611.41203
BLOCK(LOC)	BLOCK(LOC)	3562071.28
BLOCK(LOC)	GCA	-0.3570793
BLOCK(LOC)	SCA	1582.55016
BLOCK(LOC)	LOCxGCA	2.40565371
BLOCK(LOC)	ERROR	-11195.39
GCA	GCA	688588.149
GCA	SCA	0.07143599
GCA	LOCxGCA	-27143.994
GCA	ERROR	-89.260496
SCA	SCA	103061.871
SCA	LOCxGCA	-20680.698
SCA	ERROR	-66026.954
LOCxGCA	LOCxGCA	36609.6996
LOCxGCA	ERROR	-2.9506496
ERROR	ERROR	452132.047
0.98304888	0.00625435	0.07908445

TWO	(PEE Tuan - F. Beerwah)	
LOCATION	0	
BLOCK(LOC)	12104.9625	
GCA	1945.03839	
SCA	0	
LOCxGCA	196.872545	
ERROR	10340.5601	
LOCATION	LOCATION	0
LOCATION	BLOCK(LOC)	0
LOCATION	GCA	0
LOCATION	SCA	0
LOCATION	LOCxGCA	0
LOCATION	ERROR	0
BLOCK(LOC)	BLOCK(LOC)	19358083.2
BLOCK(LOC)	GCA	-13596.446
BLOCK(LOC)	SCA	0
BLOCK(LOC)	LOCxGCA	-3304.1855
BLOCK(LOC)	ERROR	-6798.1324
GCA	GCA	518225.693
GCA	SCA	0
GCA	LOCxGCA	-36985.296
GCA	ERROR	97.8715048
SCA	SCA	0
SCA	LOCxGCA	0
SCA	ERROR	0
LOCxGCA	LOCxGCA	47307.6334
LOCxGCA	ERROR	-8512.6827
ERROR	ERROR	317956.702
0.90808556	0.01080325	0.10393866

THREE	(PEE Beerwah - F. Tuan)	
LOCATION	195.19211	
BLOCK(LOC)	4255.71755	
GCA	2285.1712	
SCA	65.14134	
LOCxGCA	200.668911	
ERROR	10344.2964	
LOCATION	LOCATION	1990725.72
LOCATION	BLOCK(LOC)	-332606.55
LOCATION	GCA	-48165.515
LOCATION	SCA	2044.31839
LOCATION	LOCxGCA	-11034.158
LOCATION	ERROR	1442.23099
BLOCK(LOC)	BLOCK(LOC)	2738860.36
BLOCK(LOC)	GCA	16.2181996
BLOCK(LOC)	SCA	1118.82536
BLOCK(LOC)	LOCxGCA	29.0124226
BLOCK(LOC)	ERROR	-10007.167
GCA	GCA	718092.11
GCA	SCA	-253.44766
GCA	LOCxGCA	-46679.706
GCA	ERROR	-552.10446
SCA	SCA	75457.9128
SCA	LOCxGCA	-15457.43
SCA	ERROR	-45586.26
LOCxGCA	LOCxGCA	61195.2532
LOCxGCA	ERROR	-880.10126
ERROR	ERROR	377720.603
0.91927521	0.0102472	0.10122846

FOUR	(PEE Beerwah - F. Beerwah)	
LOCATION	0	
BLOCK(LOC)	3639.26767	
GCA	1989.90598	
SCA	25.50685	
LOCxGCA	110.942578	
ERROR	10315.507	
LOCATION	LOCATION	0
LOCATION	BLOCK(LOC)	0
LOCATION	GCA	0
LOCATION	SCA	0
LOCATION	LOCxGCA	0
LOCATION	ERROR	0
BLOCK(LOC)	BLOCK(LOC)	1685873.32
BLOCK(LOC)	GCA	-7.5470547
BLOCK(LOC)	SCA	733.945869
BLOCK(LOC)	LOCxGCA	0.06643003
BLOCK(LOC)	ERROR	-7619.1553
GCA	GCA	495050.202
GCA	SCA	-277.43279
GCA	LOCxGCA	-22408.161
GCA	ERROR	43.1346689
SCA	SCA	50729.004
SCA	LOCxGCA	-10706.749
SCA	ERROR	-31031.487
LOCxGCA	LOCxGCA	30015.8571
LOCxGCA	ERROR	32.5104318
ERROR	ERROR	299534.833
0.94719154	0.00692222	0.08319985

FIVE	(PCH Tuan - F. Tuan)	
LOCATION	0	
BLOCK(LOC)	4298.39524	
GCA	1814.52848	
SCA	65.325391	
LOCxGCA	174.804422	
ERROR	10404.3405	
LOCATION	LOCATION	0
LOCATION	BLOCK(LOC)	0
LOCATION	GCA	0
LOCATION	SCA	0
LOCATION	LOCxGCA	0
LOCATION	ERROR	0
BLOCK(LOC)	BLOCK(LOC)	3303952.93
BLOCK(LOC)	GCA	-9824.9675
BLOCK(LOC)	SCA	2555.38149
BLOCK(LOC)	LOCxGCA	-3807.5074
BLOCK(LOC)	ERROR	-10881.899
GCA	GCA	500706.413
GCA	SCA	-942.75204
GCA	LOCxGCA	-46981.337
GCA	ERROR	50.5423417
SCA	SCA	110903.912
SCA	LOCxGCA	-22226.322
SCA	ERROR	-67309.961
LOCxGCA	LOCxGCA	64222.0124
LOCxGCA	ERROR	-11.88491
ERROR	ERROR	457310.208
0.91212913	0.01638142	0.12798992

SIX	(PCH Tuan - F. Beerwah)	
LOCATION	8201.80743	
BLOCK(LOC)	3758.42496	
GCA	1567.13005	
SCA	0	
LOCxGCA	125.852684	
ERROR	10348.5174	
LOCATION	LOCATION	156766636
LOCATION	BLOCK(LOC)	-260212.99
LOCATION	GCA	-22068.964
LOCATION	SCA	0
LOCATION	LOCxGCA	-6302.9586
LOCATION	ERROR	2064.41086
BLOCK(LOC)	BLOCK(LOC)	2142714.14
BLOCK(LOC)	GCA	1.10696711
BLOCK(LOC)	SCA	0
BLOCK(LOC)	LOCxGCA	191.812909
BLOCK(LOC)	ERROR	-7731.4393
GCA	GCA	344972.648
GCA	SCA	0
GCA	LOCxGCA	-26718.523
GCA	ERROR	84.4873814
SCA	SCA	0
SCA	LOCxGCA	0
SCA	ERROR	0
LOCxGCA	LOCxGCA	34126.6224
LOCxGCA	ERROR	-8514.4004
ERROR	ERROR	320305.167
0.92566216	0.01215023	0.11022807

SEVEN	(PCH Beerwah - F. Tuan)	
LOCATION	0	
BLOCK(LOC)	13837.3817	
GCA	1494.95108	
SCA	0	
LOCxGCA	475.621969	
ERROR	10207.5205	
LOCATION	LOCATION	0
LOCATION	BLOCK(LOC)	0
LOCATION	GCA	0
LOCATION	SCA	0
LOCATION	LOCxGCA	0
LOCATION	ERROR	0
BLOCK(LOC)	BLOCK(LOC)	25224457.3
BLOCK(LOC)	GCA	-6816.3407
BLOCK(LOC)	SCA	0
BLOCK(LOC)	LOCxGCA	-9036.8017
BLOCK(LOC)	ERROR	-7602.5323
GCA	GCA	477606.712
GCA	SCA	0
GCA	LOCxGCA	-90917.196
GCA	ERROR	-1105.8893
SCA	SCA	0
SCA	LOCxGCA	0
SCA	ERROR	0
LOCxGCA	LOCxGCA	122824.246
LOCxGCA	ERROR	-9670.1431
ERROR	ERROR	333545.662
0.75863774	0.0339434	0.18423734

EIGHT	(PCH Beerwah - F. Beerwa	
LOCATION	3453.77044	
BLOCK(LOC)	2659.41287	
GCA	1221.93835	
SCA	0	
LOCxGCA	267.178161	
ERROR	10188.9848	
LOCATION	LOCATION	30648382
LOCATION	BLOCK(LOC)	-94339.305
LOCATION	GCA	-12745.17
LOCATION	SCA	0
LOCATION	LOCxGCA	-9712.5517
LOCATION	ERROR	1570.85424
BLOCK(LOC)	BLOCK(LOC)	943174.145
BLOCK(LOC)	GCA	10.353762
BLOCK(LOC)	SCA	0
BLOCK(LOC)	LOCxGCA	146.50502
BLOCK(LOC)	ERROR	-6711.2545
GCA	GCA	270099.448
GCA	SCA	0
GCA	LOCxGCA	-39052.927
GCA	ERROR	-404.81674
SCA	SCA	0
SCA	LOCxGCA	0
SCA	ERROR	0
LOCxGCA	LOCxGCA	51869.0387
LOCxGCA	ERROR	-6158.4244
ERROR	ERROR	269764.34
0.82057941	0.02485738	0.15766225

BAUB

		ONE (PEE Tuan - F. Tuan)	TWO (PEE Tuan - F. Beerwah)	THREE (PEE Beerwah - F. Tuan)	FOUR (PEE Beerwah - F. Beerwah)	FIVE (PCH Tuan - F. Tuan)	SIX (PCH Tuan - F. Beerwah)	SEVEN (PCH Beerwah - F. Tuan)	EIGHT (PCH Beerwah - F. Beerwa
LOCATION		650.503216	0	7654.20368	2560.3879	4375.40017	787.969619	1705.23633	0
BLOCK(LOC)		299.464855	546.806661	509.07613	690.447269	1008.6006	1112.38558	522.6678	684.266758
GCA		495.899078	618.045419	396.043858	647.056576	562.674115	894.713618	234.042117	506.732833
SCA		75.981166	815.89371	89.577153	658.320264	66.546028	644.314218	0	545.207727
LOCxGCA		589.762648	550.905504	375.290364	252.916853	194.124058	0	172.647168	0
ERROR		10913.8238	11175.3538	10649.7893	10986.0124	11135.2158	11336.9012	10629.0348	10974.5921
LOCATION	LOCATION	1716688.01	0	124138988	15587604.6	43396142.4	2207117.67	6951502.01	0
LOCATION	BLOCK(LOC)	-7972.892	0	-10270.423	-10561.433	-39942.072	-31374.561	-10478.607	0
LOCATION	GCA	12416.7164	0	6025.52598	1473.93971	1212.05663	-11434.471	2874.97368	0
LOCATION	SCA	3359.23756	0	2102.3587	3697.20875	3177.8243	-1494.6081	0	0
LOCATION	LOCxGCA	-35526.473	0	-18876.079	-16733.901	-13167.892	0	-8138.9536	0
LOCATION	ERROR	1872.49105	0	1543.05263	869.167566	1969.08112	1116.83122	2536.67587	0
BLOCK(LOC)	BLOCK(LOC)	55811.1109	89343.7354	84387.3825	105446.932	279597.902	258406.284	86021.9533	100787.065
BLOCK(LOC)	GCA	0.53891505	674.986763	9.44764799	0.09004783	4.26831466	-10.293061	11.4303271	-997.44256
BLOCK(LOC)	SCA	1831.82944	1444.40535	1225.21264	860.935314	1903.21915	1160.0745	0	599.95737
BLOCK(LOC)	LOCxGCA	4.9951568	-2173.686	29.465799	2.29116708	3.05495639	0	241.282376	0
BLOCK(LOC)	ERROR	-13018.154	-9968.244	-10837.444	-8836.2837	-13707.084	-10392.455	-9701.8593	-8425.1378
GCA	GCA	213684.097	265563.158	121329.452	162342.009	125574.385	144083.297	50194.5759	59348.0295
GCA	SCA	-1010.5669	-2229.6205	-488.77929	-1156.4514	-1021.8551	-23539.577	0	-15222.275
GCA	LOCxGCA	-120797.8	-137175.96	-64501.686	-59896.198	-46615.459	0	-28234.462	0
GCA	ERROR	-38.70327	369.863818	-356.08193	29.4008004	-7.8748055	558.520015	-415.54153	102.238046
SCA	SCA	128844.117	193398.173	85394.0843	133447.001	132054.039	142425.333	0	98044.7696
SCA	LOCxGCA	-25639.99	-39673.478	-16599.273	-27378.68	-25246.587	0	0	0
SCA	ERROR	-77934.069	-50009.141	-50506.458	-36675.976	-81264.85	-51276.338	0	-35819.451
LOCxGCA	LOCxGCA	184869.78	204508.992	98620.2927	89560.9282	70678.121	0	41961.9508	0
LOCxGCA	ERROR	-7.2303878	320.432982	-918.68068	25.9993262	-12.616883	0	-9828.6963	0
ERROR	ERROR	518161.694	412919.52	410786.179	347161.886	540381.855	425444.601	370785.779	342983.831
		0.45677126	0.52871802	0.51345298	0.71897298	0.74349296	1	0.57548139	1
		0.13708457	0.13503208	0.14614385	0.10287192	0.11368446	0	0.22212292	0
		0.37024933	0.36746711	0.38228766	0.32073652	0.33717126	0	0.47129918	0

JUVDENS

		ONE (PEE Tuan - F. Tuan)	TWO (PEE Tuan - F. Beerwah)	THREE (PEE Beerwah - F. Tuan)	FOUR (PEE Beerwah - F. Beerwah)	FIVE (PCH Tuan - F. Tuan)	SIX (PCH Tuan - F. Beerwah)	SEVEN (PCH Beerwah - F. Tuan)	EIGHT (PCH Beerwah - F. Beerwa
LOCATION		0	0	517.521724	0	3706.39618	4299.12691	0	6361.29603
BLOCK(LOC)		4850.07989	3908.88898	4372.04872	3488.44255	5037.5568	3815.55271	25559.7636	2679.11071
GCA		2295.56972	1816.77463	2389.71413	1982.03504	1571.5779	1474.27141	1472.63973	1189.34473
SCA		0	92.894792	97.054938	154.063101	0	0	0	33.756661
LOCxGCA		18.06543	97.715816	172.738358	192.76982	277.942249	155.374109	312.949976	293.84454
ERROR		10479.9344	10551.6002	10286.6228	10380.6558	10299.1418	10441.6726	10167.3172	10307.5655
LOCATION	LOCATION	0	0	3558408.93	0	43598411.8	49172458.6	0	93266167.4
LOCATION	BLOCK(LOC)	0	0	-349676.48	0	-668014.27	-267980.23	0	-95793.221
LOCATION	GCA	0	0	-52499.782	0	-21401.273	-19375.091	0	-11587.956
LOCATION	SCA	0	0	2121.48714	0	0	0	0	1464.52818
LOCATION	LOCxGCA	0	0	-10144.29	0	-14840.636	-7334.4821	0	-11478.212
LOCATION	ERROR	0	0	1423.26416	0	3360.51508	2104.19055	0	727.149027
BLOCK(LOC)	BLOCK(LOC)	4139673.58	2297284.31	2879438.97	1559580.01	4675780.89	2206675.28	83963425.9	957927.482
BLOCK(LOC)	GCA	-16220.466	-29.397195	15.6385679	-24.003058	22.9745746	2.00113591	-8602.0872	0.30989027
BLOCK(LOC)	SCA	0	956.588538	1108.59753	744.918951	0	0	0	715.88431
BLOCK(LOC)	LOCxGCA	-1434.8652	0.7191646	28.2779955	-4.8942925	310.499831	195.234154	-6351.7065	0.44673793
BLOCK(LOC)	ERROR	-9183.2182	-8529.8893	-9901.4703	-7722.8043	-10169.3	-7872.0518	-7417.2226	-7328.5955
GCA	GCA	636793.325	435193.822	760099.781	539884.786	438146.002	324402.21	401230.066	272293.223
GCA	SCA	0	-689.36144	-173.03457	-544.63325	0	0	0	-727.31405
GCA	LOCxGCA	-24133.792	-27037.765	-43352.92	-37210.813	-60444.148	-30637.118	-58446.313	-44342.38
GCA	ERROR	74.5685008	604.905962	-531.48781	45.8232208	-759.37022	45.2498415	-959.68074	19.9186186
SCA	SCA	0	75281.8232	78160.6122	63341.9952	0	0	0	50049.7427
SCA	LOCxGCA	0	-15801.885	-16055.617	-13545.941	0	0	0	-10479.197
SCA	ERROR	0	-41393.759	-45149.262	-31455.471	0	0	0	-30243.57
LOCxGCA	LOCxGCA	28442.9647	37361.6189	56585.0576	50156.1702	79510.9092	39559.0315	76947.2594	61713.1577
LOCxGCA	ERROR	-13397.321	-128.69178	-855.72912	33.8223859	-13201.156	-8664.3823	-9458.2945	13.4162417
ERROR	ERROR	415966.946	357078.049	373562.489	303367.137	404996.553	326103.228	330849.469	295462.587
		0.99219176	0.94895988	0.93258866	0.91136225	0.84972197	0.90465773	0.82473579	0.80188332
		0.00530801	0.01020331	0.00885118	0.01097564	0.02418806	0.01529109	0.02558076	0.02930163
		0.07285609	0.10101145	0.09408072	0.10476468	0.15552511	0.12365715	0.15993987	0.17117719

MATDENS

		ONE (PEE Tuan - F. Tuan)	TWO (PEE Tuan - F. Beerwah)	THREE (PEE Beerwah - F. Tuan)	FOUR (PEE Beerwah - F. Beerwah)	FIVE (PCH Tuan - F. Tuan)	SIX (PCH Tuan - F. Beerwah)	SEVEN (PCH Beerwah - F. Tuan)	EIGHT (PCH Beerwah - F. Beerwa
LOCATION		3098.43512	0	2142.419	0	0	7485.79133	8876.89986	0
BLOCK(LOC)		2185.60571	1991.5144	3166.63643	9585.80357	2570.12442	2434.95929	2194.34246	2005.85531
GCA		1682.3062	1404.4026	1611.65096	1819.55943	1624.69618	1541.17298	1114.07708	1179.16234
SCA		111.889165	65.078804	0	0	176.259904	42.209024	0	0
LOCxGCA		265.684082	315.626235	322.497492	120.255877	142.184273	20.060115	556.236699	176.146258
ERROR		10525.0792	10347.2312	10393.3235	10229.204	10543.7404	10367.1888	10624.2261	10424.2353
LOCATION	LOCATION	26780754.9	0	15415453.2	0	0	126364524	177001501	0
LOCATION	BLOCK(LOC)	-142620.78	0	-192108.98	0	0	-116769.28	-98739.028	0
LOCATION	GCA	-24671.13	0	-22758.272	0	0	-21251.31	-3952.5785	0
LOCATION	SCA	3166.75294	0	0	0	0	1904.72048	0	0
LOCATION	LOCxGCA	-16415.273	0	-15411.93	0	0	-4023.1583	-28629.474	0
LOCATION	ERROR	1653.9384	0	2684.61551	0	0	912.758187	2746.67579	0
BLOCK(LOC)	BLOCK(LOC)	998342.106	665548.309	1581558.45	10367728.8	1287902.97	961642.74	812815.247	558741.368
BLOCK(LOC)	GCA	-0.019458	-15.50174	25.4293258	-11403.468	-6463.622	-11.316251	29.2586888	-2509.5342
BLOCK(LOC)	SCA	1623.30507	916.583442	0	0	2553.96837	914.715915	0	0
BLOCK(LOC)	LOCxGCA	2.174578	1.70293515	256.830018	-1760.3625	-3117.5693	2.33937191	256.241744	-1202.1198
BLOCK(LOC)	ERROR	-11479.861	-8184.0549	-9330.656	-6449.7361	-11259.529	-8322.9325	-9314.8337	-6684.2645
GCA	GCA	491172.95	362065.663	462900.113	425932.016	422895.975	303352.629	370641.447	230535.88
GCA	SCA	-1026.7936	-1068.5745	0	0	-902.60393	-606.03402	0	0
GCA	LOCxGCA	-64940.606	-57179.502	-63269.617	-22153.279	-46125.583	-16057.53	-107738.42	-27779.473
GCA	ERROR	-87.007513	575.235669	-929.58345	-129.38811	71.9099812	632.917261	-1108.7295	-269.42343
SCA	SCA	117558.958	70173.0915	0	0	128234.619	67775.2099	0	0
SCA	LOCxGCA	-23761.71	-14869.537	0	0	-25653.663	-13980.365	0	0
SCA	ERROR	-67840.815	-39784.276	0	0	-69170.709	-40185.145	0	0
LOCxGCA	LOCxGCA	89618.1716	79488.0738	82727.941	27481.4657	63514.084	22807.7316	150422.739	35631.922
LOCxGCA	ERROR	-10.266387	-94.64229	-10177.493	-6382.0418	5.43382478	-206.44652	-10403.074	-6335.7302
ERROR	ERROR	464185.938	343264.474	350779.104	275086.01	469671.535	346779.652	361288.876	282309.322
		0.86361119	0.81649945	0.83326125	0.93800653	0.91952807	0.98715111	0.6669867	0.87003236
		0.02405336	0.02782433	0.02349428	0.00754557	0.02026607	0.00930596	0.05587302	0.0202238
		0.15509145	0.16680626	0.15327843	0.08686526	0.14235896	0.09646743	0.23637475	0.1422104

EVD

ONE	(PEE Tuan - F, Tuan)		TWO	(PEE Tuan - F, Beerwah)		THREE	(PEE Beerwah - F, Tuan)		FOUR	(PEE Beerwah - F, Beerwah)		FIVE	(PCH Tuan - F, Tuan)		SIX	(PCH Tuan - F, Beerwah)		SEVEN	(PCH Beerwah - F, Tuan)		EIGHT	(PCH Beerwah - F, Beerwa	
LOCATION	0		LOCATION	8717.84575		LOCATION	0		LOCATION	0		LOCATION	0		LOCATION	0		LOCATION	4766.89588		LOCATION	169.196584	
BLOCK(LOC)	6803.46031		BLOCK(LOC)	7126.03075		BLOCK(LOC)	8492.64036		BLOCK(LOC)	8523.09725		BLOCK(LOC)	6930.47927		BLOCK(LOC)	14631.0614		BLOCK(LOC)	5396.54852		BLOCK(LOC)	5619.73404	
GCA	2177.69056		GCA	1837.43036		GCA	2193.77748		GCA	1546.08933		GCA	2190.7523		GCA	2126.09514		GCA	1965.79229		GCA	1793.64468	
SCA	0		SCA	0		SCA	140.259317		SCA	45.0423		SCA	34.532452		SCA	0		SCA	0		SCA	0	
LOCxGCA	59.375972		LOCxGCA	16.700495		LOCxGCA	24.662665		LOCxGCA	206.600689		LOCxGCA	246.923141		LOCxGCA	42.174595		LOCxGCA	223.091239		LOCxGCA	0	
ERROR	10184.4107		ERROR	10331.0252		ERROR	10320.6531		ERROR	10473.0034		ERROR	10235.4461		ERROR	10374.6123		ERROR	10013.9483		ERROR	10147.8081	
LOCATION	LOCATION	0	LOCATION	LOCATION	191093810	LOCATION	LOCATION	0	LOCATION	LOCATION	0	LOCATION	LOCATION	0	LOCATION	LOCATION	0	LOCATION	LOCATION	64404116.2	LOCATION	LOCATION	1682467.15
LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	-980380.95	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	-517922.3	LOCATION	BLOCK(LOC)	-393242.03
LOCATION	GCA	0	LOCATION	GCA	-29729.268	LOCATION	GCA	0	LOCATION	GCA	0	LOCATION	GCA	0	LOCATION	GCA	0	LOCATION	GCA	-35887.054	LOCATION	GCA	-30183.307
LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	0
LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	-3307.59	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	-10355.397	LOCATION	LOCxGCA	0
LOCATION	ERROR	0	LOCATION	ERROR	2004.66021	LOCATION	ERROR	0	LOCATION	ERROR	0	LOCATION	ERROR	0	LOCATION	ERROR	0	LOCATION	ERROR	2433.08297	LOCATION	ERROR	429.328259
BLOCK(LOC)	BLOCK(LOC)	7843071.75	BLOCK(LOC)	BLOCK(LOC)	7249986.76	BLOCK(LOC)	BLOCK(LOC)	9784277.84	BLOCK(LOC)	BLOCK(LOC)	8711554.53	BLOCK(LOC)	BLOCK(LOC)	8168635.63	BLOCK(LOC)	BLOCK(LOC)	28002574.1	BLOCK(LOC)	BLOCK(LOC)	4264950.91	BLOCK(LOC)	BLOCK(LOC)	3832470.15
BLOCK(LOC)	GCA	-16526.899	BLOCK(LOC)	GCA	-9.0791159	BLOCK(LOC)	GCA	-16371.723	BLOCK(LOC)	GCA	-86.50258	BLOCK(LOC)	GCA	-15825.498	BLOCK(LOC)	GCA	-16991.867	BLOCK(LOC)	GCA	22.7477966	BLOCK(LOC)	GCA	123.845235
BLOCK(LOC)	SCA	0	BLOCK(LOC)	SCA	0	BLOCK(LOC)	SCA	1934.08827	BLOCK(LOC)	SCA	763.543048	BLOCK(LOC)	SCA	2563.32817	BLOCK(LOC)	SCA	0	BLOCK(LOC)	SCA	0	BLOCK(LOC)	SCA	0
BLOCK(LOC)	LOCxGCA	-2033.5429	BLOCK(LOC)	LOCxGCA	193.812112	BLOCK(LOC)	LOCxGCA	-2007.2489	BLOCK(LOC)	LOCxGCA	-29.149825	BLOCK(LOC)	LOCxGCA	-5165.2782	BLOCK(LOC)	LOCxGCA	-1505.9058	BLOCK(LOC)	LOCxGCA	226.342688	BLOCK(LOC)	LOCxGCA	0
BLOCK(LOC)	ERROR	-8539.0999	BLOCK(LOC)	ERROR	-7603.2822	BLOCK(LOC)	ERROR	-9463.6089	BLOCK(LOC)	ERROR	-7885.7413	BLOCK(LOC)	ERROR	-10488.984	BLOCK(LOC)	ERROR	-6903.3111	BLOCK(LOC)	ERROR	-8294.2326	BLOCK(LOC)	ERROR	-6590.5733
GCA	GCA	597079.718	GCA	GCA	401824.472	GCA	GCA	594204.242	GCA	GCA	399429.331	GCA	GCA	701465.911	GCA	GCA	531756.388	GCA	GCA	564220.5	GCA	GCA	362201.416
GCA	SCA	0	GCA	SCA	0	GCA	SCA	419.762543	GCA	SCA	-526.50217	GCA	SCA	-1119.2896	GCA	SCA	0	GCA	SCA	0	GCA	SCA	0
GCA	LOCxGCA	-27800.843	GCA	LOCxGCA	-15023.861	GCA	LOCxGCA	-24273.001	GCA	LOCxGCA	-34775.201	GCA	LOCxGCA	-58103.132	GCA	LOCxGCA	-17907.544	GCA	LOCxGCA	-44626.288	GCA	LOCxGCA	0
GCA	ERROR	-121.57351	GCA	ERROR	358.313129	GCA	ERROR	-395.33328	GCA	ERROR	47.3593207	GCA	ERROR	39.0906329	GCA	ERROR	262.541808	GCA	ERROR	-828.55563	GCA	ERROR	-5165.9074
SCA	SCA	0	SCA	SCA	0	SCA	SCA	83254.8327	SCA	SCA	54047.5718	SCA	SCA	103965.668	SCA	SCA	0	SCA	SCA	0	SCA	SCA	0
SCA	LOCxGCA	0	SCA	LOCxGCA	0	SCA	LOCxGCA	-16894.461	SCA	LOCxGCA	-11426.883	SCA	LOCxGCA	-21079.188	SCA	LOCxGCA	0	SCA	LOCxGCA	0	SCA	LOCxGCA	0
SCA	ERROR	0	SCA	ERROR	0	SCA	ERROR	-45564.417	SCA	ERROR	-32006.336	SCA	ERROR	-65147.778	SCA	ERROR	0	SCA	ERROR	0	SCA	ERROR	0
LOCxGCA	LOCxGCA	33509.7658	LOCxGCA	LOCxGCA	18243.2433	LOCxGCA	LOCxGCA	31307.0808	LOCxGCA	LOCxGCA	47188.3161	LOCxGCA	LOCxGCA	78709.3451	LOCxGCA	LOCxGCA	21917.7449	LOCxGCA	LOCxGCA	56256.2972	LOCxGCA	LOCxGCA	0
LOCxGCA	ERROR	-12594.47	LOCxGCA	ERROR	-8342.4639	LOCxGCA	ERROR	-785.35873	LOCxGCA	ERROR	34.0614182	LOCxGCA	ERROR	-21.115967	LOCxGCA	ERROR	-8581.6857	LOCxGCA	ERROR	-9256.3325	LOCxGCA	ERROR	0
ERROR	ERROR	392890.082	ERROR	ERROR	317249.64	ERROR	ERROR	376068.39	ERROR	ERROR	308830.184	ERROR	ERROR	442591.931	ERROR	ERROR	321909.418	ERROR	ERROR	320958.422	ERROR	ERROR	264356.175
0.97345811	0.00871636	0.08195337	0.99099282	0.00529899	0.07279419	0.98988288	0.00634403	0.07964941	0.888486	0.01430257	0.11959337	0.89870549	0.01368968	0.11700291	0.98054919	0.00467046	0.05834076	0.8980799	0.01239469	0.1113314	1	0	0

LVD

ONE	(PEE Tuan - F, Tuan)		TWO	(PEE Tuan - F, Beerwah)		THREE	(PEE Beerwah - F, Tuan)		FOUR	(PEE Beerwah - F, Beerwah)		FIVE	(PCH Tuan - F, Tuan)		SIX	(PCH Tuan - F, Beerwah)		SEVEN	(PCH Beerwah - F, Tuan)		EIGHT	(PCH Beerwah - F, Beerwa	
LOCATION	0		LOCATION	0		LOCATION	0		LOCATION	0		LOCATION	0		LOCATION	0		LOCATION	0		LOCATION	0	
BLOCK(LOC)	11554.08		BLOCK(LOC)	17712.9068		BLOCK(LOC)	34900.9998		BLOCK(LOC)	1669.75171		BLOCK(LOC)	2110.83564		BLOCK(LOC)	1032.02365		BLOCK(LOC)	1431.05367		BLOCK(LOC)	785.866884	
GCA	2131.79623		GCA	1652.52819		GCA	2274.00807		GCA	0		GCA	0		GCA	0		GCA	799.464039		GCA	663.470628	
SCA	0		SCA	0		SCA	0		SCA	0		SCA	0		SCA	0		SCA	61.214007		SCA	23.177608	
LOCxGCA	10.939939		LOCxGCA	225.753957		LOCxGCA	92.536295		LOCxGCA	12976.4896		LOCxGCA	21034.2365		LOCxGCA	17286.0334		LOCxGCA	855.51391		LOCxGCA	843.640426	
ERROR	10316.6096		ERROR	10110.9818		ERROR	10269.8004		ERROR	10109.8573		ERROR	10489.6405		ERROR	10248.9957		ERROR	10451.4518		ERROR	10257.9563	
LOCATION	LOCATION	0	LOCATION	LOCATION	0	LOCATION	LOCATION	0	LOCATION	LOCATION	0	LOCATION	LOCATION	0	LOCATION	LOCATION	0	LOCATION	LOCATION	0	LOCATION	LOCATION	0
LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0
LOCATION	GCA	0	LOCATION	GCA	0	LOCATION	GCA	0	LOCATION	GCA	0	LOCATION	GCA	0	LOCATION	GCA	0	LOCATION	GCA	0	LOCATION	GCA	0
LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	0
LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0
LOCATION	ERROR	0	LOCATION	ERROR	0	LOCATION	ERROR	0	LOCATION	ERROR	0	LOCATION	ERROR	0	LOCATION	ERROR	0	LOCATION	ERROR	0	LOCATION	ERROR	0
BLOCK(LOC)	BLOCK(LOC)	21770005.1	BLOCK(LOC)	BLOCK(LOC)	40703465.4	BLOCK(LOC)	BLOCK(LOC)	155565652	BLOCK(LOC)	BLOCK(LOC)	412959.404	BLOCK(LOC)	BLOCK(LOC)	939543.377	BLOCK(LOC)	BLOCK(LOC)	218220.538	BLOCK(LOC)	BLOCK(LOC)	374030.518	BLOCK(LOC)	BLOCK(LOC)	124358.592
BLOCK(LOC)	GCA	-18172.042	BLOCK(LOC)	GCA	-10605.217	BLOCK(LOC)	GCA	-22106.944	BLOCK(LOC)	GCA	0	BLOCK(LOC)	GCA	0	BLOCK(LOC)	GCA	0	BLOCK(LOC)	GCA	12.7662452	BLOCK(LOC)	GCA	0.1030779
BLOCK(LOC)	SCA	0	BLOCK(LOC)	SCA	0	BLOCK(LOC)	SCA	0	BLOCK(LOC)	SCA	0	BLOCK(LOC)	SCA	0	BLOCK(LOC)	SCA	0	BLOCK(LOC)	SCA	1068.77578	BLOCK(LOC)	SCA	703.631114
BLOCK(LOC)	LOCxGCA	-1804.9519	BLOCK(LOC)	LOCxGCA	-4004.6805	BLOCK(LOC)	LOCxGCA	-2610.1082	BLOCK(LOC)	LOCxGCA	-4492.3741	BLOCK(LOC)	LOCxGCA	-14602.758	BLOCK(LOC)	LOCxGCA	-2882.1243	BLOCK(LOC)	LOCxGCA	29.1671863	BLOCK(LOC)	LOCxGCA	0.44743433
BLOCK(LOC)	ERROR	-6562.5089	BLOCK(LOC)	ERROR	-6428.1136	BLOCK(LOC)	ERROR	-7958.7699	BLOCK(LOC)	ERROR	-6832.8678	BLOCK(LOC)	ERROR	-10545.996	BLOCK(LOC)	ERROR	-7553.7506	BLOCK(LOC)	ERROR	-9728.0834	BLOCK(LOC)	ERROR	-7203.1749
GCA	GCA	556168.381	GCA	GCA	409970.173	GCA	GCA	649558.337	GCA	GCA	0	GCA	GCA	0	GCA	GCA	0	GCA	GCA	386954.398	GCA	GCA	295960.842
GCA	SCA	0	GCA	SCA	0	GCA	SCA	0	GCA	SCA	0	GCA	SCA	0	GCA	SCA	0	GCA	SCA	-798.12047	GCA	SCA	-661.40314
GCA	LOCxGCA	-22349.185	GCA	LOCxGCA	-39756.438	GCA	LOCxGCA	-28333.66	GCA	LOCxGCA	0	GCA	LOCxGCA	0	GCA	LOCxGCA	0	GCA	LOCxGCA	-181677.41	GCA	LOCxGCA	-149507
GCA	ERROR	15.0397625	GCA	ERROR	40.6601808	GCA	ERROR	-402.65163	GCA	ERROR	0	GCA	ERROR	0	GCA	ERROR	0	GCA	ERROR	-458.42521	GCA	ERROR	13.7263285
SCA	SCA	0	SCA	SCA	0	SCA	SCA	0	SCA	SCA	0	SCA	SCA	0	SCA	SCA	0	SCA	SCA	74246.1516	SCA	SCA	46848.6354
SCA	LOCxGCA	0	SCA	LOCxGCA	0	SCA	LOCxGCA	0	SCA	LOCxGCA	0	SCA	LOCxGCA	0	SCA	LOCxGCA	0	SCA	LOCxGCA	-15261.313	SCA	LOCxGCA	-10546.394
SCA	ERROR	0	SCA	ERROR	0	SCA	ERROR	0	SCA	ERROR	0	SCA	ERROR	0	SCA	ERROR	0	SCA	ERROR	-44899.421	SCA	ERROR	29936.043
LOCxGCA	LOCxGCA	26454.2673	LOCxGCA	LOCxGCA	51578.1915	LOCxGCA	LOCxGCA	33778.8784	LOCxGCA	LOCxGCA	10717475.7	LOCxGCA	LOCxGCA	28078400.6	LOCxGCA	LOCxGCA	18841788.6	LOCxGCA	LOCxGCA	268577.949	LOCxGCA	LOCxGCA	222474.109
LOCxGCA	ERROR	-12951.581	LOCxGCA	ERROR	-8120.2946	LOCxGCA	ERROR	-9915.1598	LOCxGCA	ERROR	-7869.3414	LOCxGCA	ERROR	-17890.715	LOCxGCA	ERROR	-9966.914	LOCxGCA	ERROR	-1135.5164	LOCxGCA	ERROR	19.2529583
ERROR	ERROR	403081.209	ERROR	ERROR	303994.184	ERROR	ERROR	342407.641	ERROR	ERROR	256959.441	ERROR	ERROR	420759.151	ERROR	ERROR	314485.445	ERROR	ERROR	379330.262	ERROR	ERROR	292498.609
0.99489441	0.00575573	0.0758665	0.87980828	0.01537874	0.12401106	0.96089814	0.00612642	0.07827143	0	#DIV/0!	#DIV/0!	0	#DIV/0!	#DIV/0!	0	#DIV/0!	#DIV/0!	0.48277457	0.09374762	0.30618234	0.44022677	0.09225158	0.30372945

PCOEFF

ONE	(PEE Tuan - F, Tuan)		TWO	(PEE Tuan - F, Beerwah)		THREE	(PEE Beerwah - F, Tuan)		FOUR	(PEE Beerwah - F, Beerwah)		FIVE	(PCH Tuan - F, Tuan)		SIX	(PCH Tuan - F, Beerwah)		SEVEN	(PCH Beerwah - F, Tuan)		EIGHT	(PCH Beerwah - F, Beerwa	
LOCATION	0		LOCATION	0		LOCATION	0		LOCATION	0		LOCATION	7174.35471		LOCATION	0		LOCATION	510.68775		LOCATION	3677.82442	
BLOCK(LOC)	162.368464		BLOCK(LOC)	181.699944		BLOCK(LOC)	392.706029		BLOCK(LOC)	353.600882		BLOCK(LOC)	79.30539		BLOCK(LOC)	115.249262		BLOCK(LOC)	333.556579		BLOCK(LOC)	318.392246	
GCA	1298.46889		GCA	991.830713		GCA	1027.4894		GCA	1438.45692		GCA	1622.75707		GCA	1279.73432		GCA	1354.21275		GCA	1337.65191	
SCA	435.304458		SCA	347.450255		SCA	74.196106		SCA	91.304043		SCA	283.367548		SCA	238.987683		SCA	47.143875		SCA	72.449151	
LOCxGCA	462.624302		LOCxGCA	590.384255		LOCxGCA	628.849056		LOCxGCA	58.694253		LOCxGCA	0		LOCxGCA	115.542342		LOCxGCA	468.367699		LOCxGCA	110.129952	
ERROR	10150.3245		ERROR	10078.8312		ERROR	10922.9542		ERROR	10890.5519		ERROR	10370.9154		ERROR	10249.8109		ERROR	10287.1686		ERROR	10180.0516	
LOCATION	LOCATION	0	LOCATION	LOCATION	0	LOCATION	LOCATION	0	LOCATION	LOCATION	0	LOCATION	LOCATION	106492322	LOCATION	LOCATION	0	LOCATION	LOCATION	1329519.36	LOCATION	LOCATION	3004739.3
LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	-2702.2691	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	-5798.6986	LOCATION	BLOCK(LOC)	-3612.6952
LOCATION	GCA	0	LOCATION	GCA	0	LOCATION	GCA	0	LOCATION	GCA	0	LOCATION	GCA	-29036.683	LOCATION	GCA	0	LOCATION	GCA	-12677.754	LOCATION	GCA	-15405.767
LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	-1229.3859	LOCATION	SCA	0	LOCATION	SCA	1915.02013	LOCATION	SCA	1473.53374
LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	-23747.355	LOCATION	LOCxGCA	-5294.1974
LOCATION	ERROR	0	LOCATION	ERROR	0	LOCATION	ERROR	0	LOCATION	ERROR	0	LOCATION	ERROR	1577.7581	LOCATION	ERROR	0	LOCATION	ERROR	1392.97181	LOCATION	ERROR	697.912221
BLOCK(LOC)	BLOCK(LOC)	28295.6854	BLOCK(LOC)	BLOCK(LOC)	23486.0548	BLOCK(LOC)	BLOCK(LOC)	52941.7522	BLOCK(LOC)	BLOCK(LOC)	36174.3976	BLOCK(LOC)	BLOCK(LOC)	18911.6516	BLOCK(LOC)	BLOCK(LOC)	16863.5585	BLOCK(LOC)	BLOCK(LOC)	47699.9118	BLOCK(LOC)	BLOCK(LOC)	36122.6499
BLOCK(LOC)	GCA	-0.499694	BLOCK(LOC)	GCA	-10.751457	BLOCK(LOC)	GCA	14.1738827	BLOCK(LOC)	GCA	0.16810481	BLOCK(LOC)	GCA	2.59869179	BLOCK(LOC)	GCA	-11.727215	BLOCK(LOC)	GCA	15.822019	BLOCK(LOC)	GCA	0.09537318
BLOCK(LOC)	SCA	1491.39011	BLOCK(LOC)	SCA	862.369372	BLOCK(LOC)	SCA	1231.31135	BLOCK(LOC)	SCA	774.943032	BLOCK(LOC)	SCA	1537.13439	BLOCK(LOC)	SCA	880.486511	BLOCK(LOC)	SCA	1051.84806	BLOCK(LOC)	SCA	689.270611
BLOCK(LOC)	LOCxGCA	1.81393315	BLOCK(LOC)	LOCxGCA	-0.1500844	BLOCK(LOC)	LOCxGCA	29.9713503	BLOCK(LOC)	LOCxGCA	0.8692858	BLOCK(LOC)	LOCxGCA	0	BLOCK(LOC)	LOCxGCA	1.72217622	BLOCK(LOC)	LOCxGCA	24.417198	BLOCK(LOC)	LOCxGCA	0.29294122
BLOCK(LOC)	ERROR	-10489.973	BLOCK(LOC)	ERROR	-7631.7173	BLOCK(LOC)	ERROR	-10841.472	BLOCK(LOC)	ERROR	-7931.7607	BLOCK(LOC)	ERROR	-11023.059	BLOCK(LOC)	ERROR	-7946.0004	BLOCK(LOC)	ERROR	-9319.2401	BLOCK(LOC)	ERROR	-7028.7406
GCA	GCA	453789.421	GCA	GCA	347603.014	GCA	GCA	379132.117	GCA	GCA	284270.268	GCA	GCA	354272.643	GCA	GCA	266771.271	GCA	GCA	424911.508	GCA	GCA	261082.902
GCA	SCA	-1710.4894	GCA	SCA	-1430.5042	GCA	SCA	-845.88085	GCA	SCA	-266.95406	GCA	SCA	-19991.712	GCA	SCA	-1104.1983	GCA	SCA	-825.21494	GCA	SCA	-459.33884
GCA	LOCxGCA	-123358.49	GCA	LOCxGCA	-124824.95	GCA	LOCxGCA	-135825.63	GCA	LOCxGCA	-20106.252	GCA	LOCxGCA	0	GCA	LOCxGCA	-33026.915	GCA	LOCxGCA	-90746.9	GCA	LOCxGCA	-21360.237
GCA	ERROR	-70.056814	GCA	ERROR	444.590787	GCA	ERROR	-555.38141	GCA	ERROR	42.3887476	GCA	ERROR	2.29734238	GCA	ERROR	600.627915	GCA	ERROR	-572.60481	GCA	ERROR	18.1978914
SCA	SCA	156926.535	SCA	SCA	99817.3643	SCA	SCA	85679.6209	SCA	SCA	61066.4697	SCA	SCA	119285.146	SCA	SCA	85738.1202	SCA	SCA	70252.5103	SCA	SCA	51981.5358
SCA	LOCxGCA	-32327.851	SCA	LOCxGCA	-21522.989	SCA	LOCxGCA	-17433.401	SCA	LOCxGCA	-12682.183	SCA	LOCxGCA	0	SCA	LOCxGCA	-17667.576	SCA	LOCxGCA	-14239.906	SCA	LOCxGCA	-10786.119
SCA	ERROR	-63078.146	SCA	ERROR	-38144.565	SCA	ERROR	-50921.479	SCA	ERROR	-33379.705	SCA	ERROR	-66806.383	SCA	ERROR	-39653.992	SCA	ERROR	-43448.955	SCA	ERROR	-29470.555
LOCxGCA	LOCxGCA	176491.494	LOCxGCA	LOCxGCA	180591.265	LOCxGCA	LOCxGCA	196421.28	LOCxGCA	LOCxGCA	27553.1833	LOCxGCA	LOCxGCA	0	LOCxGCA	LOCxGCA	46796.974	LOCxGCA	LOCxGCA	126521.882	LOCxGCA	LOCxGCA	29346.462
LOCxGCA	ERROR	-19.5011139	LOCxGCA	ERROR	35.4417564	LOCxGCA	ERROR	-1027.665	LOCxGCA	ERROR	28.5336912	LOCxGCA	ERROR	0	LOCxGCA	ERROR	-135.22986	LOCxGCA	ERROR	-992.82125	LOCxGCA	ERROR	10.9620187
ERROR	ERROR	431218.807	ERROR	ERROR	325744.554	ERROR	ERROR	422183.42	ERROR	ERROR	322523.888	ERROR	ERROR	454200.208	ERROR	ERROR	339731.994	ERROR	ERROR	367531.969	ERROR	ERROR	288148.143
0.72902917	0.05543403	0.23544432	0.82686217	0.0710216	0.26649877	0.82108778	0.070776	0.26603759	0.95442113	0.01207948	0.10990668	1	0	0	0.91719037	0.02373919	0.15407527	0.74301948	0.03991835	0.19979578	0.92393258	0.01410487	0.11876392

DEV

ONE	(PEE Tuan - F, Tuan)	
LOCATION	7319.25638	
BLOCK(LOC)	156.490917	
GCA	1799.0162	
SCA	0	
LOCxGCA	188.405534	
ERROR	10496.9281	
LOCATION	LOCATION	114796915
LOCATION	BLOCK(LOC)	-4155.5403
LOCATION	GCA	-29364.075
LOCATION	SCA	0
LOCATION	LOCxGCA	-11115.387
LOCATION	ERROR	3386.82898
BLOCK(LOC)	BLOCK(LOC)	28770.6143
BLOCK(LOC)	GCA	10.1540828
BLOCK(LOC)	SCA	0
BLOCK(LOC)	LOCxGCA	318.407229
BLOCK(LOC)	ERROR	-10164.952
GCA	GCA	494139.767
GCA	SCA	0
GCA	LOCxGCA	-47257.158
GCA	ERROR	-548.31459
SCA	SCA	0
SCA	LOCxGCA	0
SCA	ERROR	0
LOCxGCA	LOCxGCA	60216.1175
LOCxGCA	ERROR	-13490.112
ERROR	ERROR	417378.007
0.90520103	0.01566939	0.12517742

TWO	(PEE Tuan - F, Beerwah)	
LOCATION	5689.52138	
BLOCK(LOC)	524.005861	
GCA	1809.94834	
SCA	0	
LOCxGCA	259.205698	
ERROR	10004.6689	
LOCATION	LOCATION	71994829.4
LOCATION	BLOCK(LOC)	-9445.7891
LOCATION	GCA	-29185.477
LOCATION	SCA	0
LOCATION	LOCxGCA	-10825.034
LOCATION	ERROR	1941.34175
BLOCK(LOC)	BLOCK(LOC)	77581.9162
BLOCK(LOC)	GCA	-1.1130715
BLOCK(LOC)	SCA	0
BLOCK(LOC)	LOCxGCA	183.53402
BLOCK(LOC)	ERROR	-7054.7212
GCA	GCA	484535.455
GCA	SCA	0
GCA	LOCxGCA	-44769.356
GCA	ERROR	12.9706524
SCA	SCA	0
SCA	LOCxGCA	0
SCA	ERROR	0
LOCxGCA	LOCxGCA	58229.1967
LOCxGCA	ERROR	-7999.0906
ERROR	ERROR	297644.425
0.87472866	0.01447409	0.12030833

THREE	(PEE Beerwah - F, Tuan)	
LOCATION	0	
BLOCK(LOC)	1030.56172	
GCA	2015.59622	
SCA	0	
LOCxGCA	192.463527	
ERROR	10474.426	
LOCATION	LOCATION	0
LOCATION	BLOCK(LOC)	0
LOCATION	GCA	0
LOCATION	SCA	0
LOCATION	LOCxGCA	0
LOCATION	ERROR	0
BLOCK(LOC)	BLOCK(LOC)	229859.012
BLOCK(LOC)	GCA	17.3031376
BLOCK(LOC)	SCA	0
BLOCK(LOC)	LOCxGCA	257.678987
BLOCK(LOC)	ERROR	-9358.8101
GCA	GCA	575092.234
GCA	SCA	0
GCA	LOCxGCA	-44172.444
GCA	ERROR	-732.95083
SCA	SCA	0
SCA	LOCxGCA	0
SCA	ERROR	0
LOCxGCA	LOCxGCA	55266.5584
LOCxGCA	ERROR	-10329.732
ERROR	ERROR	356074.935
0.91283591	0.01178345	0.1085516

FOUR	(PEE Beerwah - F, Beerwah)	
LOCATION	0	
BLOCK(LOC)	1802.33814	
GCA	4883.65475	
SCA	0	
LOCxGCA	215.492308	
ERROR	10039.1237	
LOCATION	LOCATION	0
LOCATION	BLOCK(LOC)	0
LOCATION	GCA	0
LOCATION	SCA	0
LOCATION	LOCxGCA	0
LOCATION	ERROR	0
BLOCK(LOC)	BLOCK(LOC)	468609.064
BLOCK(LOC)	GCA	-10506.226
BLOCK(LOC)	SCA	0
BLOCK(LOC)	LOCxGCA	-261.53759
BLOCK(LOC)	ERROR	-6654.2262
GCA	GCA	2504946.3
GCA	SCA	0
GCA	LOCxGCA	-37434.37
GCA	ERROR	164.887494
SCA	SCA	0
SCA	LOCxGCA	0
SCA	ERROR	0
LOCxGCA	LOCxGCA	43976.398
LOCxGCA	ERROR	-6407.3689
ERROR	ERROR	265060.271
0.95773954	0.00183998	0.04289504

FIVE	(PCH Tuan - F, Tuan)	
LOCATION	0	
BLOCK(LOC)	0	
GCA	0	
SCA	0	
LOCxGCA	3732.4705	
ERROR	10664.4087	
LOCATION	LOCATION	0
LOCATION	BLOCK(LOC)	0
LOCATION	GCA	0
LOCATION	SCA	0
LOCATION	LOCxGCA	0
LOCATION	ERROR	0
BLOCK(LOC)	BLOCK(LOC)	0
BLOCK(LOC)	GCA	0
BLOCK(LOC)	SCA	0
BLOCK(LOC)	LOCxGCA	0
BLOCK(LOC)	ERROR	0
GCA	GCA	0
GCA	SCA	0
GCA	LOCxGCA	0
GCA	ERROR	0
SCA	SCA	0
SCA	LOCxGCA	0
SCA	ERROR	0
LOCxGCA	LOCxGCA	1043998.79
LOCxGCA	ERROR	-15967.199
ERROR	ERROR	424954.994
0	#DIV/0!	#DIV/0!

SIX	(PCH Tuan - F, Beerwah)	
LOCATION	0	
BLOCK(LOC)	424.675215	
GCA	0	
SCA	0	
LOCxGCA	3809.53228	
ERROR	10166.5393	
LOCATION	LOCATION	0
LOCATION	BLOCK(LOC)	0
LOCATION	GCA	0
LOCATION	SCA	0
LOCATION	LOCxGCA	0
LOCATION	ERROR	0
BLOCK(LOC)	BLOCK(LOC)	59644.0564
BLOCK(LOC)	GCA	0
BLOCK(LOC)	SCA	0
BLOCK(LOC)	LOCxGCA	-664.29683
BLOCK(LOC)	ERROR	-7363.0871
GCA	GCA	0
GCA	SCA	0
GCA	LOCxGCA	0
GCA	ERROR	0
SCA	SCA	0
SCA	LOCxGCA	0
SCA	ERROR	0
LOCxGCA	LOCxGCA	1031220.88
LOCxGCA	ERROR	-9042.152
ERROR	ERROR	309373.43
0	#DIV/0!	#DIV/0!

SEVEN	(PCH Beerwah - F, Tuan)	
LOCATION	0	
BLOCK(LOC)	4.50119	
GCA	795.473557	
SCA	338.055307	
LOCxGCA	758.410796	
ERROR	10528.7695	
LOCATION	LOCATION	0
LOCATION	BLOCK(LOC)	0
LOCATION	GCA	0
LOCATION	SCA	0
LOCATION	LOCxGCA	0
LOCATION	ERROR	0
BLOCK(LOC)	BLOCK(LOC)	9642.43945
BLOCK(LOC)	GCA	11.6996123
BLOCK(LOC)	SCA	1090.36851
BLOCK(LOC)	LOCxGCA	22.7319716
BLOCK(LOC)	ERROR	-9558.6261
GCA	GCA	366611.163
GCA	SCA	-1070.4437
GCA	LOCxGCA	-170404.73
GCA	ERROR	-440.96145
SCA	SCA	108471.952
SCA	LOCxGCA	-22417.303
SCA	ERROR	-46057.465
LOCxGCA	LOCxGCA	253869.372
LOCxGCA	ERROR	-979.59612
ERROR	ERROR	385258.673
0.51192584	0.09899032	0.31462727

EIGHT	(PCH Beerwah - F, Beerwa	
LOCATION	0	
BLOCK(LOC)	340.701056	
GCA	654.895637	
SCA	235.2241	
LOCxGCA	1062.62581	
ERROR	10120.157	
LOCATION	LOCATION	0
LOCATION	BLOCK(LOC)	0
LOCATION	GCA	0
LOCATION	SCA	0
LOCATION	LOCxGCA	0
LOCATION	ERROR	0
BLOCK(LOC)	BLOCK(LOC)	38679.2518
BLOCK(LOC)	GCA	0.20056848
BLOCK(LOC)	SCA	679.907489
BLOCK(LOC)	LOCxGCA	-0.1390031
BLOCK(LOC)	ERROR	-6959.742
GCA	GCA	392140.095
GCA	SCA	-807.69137
GCA	LOCxGCA	-226981.97
GCA	ERROR	11.0974451
SCA	SCA	67343.3503
SCA	LOCxGCA	-14939.704
SCA	ERROR	-29164.481
LOCxGCA	LOCxGCA	342889.759
LOCxGCA	ERROR	19.1946176
ERROR	ERROR	284812.397
0.38130274	0.10409043	0.32263049

DWWI

ONE	(PEE Tuan - F, Tuan)	
LOCATION	1414.22308	
BLOCK(LOC)	258.445565	
GCA	768.368421	
SCA	0	
LOCxGCA	573.543704	
ERROR	10996.5384	
LOCATION	LOCATION	5774790.42
LOCATION	BLOCK(LOC)	-6793.2177
LOCATION	GCA	6541.88416
LOCATION	SCA	0
LOCATION	LOCxGCA	-32990.298
LOCATION	ERROR	3781.57279
BLOCK(LOC)	BLOCK(LOC)	47201.2039
BLOCK(LOC)	GCA	17.0663027
BLOCK(LOC)	SCA	0
BLOCK(LOC)	LOCxGCA	353.81832
BLOCK(LOC)	ERROR	-11366.548
GCA	GCA	280323.907
GCA	SCA	0
GCA	LOCxGCA	-119607.78
GCA	ERROR	-820.20377
SCA	SCA	0
SCA	LOCxGCA	0
SCA	ERROR	0
LOCxGCA	LOCxGCA	171831.119
LOCxGCA	ERROR	-14965.49
ERROR	ERROR	461575.699
0.5725922	0.09223437	0.30370112

TWO	(PEE Tuan - F, Beerwah)	
LOCATION	79.380192	
BLOCK(LOC)	941.553728	
GCA	773.576237	
SCA	623.84479	
LOCxGCA	621.422519	
ERROR	10734.6974	
LOCATION	LOCATION	438871.531
LOCATION	BLOCK(LOC)	-23288.773
LOCATION	GCA	10287.6516
LOCATION	SCA	4477.26629
LOCATION	LOCxGCA	-41690.856
LOCATION	ERROR	938.668182
BLOCK(LOC)	BLOCK(LOC)	191810.273
BLOCK(LOC)	GCA	-10.336524
BLOCK(LOC)	SCA	1004.97655
BLOCK(LOC)	LOCxGCA	-0.5764559
BLOCK(LOC)	ERROR	-8852.6561
GCA	GCA	318394.1
GCA	SCA	-1729.7663
GCA	LOCxGCA	-147113.37
GCA	ERROR	430.462936
SCA	SCA	148379.783
SCA	LOCxGCA	-31723.729
SCA	ERROR	-43846.094
LOCxGCA	LOCxGCA	218883.585
LOCxGCA	ERROR	90.7069703
ERROR	ERROR	371216.505
0.55453543	0.10440384	0.32311583

THREE	(PEE Beerwah - F, Tuan)	
LOCATION	6186.27225	
BLOCK(LOC)	774.616277	
GCA	510.048202	
SCA	0	
LOCxGCA	274.41059	
ERROR	10586.0291	
LOCATION	LOCATION	82536877.8
LOCATION	BLOCK(LOC)	-18083.837
LOCATION	GCA	1925.0211
LOCATION	SCA	0
LOCATION	LOCxGCA	-12625.346
LOCATION	ERROR	2618.97535
BLOCK(LOC)	BLOCK(LOC)	148473.65
BLOCK(LOC)	GCA	17.7760644
BLOCK(LOC)	SCA	0
BLOCK(LOC)	LOCxGCA	249.666868
BLOCK(LOC)	ERROR	-9569.9205
GCA	GCA	116306.611
GCA	SCA	0
GCA	LOCxGCA	-46468.94
GCA	ERROR	-703.82036
SCA	SCA	0
SCA	LOCxGCA	0
SCA	ERROR	0
LOCxGCA	LOCxGCA	65981.2675
LOCxGCA	ERROR	-10030.929
ERROR	ERROR	365282.374
0.6501912	0.10280473	0.32063176

FOUR	(PEE Beerwah - F, Beerwah)	
LOCATION	3372.20037	
BLOCK(LOC)	1249.06337	
GCA	715.566755	
SCA	482.99202	
LOCxGCA	137.108114	
ERROR	10483.5178	
LOCATION	LOCATION	26354627.8
LOCATION	BLOCK(LOC)	-25579.533
LOCATION	GCA	-2514.6427
LOCATION	SCA	2737.82813
LOCATION	LOCxGCA	-9393.7414
LOCATION	ERROR	766.314974
BLOCK(LOC)	BLOCK(LOC)	255615.222
BLOCK(LOC)	GCA	0.73544303
BLOCK(LOC)	SCA	757.27958
BLOCK(LOC)	LOCxGCA	1.89263478
BLOCK(LOC)	ERROR	-7830.5322
GCA	GCA	135215.944
GCA	SCA	-797.85097
GCA	LOCxGCA	-34933.76
GCA	ERROR	35.1068596
SCA	SCA	99882.6975
SCA	LOCxGCA	-20388.989
SCA	ERROR	-32182.586
LOCxGCA	LOCxGCA	51197.9038
LOCxGCA	ERROR	21.2659008
ERROR	ERROR	309945.123
0.83920235	0.06736888	0.25955515

FIVE	(PCH Tuan - F, Tuan)	
LOCATION	3910.6265	
BLOCK(LOC)	1125.52342	
GCA	303.973017	
SCA	128.482833	
LOCxGCA	179.257314	
ERROR	11031.6072	
LOCATION	LOCATION	35029889.8
LOCATION	BLOCK(LOC)	-46899.523
LOCATION	GCA	3861.9009
LOCATION	SCA	3065.04923
LOCATION	LOCxGCA	-12038.636
LOCATION	ERROR	1851.14591
BLOCK(LOC)	BLOCK(LOC)	328295.716
BLOCK(LOC)	GCA	3.25334047
BLOCK(LOC)	SCA	1797.81465
BLOCK(LOC)	LOCxGCA	-1.3846419
BLOCK(LOC)	ERROR	-12884.569
GCA	GCA	73964.0726
GCA	SCA	-724.69425
GCA	LOCxGCA	-40034.761
GCA	ERROR	-11.769105
SCA	SCA	131749.134
SCA	LOCxGCA	-24833.465
SCA	ERROR	-76365.337
LOCxGCA	LOCxGCA	63917.8895
LOCxGCA	ERROR	-22.684241
ERROR	ERROR	517240.639
0.62904374	0.23191222	0.48157266

SIX	(PCH Tuan - F, Beerwah)	
LOCATION	1722.60577	
BLOCK(LOC)	1616.89659	
GCA	564.297714	
SCA	632.828628	
LOCxGCA	0	
ERROR	10758.4519	
LOCATION	LOCATION	8127043.89
LOCATION	BLOCK(LOC)	-57063.804
LOCATION	GCA	-5665.1402
LOCATION	SCA	-1406.0544
LOCATION	LOCxGCA	0
LOCATION	ERROR	970.576612
BLOCK(LOC)	BLOCK(LOC)	469950.148
BLOCK(LOC)	GCA	-8.2095146
BLOCK(LOC)	SCA	1003.07533
BLOCK(LOC)	LOCxGCA	0
BLOCK(LOC)	ERROR	-9002.4937
GCA	GCA	73790.9767
GCA	SCA	-19933.627
GCA	LOCxGCA	0
GCA	ERROR	425.492182
SCA	SCA	126509.573
SCA	LOCxGCA	0
SCA	ERROR	-44249.738
LOCxGCA	LOCxGCA	0
LOCxGCA	ERROR	0
ERROR	ERROR	374543.214
1	0	0

SEVEN	(PCH Beerwah - F, Tuan)	
LOCATION	1706.94621	
BLOCK(LOC)	683.285907	
GCA	138.387405	
SCA	60.175823	
LOCxGCA	173.038028	
ERROR	10585.3577	
LOCATION	LOCATION	7056901.92
LOCATION	BLOCK(LOC)	-14851.695
LOCATION	GCA	3465.31469
LOCATION	SCA	1640.62864
LOCATION	LOCxGCA	-8321.9312
LOCATION	ERROR	1377.87997
BLOCK(LOC)	BLOCK(LOC)	122274.542
BLOCK(LOC)	GCA	4.58341508
BLOCK(LOC)	SCA	1140.10176
BLOCK(LOC)	LOCxGCA	18.1596197
BLOCK(LOC)	ERROR	-10033.455
GCA	GCA	38100.7106
GCA	SCA	-168.83318
GCA	LOCxGCA	-26546.49
GCA	ERROR	-152.40905
SCA	SCA	75205.065
SCA	LOCxGCA	-13846.671
SCA	ERROR	-46791.754
LOCxGCA	LOCxGCA	43482.8516
LOCxGCA	ERROR	-708.72865
ERROR	ERROR	391629.254
0.44436771	0.34497722	0.58734761

EIGHT	(PCH Beerwah - F, Beerwa	
LOCATION	358.764122	
BLOCK(LOC)	1189.84019	
GCA	368.689056	
SCA	573.520063	
LOCxGCA	0	
ERROR	10458.6818	
LOCATION	LOCATION	604613.413
LOCATION	BLOCK(LOC)	-23397.603
LOCATION	GCA	-2946.3985
LOCATION	SCA	-1096.3953
LOCATION	LOCxGCA	0
LOCATION	ERROR	753.529268
BLOCK(LOC)	BLOCK(LOC)	233968.596
BLOCK(LOC)	GCA	0.87483037
BLOCK(LOC)	SCA	738.613514
BLOCK(LOC)	LOCxGCA	0
BLOCK(LOC)	ERROR	-7564.0055
GCA	GCA	39339.6137
GCA	SCA	-13660.518
GCA	LOCxGCA	0
GCA	ERROR	14.9201918
SCA	SCA	91999.5875
SCA	LOCxGCA	0
SCA	ERROR	-31311.912
LOCxGCA	LOCxGCA	0
LOCxGCA	ERROR	0
ERROR	ERROR	305049.565
1	0	0

LWP

ONE	(PEE Tuan - F, Tuan)	
LOCATION	8442.68169	
BLOCK(LOC)	0	
GCA	456.814809	
SCA	175.892251	
LOCxGCA	1292.8265	
ERROR	10622.5301	
LOCATION	LOCATION	156526756
LOCATION	BLOCK(LOC)	0
LOCATION	GCA	45277.4065
LOCATION	SCA	3998.50081
LOCATION	LOCxGCA	-101936.12
LOCATION	ERROR	21.2699118
BLOCK(LOC)	BLOCK(LOC)	0
BLOCK(LOC)	GCA	0
BLOCK(LOC)	SCA	0
BLOCK(LOC)	LOCxGCA	0
BLOCK(LOC)	ERROR	0
GCA	GCA	460692.036
GCA	SCA	-832.36418
GCA	LOCxGCA	-334592.14
GCA	ERROR	-31.715479
SCA	SCA	128350.038
SCA	LOCxGCA	-27280.51
SCA	ERROR	-67425.614
LOCxGCA	LOCxGCA	521928.101
LOCxGCA	ERROR	-58.609802
ERROR	ERROR	461280.798
0.26109055	0.1359615	0.36872958

TWO	(PEE Tuan - F, Beerwah)	
LOCATION	0	
BLOCK(LOC)	190.256284	
GCA	521.191285	
SCA	101.799288	
LOCxGCA	542.356209	
ERROR	10701.9805	
LOCATION	LOCATION	0
LOCATION	BLOCK(LOC)	0
LOCATION	GCA	0
LOCATION	SCA	0
LOCATION	LOCxGCA	0
LOCATION	ERROR	0
BLOCK(LOC)	BLOCK(LOC)	26354.5511
BLOCK(LOC)	GCA	-9.2730986
BLOCK(LOC)	SCA	960.648493
BLOCK(LOC)	LOCxGCA	0.27537723
BLOCK(LOC)	ERROR	-8589.3542
GCA	GCA	181491.178
GCA	SCA	-899.67251
GCA	LOCxGCA	-95397.408
GCA	ERROR	385.891936
SCA	SCA	78889.7209
SCA	LOCxGCA	-16645.104
SCA	ERROR	-42536.442
LOCxGCA	LOCxGCA	142993.866
LOCxGCA	ERROR	19.5271241
ERROR	ERROR	367014.895
0.49004985	0.1142361	0.33798832

THREE	(PEE Beerwah - F, Tuan)	
LOCATION	2309.23643	
BLOCK(LOC)	220.919658	
GCA	525.964539	
SCA	136.712687	
LOCxGCA	1396.47588	
ERROR	11048.5003	
LOCATION	LOCATION	15324519.9
LOCATION	BLOCK(LOC)	-4220.9016
LOCATION	GCA	48232.3945
LOCATION	SCA	2777.54932
LOCATION	LOCxGCA	-111339.63
LOCATION	ERROR	1667.28848
BLOCK(LOC)	BLOCK(LOC)	34565.4848
BLOCK(LOC)	GCA	7.69829967
BLOCK(LOC)	SCA	1253.07693
BLOCK(LOC)	LOCxGCA	37.0597297
BLOCK(LOC)	ERROR	-10986.701
GCA	GCA	522664.869
GCA	SCA	-615.83021
GCA	LOCxGCA	-367091.89
GCA	ERROR	-309.67218
SCA	SCA	94277.9503
SCA	LOCxGCA	-20092.667
SCA	ERROR	-52038.996
LOCxGCA	LOCxGCA	569672.355
LOCxGCA	ERROR	-1338.9094
ERROR	ERROR	430833
0.27359211	0.12564246	0.3544608

FOUR	(PEE Beerwah - F, Beerwah)	
LOCATION	7262.48967	
BLOCK(LOC)	376.883764	
GCA	875.949657	
SCA	79.70783	
LOCxGCA	405.085713	
ERROR	10988.958	
LOCATION	LOCATION	112638450
LOCATION	BLOCK(LOC)	-4754.8716
LOCATION	GCA	-2167.0022
LOCATION	SCA	1818.02607
LOCATION	LOCxGCA	-17945.006
LOCATION	ERROR	823.240195
BLOCK(LOC)	BLOCK(LOC)	47409.3159
BLOCK(LOC)	GCA	-0.0389756
BLOCK(LOC)	SCA	818.951509
BLOCK(LOC)	LOCxGCA	1.20877644
BLOCK(LOC)	ERROR	-8391.8128
GCA	GCA	225796.646
GCA	SCA	-779.65803
GCA	LOCxGCA	-66520.726
GCA	ERROR	45.205382
SCA	SCA	62355.054
SCA	LOCxGCA	-13064.096
SCA	ERROR	-35200.454
LOCxGCA	LOCxGCA	95221.5139
LOCxGCA	ERROR	36.879071
ERROR	ERROR	339971.619
0.68378257	0.05841777	0.24169768

FIVE	(PCH Tuan - F, Tuan)	
LOCATION	0	
BLOCK(LOC)	265.570738	
GCA	577.116246	
SCA	95.743509	
LOCxGCA	689.483463	
ERROR	10698.8283	
LOCATION	LOCATION	0
LOCATION	BLOCK(LOC)	0
LOCATION	GCA	0
LOCATION	SCA	0
LOCATION	LOCxGCA	0
LOCATION	ERROR	0
BLOCK(LOC)	BLOCK(LOC)	45996.8764
BLOCK(LOC)	GCA	2.58856306
BLOCK(LOC)	SCA	1650.23407
BLOCK(LOC)	LOCxGCA	-0.3624316
BLOCK(LOC)	ERROR	-11833.019
GCA	GCA	265853.995
GCA	SCA	-1132.1151
GCA	LOCxGCA	-146000.57
GCA	ERROR	-0.6498008
SCA	SCA	123035.087
SCA	LOCxGCA	-24848.107
SCA	ERROR	-70977.939
LOCxGCA	LOCxGCA	222153.082
LOCxGCA	ERROR	-22.018567
ERROR	ERROR	482529.868
0.45564217	0.12300025	0.35071391

SIX	(PCH Tuan - F, Beerwah)	
LOCATION	0	
BLOCK(LOC)	442.889501	
GCA	453.267254	
SCA	57.538927	
LOCxGCA	191.968969	
ERROR	10696.4029	
LOCATION	LOCATION	0
LOCATION	BLOCK(LOC)	0
LOCATION	GCA	0
LOCATION	SCA	0
LOCATION	LOCxGCA	0
LOCATION	ERROR	0
BLOCK(LOC)	BLOCK(LOC)	62586.972
BLOCK(LOC)	GCA	-9.3332241
BLOCK(LOC)	SCA	960.890293
BLOCK(LOC)	LOCxGCA	2.03308917
BLOCK(LOC)	ERROR	-8745.8589
GCA	GCA	83326.374
GCA	SCA	-852.94899
GCA	LOCxGCA	-32404.376
GCA	ERROR	495.139471
SCA	SCA	74090.9683
SCA	LOCxGCA	-14899.779
SCA	ERROR	-42726.571
LOCxGCA	LOCxGCA	48730.2582
LOCxGCA	ERROR	-156.91291
ERROR	ERROR	369143.267
0.70248265	0.10801135	0.32865081

SEVEN	(PCH Beerwah - F, Tuan)	
LOCATION	0	
BLOCK(LOC)	169.278396	
GCA	846.320871	
SCA	520.412963	
LOCxGCA	344.099232	
ERROR	10833.7066	
LOCATION	LOCATION	0
LOCATION	BLOCK(LOC)	0
LOCATION	GCA	0
LOCATION	SCA	0
LOCATION	LOCxGCA	0
LOCATION	ERROR	0
BLOCK(LOC)	BLOCK(LOC)	29180.7874
BLOCK(LOC)	GCA	13.3600109
BLOCK(LOC)	SCA	1183.66087
BLOCK(LOC)	LOCxGCA	18.9623103
BLOCK(LOC)	ERROR	-10302.711
GCA	GCA	251924.543
GCA	SCA	-1093.9339
GCA	LOCxGCA	-83974.444
GCA	ERROR	-477.02371
SCA	SCA	137528.619
SCA	LOCxGCA	-27654.276
SCA	ERROR	-49158.707
LOCxGCA	LOCxGCA	123049.822
LOCxGCA	ERROR	-793.13557
ERROR	ERROR	408195.861
0.71094303	0.08309759	0.28826652

EIGHT	(PCH Beerwah - F, Beerwa	
LOCATION	6172.57212	
BLOCK(LOC)	353.09252	
GCA	212.185711	
SCA	367.374326	
LOCxGCA	497.781217	
ERROR	10817.2878	
LOCATION	LOCATION	81566637.8
LOCATION	BLOCK(LOC)	-4283.7712
LOCATION	GCA	10728.1549
LOCATION	SCA	2499.12967
LOCATION	LOCxGCA	-24411.224
LOCATION	ERROR	789.403496
BLOCK(LOC)	BLOCK(LOC)	42832.5373
BLOCK(LOC)	GCA	0.0601553
BLOCK(LOC)	SCA	776.300894
BLOCK(LOC)	LOCxGCA	0.53429088
BLOCK(LOC)	ERROR	-7948.3796
GCA	GCA	107426.156
GCA	SCA	-452.65017
GCA	LOCxGCA	-78677.873
GCA	ERROR	6.64547725
SCA	SCA	88657.5398
SCA	LOCxGCA	-18458.014
SCA	ERROR	-33308.831
LOCxGCA	LOCxGCA	125666.347
LOCxGCA	ERROR	16.8397884
ERROR	ERROR	325380.776
0.29886704	0.19245445	0.4386963

OBVOL

ONE	(PEE Tuan - F, Tuan)		TWO	(PEE Tuan - F, Beerwah)		THREE	(PEE Beerwah - F, Tuan)		FOUR	(PEE Beerwah - F, Beerwah)		FIVE	(PCH Tuan - F, Tuan)		SIX	(PCH Tuan - F, Beerwah)		SEVEN	(PCH Beerwah - F, Tuan)		EIGHT	(PCH Beerwah - F, Beerwa	
LOCATION	2079.76815		LOCATION	647.96129		LOCATION	0		LOCATION	0		LOCATION	4002.23595		LOCATION	2115.11091		LOCATION	4057.14425		LOCATION	2146.42078	
BLOCK(LOC)	322.246333		BLOCK(LOC)	284.418472		BLOCK(LOC)	1093.00401		BLOCK(LOC)	919.026179		BLOCK(LOC)	1221.54449		BLOCK(LOC)	964.823862		BLOCK(LOC)	624.196509		BLOCK(LOC)	529.192724	
GCA	470.440498		GCA	150.857879		GCA	441.951418		GCA	429.049054		GCA	335.429847		GCA	559.995691		GCA	158.596225		GCA	446.203596	
SCA	120.813274		SCA	1056.93303		SCA	14.224444		SCA	737.353965		SCA	116.889232		SCA	969.30504		SCA	0		SCA	728.585133	
LOCxGCA	521.636398		LOCxGCA	670.431863		LOCxGCA	570.16076		LOCxGCA	634.880965		LOCxGCA	124.874584		LOCxGCA	0		LOCxGCA	242.032024		LOCxGCA	11.970448	
ERROR	10705.9468		ERROR	10583.2724		ERROR	10921.103		ERROR	10839.1301		ERROR	10986.8895		ERROR	10785.4871		ERROR	10694.0629		ERROR	10657.1215	
LOCATION	LOCATION	10920908.7	LOCATION	LOCATION	1898831.33	LOCATION	LOCATION	0	LOCATION	LOCATION	0	LOCATION	LOCATION	96610772.4	LOCATION	LOCATION	10917016.4	LOCATION	LOCATION	35919851.7	LOCATION	LOCATION	10429111.3
LOCATION	BLOCK(LOC)	-8098.3675	LOCATION	BLOCK(LOC)	-4625.2701	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	-53167.388	LOCATION	BLOCK(LOC)	-24256.141	LOCATION	BLOCK(LOC)	-12914.325	LOCATION	BLOCK(LOC)	-6907.17
LOCATION	GCA	10142.2261	LOCATION	GCA	32200.5721	LOCATION	GCA	0	LOCATION	GCA	0	LOCATION	GCA	2455.22619	LOCATION	GCA	-8208.0976	LOCATION	GCA	4271.03911	LOCATION	GCA	-14.040653
LOCATION	SCA	3093.23054	LOCATION	SCA	6425.22985	LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	2899.12732	LOCATION	SCA	-1957.1832	LOCATION	SCA	0	LOCATION	SCA	3262.12021
LOCATION	LOCxGCA	-29759.796	LOCATION	LOCxGCA	-56445.349	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	-9577.0857	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	-9974.419	LOCATION	LOCxGCA	-6508.8561
LOCATION	ERROR	1621.88284	LOCATION	ERROR	858.422687	LOCATION	ERROR	0	LOCATION	ERROR	0	LOCATION	ERROR	1755.8906	LOCATION	ERROR	965.785077	LOCATION	ERROR	2337.55326	LOCATION	ERROR	750.875042
BLOCK(LOC)	BLOCK(LOC)	56690.6387	BLOCK(LOC)	BLOCK(LOC)	38121.1613	BLOCK(LOC)	BLOCK(LOC)	247444.291	BLOCK(LOC)	BLOCK(LOC)	155475.857	BLOCK(LOC)	BLOCK(LOC)	372180.47	BLOCK(LOC)	BLOCK(LOC)	139781.882	BLOCK(LOC)	BLOCK(LOC)	106098.896	BLOCK(LOC)	BLOCK(LOC)	69071.9353
BLOCK(LOC)	GCA	-0.6097096	BLOCK(LOC)	GCA	-2.3161347	BLOCK(LOC)	GCA	8.84868292	BLOCK(LOC)	GCA	0.76828498	BLOCK(LOC)	GCA	1.32490624	BLOCK(LOC)	GCA	-9.0790981	BLOCK(LOC)	GCA	7.25572025	BLOCK(LOC)	GCA	0.05891845
BLOCK(LOC)	SCA	1612.85196	BLOCK(LOC)	SCA	975.838819	BLOCK(LOC)	SCA	1143.43492	BLOCK(LOC)	SCA	779.229449	BLOCK(LOC)	SCA	1739.24254	BLOCK(LOC)	SCA	1023.92386	BLOCK(LOC)	SCA	0	BLOCK(LOC)	SCA	749.667093
BLOCK(LOC)	LOCxGCA	-1.1466969	BLOCK(LOC)	LOCxGCA	-7.5645651	BLOCK(LOC)	LOCxGCA	23.8871224	BLOCK(LOC)	LOCxGCA	-1.8633613	BLOCK(LOC)	LOCxGCA	-3.4372898	BLOCK(LOC)	LOCxGCA	0	BLOCK(LOC)	LOCxGCA	222.068956	BLOCK(LOC)	LOCxGCA	-0.009681
BLOCK(LOC)	ERROR	-11359.486	BLOCK(LOC)	ERROR	-8355.6758	BLOCK(LOC)	ERROR	-10030.941	BLOCK(LOC)	ERROR	-7784.2206	BLOCK(LOC)	ERROR	-12368.653	BLOCK(LOC)	ERROR	-8945.4849	BLOCK(LOC)	ERROR	-8634.8904	BLOCK(LOC)	ERROR	-7491.4183
GCA	GCA	182758.678	GCA	GCA	238312.917	GCA	GCA	174501.237	GCA	GCA	214219.368	GCA	GCA	67890.5907	GCA	GCA	82307.3398	GCA	GCA	47695.4217	GCA	GCA	68888.309
GCA	SCA	-930.7626	GCA	SCA	-924.44488	GCA	SCA	-464.21733	GCA	SCA	-990.50519	GCA	SCA	-731.17302	GCA	SCA	-26786.112	GCA	SCA	0	GCA	SCA	-647.47078
GCA	LOCxGCA	-101398.66	GCA	LOCxGCA	-208181.69	GCA	LOCxGCA	-97849.072	GCA	LOCxGCA	-132389.68	GCA	LOCxGCA	-32312.337	GCA	LOCxGCA	0	GCA	LOCxGCA	-32982.611	GCA	LOCxGCA	-22837.341
GCA	ERROR	-10.608459	GCA	ERROR	99.8348865	GCA	ERROR	-365.03767	GCA	ERROR	-4.6143504	GCA	ERROR	31.6647006	GCA	ERROR	420.106829	GCA	ERROR	-297.819	GCA	ERROR	-4.7329362
SCA	SCA	118590.052	SCA	SCA	214749.901	SCA	SCA	70422.9359	SCA	SCA	134069.025	SCA	SCA	125054.764	SCA	SCA	172645.796	SCA	SCA	0	SCA	SCA	128030.971
SCA	LOCxGCA	-23584.627	SCA	LOCxGCA	-46343.09	SCA	LOCxGCA	-13940.603	SCA	LOCxGCA	-28359.913	SCA	LOCxGCA	-23512.588	SCA	LOCxGCA	0	SCA	LOCxGCA	0	SCA	LOCxGCA	-26276.11
SCA	ERROR	-67953.121	SCA	ERROR	-42103.392	SCA	ERROR	-46243.651	SCA	ERROR	-32327.33	SCA	ERROR	-73098.548	SCA	ERROR	-44323.243	SCA	ERROR	0	SCA	ERROR	-31243.657
LOCxGCA	LOCxGCA	155132.397	LOCxGCA	LOCxGCA	339681.466	LOCxGCA	LOCxGCA	148917.184	LOCxGCA	LOCxGCA	204967.992	LOCxGCA	LOCxGCA	51362.8062	LOCxGCA	LOCxGCA	0	LOCxGCA	LOCxGCA	50885.1887	LOCxGCA	LOCxGCA	36105.3458
LOCxGCA	ERROR	10.4915717	LOCxGCA	ERROR	323.953709	LOCxGCA	ERROR	-1085.0446	LOCxGCA	ERROR	-8.1391268	LOCxGCA	ERROR	17.5193749	LOCxGCA	ERROR	-9077.5196	LOCxGCA	ERROR	-9077.5196	LOCxGCA	ERROR	-2.9134807
ERROR	ERROR	471530.414	ERROR	ERROR	357513.251	ERROR	ERROR	401651.875	ERROR	ERROR	321055.394	ERROR	ERROR	502549.925	ERROR	ERROR	374831.359	ERROR	ERROR	355051.112	ERROR	ERROR	310298.011
0.47419762	0.13915543	0.37169265	0.14771311	0.22332762	0.47257552	0.43666248	0.12877359	0.35865037	0.40326812	0.15312676	0.39131414	0.72871305	0.21253659	0.46101691	1	0	0	0.39587182	0.25642849	0.50630769	0.97387358	0.16888315	0.41095395

FROT

ONE	(PEE Tuan - F, Tuan)		TWO	(PEE Tuan - F, Beerwah)		THREE	(PEE Beerwah - F, Tuan)		FOUR	(PEE Beerwah - F, Beerwah)		FIVE	(PCH Tuan - F, Tuan)		SIX	(PCH Tuan - F, Beerwah)		SEVEN	(PCH Beerwah - F, Tuan)		EIGHT	(PCH Beerwah - F, Beerwa	
LOCATION	410.775368		LOCATION	3316.68302		LOCATION	1198.75132		LOCATION	0		LOCATION	0		LOCATION	0		LOCATION	2097.81446		LOCATION	99.83986	
BLOCK(LOC)	2698.38314		BLOCK(LOC)	2652.08455		BLOCK(LOC)	1573.71391		BLOCK(LOC)	1657.83694		BLOCK(LOC)	1212.63685		BLOCK(LOC)	1489.04352		BLOCK(LOC)	1335.49037		BLOCK(LOC)	1535.19614	
GCA	473.187982		GCA	622.005582		GCA	179.816019		GCA	303.830049		GCA	775.998626		GCA	716.440693		GCA	251.244443		GCA	376.232781	
SCA	344.278957		SCA	146.877607		SCA	227.980325		SCA	145.341594		SCA	775.95106		SCA	500.082417		SCA	287.130553		SCA	104.000364	
LOCxGCA	2.201728		LOCxGCA	0		LOCxGCA	0		LOCxGCA	0		LOCxGCA	51.54455		LOCxGCA	130.446433		LOCxGCA	0		LOCxGCA	0	
ERROR	10245.4286		ERROR	10482.7741		ERROR	10264.0644		ERROR	10428.0972		ERROR	10369.2192		ERROR	10615.6581		ERROR	10421.3921		ERROR	10570.2975	
LOCATION	LOCATION	1582012.35	LOCATION	LOCATION	27785295.6	LOCATION	LOCATION	4154841.92	LOCATION	LOCATION	0	LOCATION	LOCATION	0	LOCATION	LOCATION	0	LOCATION	LOCATION	10752792.6	LOCATION	LOCATION	164072.772
LOCATION	BLOCK(LOC)	-207166.59	LOCATION	BLOCK(LOC)	-136311.61	LOCATION	BLOCK(LOC)	-54308.425	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	0	LOCATION	BLOCK(LOC)	-41300.054	LOCATION	BLOCK(LOC)	-35724.198
LOCATION	GCA	-315.81639	LOCATION	GCA	-5419.0802	LOCATION	GCA	-1173.2749	LOCATION	GCA	0	LOCATION	GCA	0	LOCATION	GCA	0	LOCATION	GCA	-1601.4071	LOCATION	GCA	-2439.1656
LOCATION	SCA	3205.97399	LOCATION	SCA	-716.46896	LOCATION	SCA	-1003.2182	LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	0	LOCATION	SCA	-1080.5276	LOCATION	SCA	-552.51786
LOCATION	LOCxGCA	-4927.7261	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0	LOCATION	LOCxGCA	0
LOCATION	ERROR	1507.94783	LOCATION	ERROR	890.903663	LOCATION	ERROR	1098.37933	LOCATION	ERROR	0	LOCATION	ERROR	0	LOCATION	ERROR	0	LOCATION	ERROR	1139.80736	LOCATION	ERROR	743.248225
BLOCK(LOC)	BLOCK(LOC)	1450167.28	BLOCK(LOC)	BLOCK(LOC)	1122589.35	BLOCK(LOC)	BLOCK(LOC)	447241.533	BLOCK(LOC)	BLOCK(LOC)	390016.826	BLOCK(LOC)	BLOCK(LOC)	346759.272	BLOCK(LOC)	BLOCK(LOC)	394083.969	BLOCK(LOC)	BLOCK(LOC)	340112.217	BLOCK(LOC)	BLOCK(LOC)	357241.802
BLOCK(LOC)	GCA	-0.5980655	BLOCK(LOC)	GCA	-9.2547082	BLOCK(LOC)	GCA	8.25092209	BLOCK(LOC)	GCA	-738.30402	BLOCK(LOC)	GCA	-690.90109	BLOCK(LOC)	GCA	-453.19269	BLOCK(LOC)	GCA	10.2737542	BLOCK(LOC)	GCA	0.14754696
BLOCK(LOC)	SCA	1499.79985	BLOCK(LOC)	SCA	951.525335	BLOCK(LOC)	SCA	1036.34468	BLOCK(LOC)	SCA	482.626763	BLOCK(LOC)	SCA	2953.38872	BLOCK(LOC)	SCA	1800.86773	BLOCK(LOC)	SCA	1088.8617	BLOCK(LOC)	SCA	742.623827
BLOCK(LOC)	LOCxGCA	-0.58516	BLOCK(LOC)	LOCxGCA	0	BLOCK(LOC)	LOCxGCA	0	BLOCK(LOC)	LOCxGCA	0	BLOCK(LOC)	LOCxGCA	-3196.4957	BLOCK(LOC)	LOCxGCA	-2531.7542	BLOCK(LOC)	LOCxGCA	0	BLOCK(LOC)	LOCxGCA	0
BLOCK(LOC)	ERROR	-10555.843	BLOCK(LOC)	ERROR	-8316.1417	BLOCK(LOC)	ERROR	-8875.7139	BLOCK(LOC)	ERROR	-6935.4583	BLOCK(LOC)	ERROR	-10600.261	BLOCK(LOC)	ERROR	-8435.1293	BLOCK(LOC)	ERROR	-9145.7038	BLOCK(LOC)	ERROR	-7421.2739
GCA	GCA	72665.4288	GCA	GCA	68203.3419	GCA	GCA	16807.6092	GCA	GCA	24168.7178	GCA	GCA	166426.518	GCA	GCA	141701.756	GCA	GCA	24774.8567	GCA	GCA	31365.5405
GCA	SCA	-551.1948	GCA	SCA	-10897.334	GCA	SCA	-9363.0111	GCA	SCA	-7360.2557	GCA	SCA	-1188.2189	GCA	SCA	-1300.1165	GCA	SCA	-10828.544	GCA	SCA	-7228.25
GCA	LOCxGCA	-22896.491	GCA	LOCxGCA	0	GCA	LOCxGCA	0	GCA	LOCxGCA	0	GCA	LOCxGCA	-44839.612	GCA	LOCxGCA	-39599.544	GCA	LOCxGCA	0	GCA	LOCxGCA	0
GCA	ERROR	-13.529696	GCA	ERROR	396.798622	GCA	ERROR	-362.59229	GCA	ERROR	6.84294886	GCA	ERROR	50.162182	GCA	ERROR	547.497539	GCA	ERROR	-442.02289	GCA	ERROR	-7.3063006
SCA	SCA	136880.091	SCA	SCA	67081.6488	SCA	SCA	73062.4497	SCA	SCA	49841.3261	SCA	SCA	212306.154	SCA	SCA	126129.686	SCA	SCA	81249.1063	SCA	SCA	47941.4936
SCA	LOCxGCA	-25920.602	SCA	LOCxGCA	0	SCA	LOCxGCA	0	SCA	LOCxGCA	0	SCA	LOCxGCA	-41537.993	SCA	LOCxGCA	-25588.967	SCA	LOCxGCA	0	SCA	LOCxGCA	0
SCA	ERROR	-62231.728	SCA	ERROR	-40447.905	SCA	ERROR	-41867.157	SCA	ERROR	-29801.239	SCA	ERROR	-65139.861	SCA	ERROR	-42444.269	SCA	ERROR	-43231.193	SCA	ERROR	-30725.167
LOCxGCA	LOCxGCA	35964.0838	LOCxGCA	LOCxGCA	0	LOCxGCA	LOCxGCA	0	LOCxGCA	LOCxGCA	0	LOCxGCA	LOCxGCA	57482.3441	LOCxGCA	LOCxGCA	58550.2686	LOCxGCA	LOCxGCA	0	LOCxGCA	LOCxGCA	0
LOCxGCA	ERROR	6.4440947	LOCxGCA	ERROR	0	LOCxGCA	ERROR	0	LOCxGCA	ERROR	0	LOCxGCA	ERROR	110.284904	LOCxGCA	ERROR	-66.90029	LOCxGCA	ERROR	0	LOCxGCA	ERROR	0
ERROR	ERROR	431804.619	ERROR	ERROR	350304.078	ERROR	ERROR	354888.84	ERROR	ERROR	297091.721	ERROR	ERROR	446873.896	ERROR	ERROR	362306.918	ERROR	ERROR	365952.185	ERROR	ERROR	305253.595
0.99536858	0.15816834	0.39770383	1	0	0	1	0	0	1	0	0	0.93769118	0.09530545	0.30871581	0.84598952	0.07749891	0.27838806	1	0	0	1	0	0

Appendix 15 SAS code for REML analysis of variance in PEE, PCH and F_1, pooled across-site analysis of standardised data, Chapter 5 traits.

PATH: D:\ACRSITE\ACROSS-SITE\ACROSS-SITE CODE 1

```
/*********************************************************************
******** ACROSS-SITE ANALYSIS, STANDARDISED DATA, CH5 TRAITS ********
*********************************************************************/

libname FINAL 'D:\FINAL';

data TOTAL; set FINAL.TOTAL;

T=TAXON;
S=SITE;
R=REP;
F=FEMALE;
M=MALE;
PROT= SQRT(((SPGN+SPGS)/2)**2); * mean bark window spiral angle;
UBVOL= ((BAUB*(HT*1000))/2)/(1000);

/* STANDARDISING DATA TO REMOVE HETEROGENEITY OF VARIANCES BETWEEN SITES */

** Note: all standardised variables are denoted VARNAME_S

if taxon =1 and site =1 then CMBA89_S=(CMBA89/0.05882)*100;
else if taxon =1 and site =2 then CMBA89_S=(CMBA89/0.02367)*100;
else if taxon =2 and site =1 then CMBA89_S=(CMBA89/0.14576)*100;
else if taxon =2 and site =2 then CMBA89_S=(CMBA89/0.09071)*100;
else if taxon =3 and site =1 then CMBA89_S=(CMBA89/0.24508)*100;
else if taxon =3 and site =2 then CMBA89_S=(CMBA89/0.07399)*100;

if taxon =1 and site =1 then CMBA90_S=(CMBA90/0.41437)*100;
else if taxon =1 and site =2 then CMBA90_S=(CMBA90/0.29469)*100;
else if taxon =2 and site =1 then CMBA90_S=(CMBA90/0.80924)*100;
else if taxon =2 and site =2 then CMBA90_S=(CMBA90/0.54321)*100;
else if taxon =3 and site =1 then CMBA90_S=(CMBA90/1.18836)*100;
else if taxon =3 and site =2 then CMBA90_S=(CMBA90/0.67271)*100;

if taxon =1 and site =1 then CMBA91_S=(CMBA91/0.72646)*100;
else if taxon =1 and site =2 then CMBA91_S=(CMBA91/0.76628)*100;
else if taxon =2 and site =1 then CMBA91_S=(CMBA91/1.54427)*100;
else if taxon =2 and site =2 then CMBA91_S=(CMBA91/1.36175)*100;
else if taxon =3 and site =1 then CMBA91_S=(CMBA91/2.32299)*100;
else if taxon =3 and site =2 then CMBA91_S=(CMBA91/2.02029)*100;

/* similar standardisation code for all traits analysed in the statistical models below
.................
.................                                                    */

if taxon =1 and site =1 then PILMN_S=(PILMN/1.39685)*100;
else if taxon =1 and site =2 then PILMN_S=(PILMN/1.34743)*100;
else if taxon =2 and site =1 then PILMN_S=(PILMN/1.77571)*100;
else if taxon =2 and site =2 then PILMN_S=(PILMN/1.63819)*100;
else if taxon =3 and site =1 then PILMN_S=(PILMN/1.68042)*100;
else if taxon =3 and site =2 then PILMN_S=(PILMN/1.55707)*100;
```

```
/*********** OBTAINING TYPE III EMS COEFFICIENTS  ***************
 **************** ACROSS-SITE USING PROC GLM ********************/

PROC SORT; BY T;

PROC GLM;
BY T;
CLASS S R F M;
model

CMBA88_S CMBA89_S CMBA90_S CMBA91_S CMBA92_S CMBA93_S
CMBA94_S CMBA95_S CMBA96_S CMBA97_S CMBA98_S
CUMRD88_S CUMRD89_S CUMRD90_S CUMRD91_S CUMRD92_S CUMRD93_S
CUMRD94_S CUMRD95_S CUMRD96_S CUMRD97_S CUMRD98_S
RD88_S RD89_S RD90_S RD91_S RD92_S RD93_S RD94_S RD95_S RD96_S
RD97_S RD98_S
cumrd1_S cumrd2_S cumrd3_S cumrd4_S cumrd5_S cumrd6_S cumrd7_S
cumrd8_S cumrd9_S cumrd10_S cumrd11_S
rd1_S rd2_S rd3_S rd4_S rd5_S rd6_S rd7_S rd8_S rd9_S rd10_S rd11_S
PILN1_S PILN2_S PILS1_S PILS2_S PILNTH_S PILSTH_S PILMN_S
SG90_S SG91_S SG92_S SG93_S SG94_S SG96_S
SGMEAN_S SGSD_S HT_S DBHOB_S OBVOL_S STR_S DENS_S SLOPE_S DEV_S
JUVDENS_S MATDENS_S LWP_S EWD_S LWD_S DWWI_S

 = S R(S) F F*S F*R(S) M M*S M*R(S) F*M F*M*S;
RANDOM S R(S) F F*S F*R(S) M M*S M*R(S) F*M F*M*S;
RUN;


/****************** ESTIMATING VARIANCE COMPONENTS ******************
 ************** ACROSS-SITE USING PROC VARCOMP ***********************/

PROC VARCOMP METHOD=REML; OPTIONS NODATE PAGESIZE=MAX LINESIZE=MAX;
BY T;
CLASS S R F M;
MODEL

CMBA88_S CMBA89_S CMBA90_S CMBA91_S CMBA92_S CMBA93_S
CMBA94_S CMBA95_S CMBA96_S CMBA97_S CMBA98_S
CUMRD88_S CUMRD89_S CUMRD90_S CUMRD91_S CUMRD92_S CUMRD93_S
CUMRD94_S CUMRD95_S CUMRD96_S CUMRD97_S CUMRD98_S
RD88_S RD89_S RD90_S RD91_S RD92_S RD93_S RD94_S RD95_S RD96_S
RD97_S RD98_S
cumrd1_S cumrd2_S cumrd3_S cumrd4_S cumrd5_S cumrd6_S cumrd7_S
cumrd8_S cumrd9_S cumrd10_S cumrd11_S
rd1_S rd2_S rd3_S rd4_S rd5_S rd6_S rd7_S rd8_S rd9_S rd10_S rd11_S
PILN1_S PILN2_S PILS1_S PILS2_S PILNTH_S PILSTH_S PILMN_S
SG90_S SG91_S SG92_S SG93_S SG94_S SG96_S
SGMEAN_S SGSD_S HT_S DBHOB_S OBVOL_S STR_S DENS_S SLOPE_S DEV_S
JUVDENS_S MATDENS_S LWP_S EWD_S LWD_S DWWI_S

 = S R(S) F F*S F*R(S) M M*S M*R(S) F*M F*M*S;
RUN;
```

Appendix 16 Variance components and genetic parameters estimated from across-site REML analysis of variance, Chapter 5 traits

taxon	trait	Var(S)	Var(R(S))	Var(F)	Var(S*F)	Var(R*F(S)	Var(M)	Var(S*M)	Var(R*M(S)	Var(F*M)	Var(S*F*M	Var(Error)	Var(Var(F))	Var(Var(M))	cov(Var(F),Var(M))	Var(Var(FM))	var(add)	var(dom)	var(phen)	h^2_i	se(h^2_i)	d^2	se(d^2)	H^2_i
1	UBVOL	847.650	92.570	374.885	0.000	0.000	186.282	0.000	0.000	47.194	0.000	1215.100	62582.93	17117.64	36.89	1248.96	1122.334	188.776	1823.461	0.6155	0.2168	0.1035	0.0775	0.7190
2	UBVOL	253.011	83.239	5.610	0.000	15.647	78.181	48.973	0.000	2.283	23.084	509.672	86.91	5221.57	0.96	294.72	167.581	9.133	683.449	0.2452	0.1923	0.0134	0.1005	0.2586
3	UBVOL	11.766	22.057	7.994	5.093	0.000	15.038	0.000	34.908	16.933	0.414	338.172	110.80	141.80	14.27	175.51	46.064	67.730	418.552	0.1101	0.0776	0.1618	0.1266	0.2719
1	GRAV	0.000	113.750	420.510	6.732	0.000	1356.000	76.032	26.525	9.207	0.000	2030.100	79872.25	806073.61	161.56	1526.37	3553.020	36.830	3925.106	0.9052	0.2663	0.0094	0.0398	0.9146
2	GRAV	14815.900	57.232	155.140	13.402	16.340	193.711	60.061	0.000	20.150	0.000	1654.400	13735.40	24462.70	28.35	1175.15	697.702	80.601	2113.204	0.3302	0.1579	0.0381	0.0649	0.3683
3	GRAV	43795.500	81.335	601.289	73.607	13.647	660.614	12.539	73.763	3.541	43.512	2165.400	88980.60	94761.20	-2874.50	3550.60	2523.806	14.163	3647.912	0.6918	0.1572	0.0039	0.0653	0.6957
1	SLOPE	43.098	25.859	82.143	5.273	15.394	92.602	0.000	5.537	0.541	12.968	556.395	3468.40	3988.75	1.79	247.17	349.489	2.164	770.853	0.4534	0.1765	0.0028	0.0816	0.4562
2	SLOPE	0.000	9.906	96.806	0.656	22.823	64.081	11.102	0.000	2.604	11.423	457.782	4372.46	2345.65	1.40	182.44	321.774	10.417	667.277	0.4822	0.1901	0.0156	0.0810	0.4978
3	SLOPE	0.000	3.761	28.837	21.300	0.000	83.379	9.257	9.656	13.376	0.000	470.341	534.95	1839.43	9.68	134.95	224.432	53.505	636.146	0.3528	0.1309	0.0841	0.0730	0.4369
1	DEV	597.783	115.377	384.437	0.000	0.000	189.773	0.000	0.000	11.453	0.000	1063.900	63115.59	16427.26	45.74	476.13	1148.420	45.811	1649.563	0.6962	0.2251	0.0278	0.0529	0.7240
2	DEV	737.214	0.000	174.131	26.988	22.614	68.642	57.506	24.201	0.000	0.000	1385.200	16742.26	5941.19	-4.24	0.00	485.546	0.000	1759.282	0.2760	0.1512	0.0000	0.0000	0.2760
3	DEV	981.692	21.632	179.738	0.000	0.000	179.070	0.000	44.984	16.875	0.000	1001.400	7738.22	7757.43	540.47	498.83	717.618	67.498	1422.068	0.5046	0.1385	0.0475	0.0628	0.5521
1	BAUB89	32098.100	33306.100	20874.200	0.000	0.000	8933.600	0.000	0.000	6985.700	0.000	301626.400	265837218.50	76138755.62	3664336.25	67568618.21	59615.600	27942.800	338419.900	0.1762	0.1020	0.0826	0.0972	0.2587
1	BAUB90	0.000	5039.600	3443.300	0.000	0.000	951.032	158.866	262.373	169.856	0.000	29967.400	5715684.16	811547.88	7053.72	334461.13	8788.664	679.425	34952.827	0.2514	0.1294	0.0194	0.0662	0.2709
1	BAUB91	0.000	2196.600	1907.500	0.000	0.000	676.642	102.617	220.024	0.000	188.861	13407.400	1697990.82	334468.81	-1231.75	0.00	5168.285	0.000	16503.044	0.3132	0.1475	0.0000	0.0000	0.3132
1	BAUB92	59.893	731.392	961.940	0.000	0.000	388.815	35.139	175.900	0.000	111.039	5912.600	425793.51	97494.77	-326.18	0.00	2701.510	0.000	7585.433	0.3561	0.1587	0.0000	0.0000	0.3561
1	BAUB93	93.272	443.414	731.159	0.000	0.000	341.175	10.228	62.498	0.000	94.880	3768.000	241907.86	63681.62	-139.88	0.00	2144.669	0.000	5007.941	0.4283	0.1756	0.0000	0.0000	0.4283
1	BAUB94	895.733	223.335	440.440	0.000	0.000	242.373	0.000	9.417	0.000	67.463	2230.100	87966.24	29507.03	3.84	0.00	1365.626	0.000	2989.793	0.4568	0.1790	0.0000	0.0000	0.4568
1	BAUB95	1372.700	141.972	323.500	0.000	0.000	200.790	0.000	0.000	0.561	44.046	1561.100	47158.53	19492.28	24.59	2004.32	1048.580	2.245	2129.997	0.4923	0.1849	0.0011	0.0841	0.4933
1	BAUB96	1339.700	87.991	244.927	0.000	0.000	164.630	0.000	0.000	9.968	26.357	1152.300	27178.13	13025.29	16.98	1174.64	819.112	39.873	1598.181	0.5125	0.1889	0.0249	0.0858	0.5375
1	BAUB97	937.191	57.923	204.736	0.000	0.000	144.529	0.000	0.000	12.890	24.414	924.965	19103.07	10027.52	13.81	851.88	698.530	51.559	1311.534	0.5326	0.1934	0.0393	0.0890	0.5719
1	BAUB98	934.480	44.236	163.767	0.000	0.000	122.662	0.000	0.000	20.956	11.830	767.202	12439.64	7307.71	11.30	657.88	572.859	83.822	1086.417	0.5273	0.1931	0.0772	0.0944	0.6044
2	BAUB89	3419.500	11856.600	1453.400	0.000	0.000	2454.100	120.078	2593.800	1742.500	0.000	93077.500	3098731.30	6796475.93	91510.89	5074801.79	7815.000	6970.000	101441.378	0.0770	0.0610	0.0687	0.0888	0.1457
2	BAUB90	6762.500	4078.300	0.000	0.000	0.000	670.975	0.000	0.000	593.314	0.000	15819.000	0.00	350204.29	0.00	162749.05	1341.951	2373.257	17083.290	0.0786	0.0669	0.1389	0.0945	0.2175
2	BAUB91	2141.900	2307.700	0.000	0.000	0.000	440.841	54.731	0.000	201.778	114.176	7014.800	0.00	138894.00	0.00	46144.90	881.682	807.112	7826.326	0.1127	0.0906	0.1031	0.1098	0.2158
2	BAUB92	194.031	1094.800	0.000	0.000	0.000	283.835	68.312	0.000	23.592	133.708	3428.700	0.00	56066.02	0.00	10711.51	567.671	94.366	3938.147	0.1441	0.1127	0.0240	0.1051	0.1681
2	BAUB93	0.000	575.820	3.613	0.000	0.000	177.568	105.257	0.000	0.000	103.077	2092.900	492.10	29002.35	-29.32	0.00	362.361	0.000	2482.415	0.1460	0.1302	0.0000	0.0000	0.1460
2	BAUB94	0.000	307.276	7.269	0.000	0.000	106.657	98.399	0.000	0.000	65.585	1239.400	275.76	13528.78	-9.11	0.00	227.852	0.000	1517.310	0.1502	0.1464	0.0000	0.0000	0.1502
2	BAUB95	0.000	162.720	6.656	0.000	0.000	71.595	66.351	0.000	0.000	51.322	841.837	161.19	6195.72	-3.80	0.00	156.502	0.000	1037.761	0.1508	0.1453	0.0000	0.0000	0.1508
2	BAUB96	62.493	108.796	4.733	0.000	6.074	55.960	55.839	0.000	0.000	38.979	646.074	95.65	4009.61	-2.23	0.00	121.386	0.000	807.660	0.1503	0.1505	0.0000	0.0000	0.1503
2	BAUB97	102.421	66.436	5.480	0.000	10.322	52.292	43.362	0.000	2.861	25.809	501.257	83.09	2967.79	3.15	292.17	115.544	11.444	641.384	0.1801	0.1612	0.0178	0.1066	0.1980
2	BAUB98	72.022	48.386	4.378	0.543	9.544	47.033	32.704	0.000	2.731	20.386	419.871	87.46	2130.65	3.63	224.19	102.822	10.926	537.189	0.1914	0.1631	0.0203	0.1115	0.2117
3	BAUB89	18442.800	20189.900	2652.400	3366.300	1492.000	1396.500	685.941	0.000	0.000	850.969	96097.100	10232605.59	3628324.34	122853.63	0.00	8097.800	0.000	106541.210	0.0760	0.0695	0.0000	0.0000	0.0760
3	BAUB90	2089.000	1994.100	324.024	10.760	292.672	329.800	0.000	53.714	0.000	337.121	12477.200	85886.72	63034.92	-435.06	0.00	1307.647	0.000	13825.289	0.0946	0.0542	0.0000	0.0000	0.0946
3	BAUB91	137.057	511.370	75.350	28.846	22.122	205.420	0.000	85.268	12.619	46.314	4807.200	9247.75	16530.93	143.42	16335.18	561.540	50.477	5283.139	0.1063	0.0593	0.0096	0.0968	0.1158
3	BAUB92	0.000	216.130	34.065	19.736	0.000	88.265	0.000	63.568	44.185	0.000	2237.700	2245.77	3681.72	48.82	2475.87	244.661	176.742	2487.520	0.0984	0.0606	0.0711	0.0800	0.1694
3	BAUB93	16.180	134.012	27.304	11.919	0.000	58.216	0.000	49.479	34.800	0.000	1389.300	1077.39	1616.53	28.33	1096.23	171.041	139.200	1571.019	0.1089	0.0646	0.0886	0.0843	0.1975
3	BAUB94	149.883	66.251	14.793	10.798	0.000	28.803	0.000	43.410	29.025	0.000	781.070	425.22	503.72	17.67	454.58	87.192	116.101	907.898	0.0960	0.0666	0.1279	0.0939	0.2239
3	BAUB95	223.944	39.776	9.978	9.838	1.351	19.272	0.000	35.616	23.609	0.000	548.764	238.57	253.47	16.70	256.84	58.501	94.438	648.428	0.0902	0.0691	0.1456	0.0989	0.2359
3	BAUB96	110.125	26.186	8.184	7.437	3.032	13.697	0.000	33.156	16.990	2.894	412.090	151.79	141.99	12.26	226.80	43.763	67.961	497.482	0.0880	0.0702	0.1366	0.1211	0.2246
3	BAUB97	78.129	15.571	7.333	5.107	3.859	9.833	0.000	31.408	14.657	3.818	330.916	107.15	89.97	11.98	166.41	34.331	58.629	406.931	0.0844	0.0716	0.1441	0.1268	0.2284
3	BAUB98	123.937	13.840	7.307	3.649	4.938	10.683	0.000	36.632	11.971	4.893	291.483	88.96	89.84	10.14	137.52	35.979	47.885	371.557	0.0968	0.0741	0.1289	0.1262	0.2257

taxon	trait	Var(S)	Var(R(S))	Var(F)	Var(S*F)	Var(R*F(S)	Var(M)	Var(S*M)	Var(R*M(S)	Var(F*M)	Var(S*F*M	Var(Error)	Var(Var(F))	Var(Var(M))	cov(Var(F) ,Var(M))	Var(Var(FM))	var(add)	var(dom)	var(phen)	h^2_i	se(h^2_i)	d^2	se(d^2)	H^2_i
1	DENS89	9629.200	420.148	17.182	0.791	32.742	296.815	119.451	60.167	9.086	8.009	1250.900	665.14	59122.90	6.26	1601.70	627.994	36.343	1795.143	0.3498	0.2311	0.0202	0.0892	0.3701
1	DENS90	441.247	626.820	59.594	42.604	0.000	974.801	0.000	83.709	0.000	0.000	1627.000	4458.48	397102.21	44.16	0.00	2068.789	0.000	2787.708	0.7421	0.2886	0.0000	0.0000	0.7421
1	DENS91	1647.600	676.888	64.100	49.455	1.305	1036.500	0.000	58.669	0.000	0.000	1647.200	5257.34	446692.43	33.55	0.00	2201.200	0.000	2857.229	0.7704	0.2924	0.0000	0.0000	0.7704
1	DENS92	613.015	499.796	90.334	15.761	0.000	854.134	2.963	9.798	0.000	26.417	1370.500	5523.55	304795.00	19.84	0.00	1888.936	0.000	2369.906	0.7971	0.2857	0.0000	0.0000	0.7971
1	DENS93	767.393	449.392	87.737	19.725	0.000	789.721	21.178	2.382	0.000	29.307	1314.300	5461.80	267207.33	12.79	0.00	1754.917	0.000	2264.351	0.7750	0.2859	0.0000	0.0000	0.7750
1	DENS94	60.842	370.401	112.854	0.000	0.000	725.903	28.862	2.205	0.000	24.904	1238.700	6524.66	228783.40	14.54	0.00	1677.514	0.000	2133.428	0.7863	0.2791	0.0000	0.0000	0.7863
1	DENS95	0.000	354.785	129.438	0.000	0.000	690.525	26.515	0.000	0.000	20.984	1215.000	8264.60	206803.22	19.72	0.00	1639.927	0.000	2082.462	0.7875	0.2728	0.0000	0.0000	0.7875
1	DENS96	0.000	326.555	134.358	1.453	1.240	597.324	38.772	0.370	0.000	16.735	1141.200	8893.78	159329.82	14.54	0.00	1463.364	0.000	1931.452	0.7576	0.2680	0.0000	0.0000	0.7576
1	DENS97	38.225	324.767	131.135	0.000	0.000	560.106	29.355	2.702	0.000	16.735	1101.800	8286.89	138616.40	22.13	0.00	1382.483	0.000	1841.834	0.7506	0.2634	0.0000	0.0000	0.7506
1	DENS98	34.222	333.972	132.696	0.000	0.000	538.378	23.267	11.390	0.000	13.235	1093.100	8457.63	127339.64	34.03	0.00	1342.148	0.000	1812.066	0.7407	0.2594	0.0000	0.0000	0.7407
2	DENS89	19099.600	434.775	31.562	21.829	0.000	129.228	56.469	0.000	28.080	47.424	1352.400	2079.82	13813.81	38.75	2714.81	321.579	112.320	1666.991	0.1929	0.1402	0.0674	0.1250	0.2603
2	DENS90	3436.200	336.896	0.000	50.779	0.000	161.361	55.236	0.000	19.821	0.000	1423.900	0.00	17562.55	0.00	894.67	322.722	79.283	1711.097	0.1886	0.1418	0.0463	0.0699	0.2349
2	DENS91	9616.000	471.454	0.000	52.455	0.000	139.119	74.773	0.000	21.912	0.000	1416.800	0.00	15938.88	0.00	918.49	278.239	87.648	1705.059	0.1632	0.1379	0.0514	0.0711	0.2146
2	DENS92	15115.400	295.475	0.458	31.216	0.000	81.723	116.746	0.000	0.616	0.000	1114.800	671.08	10920.54	15.33	392.73	164.360	2.465	1345.559	0.1222	0.1546	0.0018	0.0589	0.1240
2	DENS93	21920.000	323.858	32.961	12.053	0.000	76.264	149.260	0.000	11.326	0.000	1075.200	1259.93	13435.26	13.39	489.41	218.450	45.302	1357.064	0.1610	0.1711	0.0334	0.0652	0.1944
2	DENS94	13154.600	222.138	75.002	0.000	2.012	87.077	100.437	0.000	1.642	0.000	976.363	2915.36	10010.07	6.39	317.55	324.157	6.569	1242.532	0.2609	0.1661	0.0053	0.0574	0.2662
2	DENS95	6359.900	196.045	79.452	0.000	8.476	95.798	83.152	0.000	0.000	0.000	914.682	3182.79	9533.94	-2.99	0.00	350.499	0.000	1181.560	0.2966	0.1688	0.0000	0.0000	0.2966
2	DENS96	10386.100	198.284	89.462	0.000	14.380	94.890	97.628	0.000	3.785	0.000	903.222	4012.45	10653.84	1.20	292.02	368.705	15.139	1203.367	0.3064	0.1781	0.0126	0.0568	0.3190
2	DENS97	14209.300	209.917	92.305	0.000	15.744	112.872	100.633	0.000	7.711	0.000	922.276	4324.99	13381.32	6.41	343.02	410.354	30.845	1251.541	0.3279	0.1856	0.0246	0.0592	0.3525
2	DENS98	13689.200	217.574	90.650	0.000	18.629	119.174	97.094	0.000	5.907	0.000	918.527	4196.44	13922.07	21.46	335.50	419.650	23.627	1249.981	0.3357	0.1870	0.0189	0.0586	0.3546
3	DENS89	16432.000	465.430	146.288	0.000	0.000	50.418	78.169	20.701	11.279	0.000	1104.900	6081.17	2982.68	-224.03	556.54	393.412	45.117	1411.755	0.2787	0.1177	0.0320	0.0668	0.3106
3	DENS90	7345.300	839.924	235.124	22.902	0.000	119.591	23.348	66.679	0.000	0.000	1456.000	14611.81	5033.63	21.99	0.00	709.429	0.000	1923.644	0.3688	0.1220	0.0000	0.0000	0.3688
3	DENS91	13612.900	1063.900	290.496	63.738	0.000	107.327	0.000	74.990	23.997	0.000	1514.600	25358.82	3908.41	2.27	1094.35	795.646	95.987	2075.348	0.3834	0.1368	0.0463	0.0638	0.4296
3	DENS92	17085.100	736.777	281.064	36.442	0.000	126.318	5.882	83.842	6.381	0.000	1318.000	20489.80	4710.01	-48.26	611.48	814.762	25.523	1857.928	0.4385	0.1365	0.0137	0.0532	0.4523
3	DENS93	21274.800	805.534	282.968	34.083	0.000	143.622	24.152	77.525	19.336	0.000	1296.300	21171.96	6682.08	-523.05	755.87	853.180	77.346	1877.987	0.4543	0.1385	0.0412	0.0586	0.4955
3	DENS94	13906.400	653.139	263.973	12.058	0.000	153.072	22.117	56.808	12.866	0.000	1201.600	16794.64	6830.26	-402.89	583.33	834.091	51.465	1722.494	0.4842	0.1364	0.0299	0.0561	0.5141
3	DENS95	14168.500	579.496	256.204	11.198	0.000	163.853	18.656	47.590	12.937	0.000	1133.200	15681.22	7286.03	-272.30	532.76	840.114	51.750	1643.638	0.5111	0.1391	0.0315	0.0562	0.5426
3	DENS96	10507.200	501.945	213.925	4.434	0.000	160.706	2.242	48.343	13.108	0.000	1053.200	10981.68	6345.78	-219.48	475.80	749.262	52.430	1495.958	0.5009	0.1334	0.0350	0.0583	0.5359
3	DENS97	8831.200	490.647	203.275	6.081	0.000	162.762	0.000	48.840	14.937	0.000	1024.100	10144.45	6431.88	-219.54	476.94	732.074	59.750	1459.995	0.5014	0.1335	0.0409	0.0598	0.5423
3	DENS98	6580.200	463.462	196.096	7.183	0.000	167.940	0.000	33.425	12.840	0.000	1009.000	9562.89	6700.86	-243.50	453.66	728.073	51.359	1426.484	0.5104	0.1344	0.0360	0.0597	0.5464
1	RINGDENS89	9054.300	410.371	12.369	2.215	41.492	287.672	108.406	61.025	15.397	6.494	1247.200	610.69	54738.60	3.63	1677.00	600.081	61.588	1782.270	0.3367	0.2252	0.0346	0.0919	0.3713
1	RINGDENS90	239.360	375.029	56.116	25.162	0.000	698.123	0.000	44.641	9.707	0.000	1262.300	3110.63	204647.56	38.84	648.51	1508.478	38.830	2096.049	0.7197	0.2811	0.0185	0.0486	0.7382
1	RINGDENS91	603.247	284.860	33.208	18.819	22.998	485.667	10.567	0.000	0.000	0.000	1026.500	1419.01	100837.34	0.75	0.00	1037.750	0.000	1597.759	0.6495	0.2731	0.0000	0.0000	0.6495
1	RINGDENS92	1935.300	96.322	50.469	0.000	4.996	222.204	8.469	0.000	0.000	15.692	594.003	1355.30	22037.42	-0.92	0.00	545.346	0.000	895.833	0.6088	0.2405	0.0000	0.0000	0.6088
1	RINGDENS93	18.466	108.336	29.460	12.321	0.000	185.591	30.465	0.000	0.000	14.951	628.644	834.71	17708.41	-0.69	0.00	430.101	0.000	901.431	0.4771	0.2346	0.0000	0.0000	0.4771
1	RINGDENS94	0.000	67.892	42.572	0.000	0.000	226.942	3.039	2.113	0.000	0.000	618.304	955.82	22094.91	2.28	0.00	539.029	0.000	892.970	0.6036	0.2394	0.0000	0.0000	0.6036
1	RINGDENS95	657.659	174.988	66.077	7.269	0.000	199.461	4.987	0.000	2.461	0.000	635.828	2417.46	17528.94	12.05	142.84	531.077	9.843	916.083	0.5797	0.2219	0.0107	0.0522	0.5905
1	RINGDENS96	547.990	81.207	56.122	2.842	3.495	102.986	34.027	0.940	3.319	0.000	508.707	1638.00	6549.70	1.15	98.44	318.216	13.276	712.437	0.4467	0.2031	0.0186	0.0557	0.4653
1	RINGDENS97	0.000	60.212	30.780	0.000	0.882	113.566	0.000	10.873	0.000	21.767	452.312	560.29	5827.58	4.32	0.00	288.692	0.000	630.180	0.4581	0.1979	0.0000	0.0000	0.4581
1	RINGDENS98	12.004	80.892	30.392	0.000	21.822	77.270	0.000	0.000	0.000	0.000	413.807	524.12	2665.08	2.34	0.00	215.325	0.000	543.291	0.3963	0.1684	0.0000	0.0000	0.3963

taxon	trait	Var(S)	Var(R(S))	Var(F)	Var(S*F)	Var(R*F(S)	Var(M)	Var(S*M)	Var(R*M(S)	Var(F*M)	Var(S*F*M	Var(Error)	Var(Var(F))	Var(Var(M))	cov(Var(F) ,Var(M))	Var(Var(FM))	var(add)	var(dom)	var(phen)	h^2_i	se(h^2_i)	d^2	se(d^2)	H^2_i
2	RINGDENS89	13871.500	374.124	28.749	19.785	0.000	118.648	62.392	0.000	26.122	41.963	1278.500	1760.16	12575.01	34.90	2387.92	294.794	104.488	1576.159	0.1870	0.1523	0.0663	0.1240	0.2533
2	RINGDENS90	1008.300	197.179	0.000	29.439	0.000	125.147	35.224	0.000	4.841	0.000	1153.100	0.00	9866.66	0.00	436.15	250.295	19.366	1347.751	0.1857	0.1350	0.0144	0.0620	0.2001
2	RINGDENS91	11530.700	368.044	7.697	40.883	1.298	50.836	71.671	0.000	19.723	0.000	1121.300	1179.74	4868.79	13.12	643.04	117.066	78.893	1313.409	0.0891	0.1159	0.0601	0.0772	0.1492
2	RINGDENS92	2016.100	57.260	28.250	8.600	0.000	14.083	59.355	14.033	0.000	0.000	548.605	630.16	1503.43	3.30	0.00	84.665	0.000	672.926	0.1258	0.1339	0.0000	0.0000	0.1258
2	RINGDENS93	23597.600	203.550	92.732	0.000	41.071	37.947	127.423	0.000	24.707	0.000	715.316	4543.55	7047.10	7.72	383.49	261.359	98.827	1039.195	0.2515	0.1925	0.0951	0.0754	0.3466
2	RINGDENS94	3333.400	64.167	67.874	0.000	19.672	54.482	27.901	0.000	0.000	0.000	542.163	2220.10	2320.46	-1.70	0.00	244.712	0.000	712.091	0.3437	0.1605	0.0000	0.0000	0.3437
2	RINGDENS95	483.916	82.034	47.748	0.000	33.576	72.247	36.149	0.000	0.000	7.098	501.350	1228.36	3921.77	-2.64	0.00	239.990	0.000	698.168	0.3437	0.1753	0.0000	0.0000	0.3437
2	RINGDENS96	14614.500	71.583	75.012	21.632	30.347	45.128	80.009	0.000	22.456	0.000	571.233	3871.68	4372.98	0.88	265.33	240.280	89.825	845.817	0.2841	0.1933	0.1062	0.0770	0.3903
2	RINGDENS97	23450.100	126.775	73.995	1.892	14.660	145.706	76.725	23.851	7.015	29.837	721.382	3047.50	16262.70	10.87	543.30	439.402	28.059	1095.062	0.4013	0.2113	0.0256	0.0851	0.4269
2	RINGDENS98	4642.700	163.798	68.173	3.682	1.462	94.359	46.133	0.000	2.483	18.460	654.501	2528.45	6701.06	17.84	405.26	325.063	9.930	889.252	0.3655	0.1829	0.0112	0.0906	0.3767
3	RINGDENS89	13037.500	450.314	132.236	0.000	0.000	34.535	92.339	20.949	6.062	0.000	1072.100	4965.51	2697.68	-149.05	466.35	333.543	24.248	1358.222	0.2456	0.1157	0.0179	0.0636	0.2634
3	RINGDENS90	6031.200	656.675	179.603	35.768	0.000	131.239	29.543	52.439	0.970	0.000	1261.300	9799.27	5659.56	22.14	508.86	621.683	3.880	1690.862	0.3677	0.1241	0.0023	0.0534	0.3700
3	RINGDENS91	9457.800	650.089	194.464	88.661	0.000	64.015	5.857	42.831	25.518	0.000	1146.000	14558.96	1784.46	-194.31	697.00	516.958	102.071	1567.345	0.3298	0.1391	0.0651	0.0674	0.3950
3	RINGDENS92	2349.400	114.226	96.529	11.920	0.000	66.669	9.637	10.183	3.709	7.312	637.816	2576.13	1360.14	-27.68	301.08	326.397	14.835	843.776	0.3868	0.1232	0.0176	0.0823	0.4044
3	RINGDENS93	7543.900	387.998	116.461	15.470	0.000	115.318	33.983	17.543	23.539	20.423	786.896	4532.39	4949.83	-650.86	689.92	463.559	94.158	1129.633	0.4104	0.1324	0.0834	0.0930	0.4937
3	RINGDENS94	316.315	143.508	94.246	0.000	0.000	70.851	15.191	6.310	0.455	10.551	644.660	2199.33	1584.21	-70.66	271.39	330.193	1.819	842.263	0.3920	0.1188	0.0022	0.0782	0.3942
3	RINGDENS95	3340.200	144.190	96.154	13.371	0.000	88.756	1.298	28.349	1.581	0.000	581.106	2472.84	1873.22	-35.00	111.97	369.819	6.323	810.614	0.4562	0.1279	0.0078	0.0522	0.4640
3	RINGDENS96	1131.000	88.559	38.078	0.000	10.545	50.981	0.000	11.907	1.082	7.039	463.880	449.13	680.62	-24.91	123.23	178.118	4.329	583.512	0.3053	0.0980	0.0074	0.0761	0.3127
3	RINGDENS97	1142.300	148.869	48.516	17.304	0.000	57.942	0.000	16.420	0.559	0.000	494.551	873.68	860.64	-14.63	76.71	212.917	2.235	635.293	0.3351	0.1114	0.0035	0.0551	0.3387
3	RINGDENS98	513.128	171.871	62.734	5.119	10.546	79.079	13.671	0.000	0.000	29.723	541.953	1268.56	1923.81	-98.85	0.00	283.627	0.000	742.825	0.3818	0.1234	0.0000	0.0000	0.3818
1	RINGDENS1	1508.100	424.620	19.318	8.644	40.408	209.194	0.000	24.643	6.986	17.815	976.164	691.62	19973.17	14.86	820.85	457.024	27.943	1303.172	0.3507	0.1843	0.0214	0.0879	0.3721
1	RINGDENS2	5702.100	406.215	57.398	17.819	0.000	295.106	64.382	3.690	0.000	0.000	1037.200	2520.13	46871.17	2.89	0.00	705.008	0.000	1475.595	0.4778	0.2346	0.0000	0.0000	0.4778
1	RINGDENS3	3554.300	298.595	55.109	0.000	0.000	214.932	0.000	4.463	0.000	0.000	787.897	1595.80	19929.37	3.60	0.00	540.082	0.000	1062.401	0.5084	0.2077	0.0000	0.0000	0.5084
1	RINGDENS4	17167.900	102.498	16.862	10.004	0.000	56.011	83.292	0.000	0.000	20.218	470.795	385.96	5378.01	-3.79	0.00	145.747	0.000	657.182	0.2218	0.2161	0.0000	0.0000	0.2218
1	RINGDENS5	5110.700	45.594	20.376	2.628	0.000	121.871	28.977	0.333	0.000	0.000	462.670	309.47	8200.32	-1.20	0.00	284.493	0.000	636.855	0.4467	0.2301	0.0000	0.0000	0.4467
1	RINGDENS6	0.000	143.208	35.216	0.000	14.345	97.465	10.513	14.641	3.907	0.000	529.174	714.81	4883.38	4.14	110.22	265.360	15.628	705.260	0.3763	0.1751	0.0222	0.0595	0.3984
1	RINGDENS7	1470.500	158.242	47.400	35.368	0.000	149.495	6.856	0.042	0.000	0.000	591.139	2266.78	10208.87	2.76	0.00	393.792	0.000	830.300	0.4743	0.2106	0.0000	0.0000	0.4743
1	RINGDENS8	302.179	90.067	48.763	0.000	2.738	115.569	25.509	1.604	0.000	0.356	514.321	1178.67	7290.97	1.09	0.00	328.665	0.000	708.860	0.4637	0.2039	0.0000	0.0000	0.4637
1	RINGDENS9	174.449	43.570	33.144	3.040	0.000	107.815	0.000	8.994	5.897	0.566	428.016	659.29	5178.40	4.96	129.09	281.919	23.590	587.473	0.4799	0.2004	0.0402	0.0774	0.5200
1	RINGDENS10	39.542	59.006	26.687	0.000	26.064	66.325	0.000	0.000	0.248	0.000	393.415	449.69	2022.31	3.96	62.30	186.023	0.991	512.738	0.3628	0.1609	0.0019	0.0616	0.3647
2	RINGDENS1	124.658	308.968	31.652	21.694	0.000	88.351	0.000	17.534	0.000	0.000	968.491	1265.12	3943.11	-6.93	0.00	240.005	0.000	1127.721	0.2128	0.1160	0.0000	0.0000	0.2128
2	RINGDENS2	1520.500	195.570	0.000	24.984	0.000	112.968	45.592	0.000	21.197	0.000	989.786	0.00	9226.72	0.00	508.00	225.935	84.787	1194.527	0.1891	0.1474	0.0710	0.0755	0.2601
2	RINGDENS3	2148.400	206.353	0.000	34.810	0.000	71.440	31.210	0.000	18.101	0.000	845.066	0.00	4049.46	0.00	392.84	142.881	72.402	1000.627	0.1428	0.1194	0.0724	0.0792	0.2151
2	RINGDENS4	2535.500	89.284	8.353	31.682	7.121	5.086	91.568	9.471	15.367	0.000	566.937	646.16	2462.24	1.85	206.98	26.878	61.469	735.586	0.0365	0.1512	0.0836	0.0782	0.1201
2	RINGDENS5	3629.200	73.809	49.118	11.584	4.781	16.150	33.035	0.000	2.085	0.000	537.158	1539.78	782.32	3.46	103.40	130.537	8.339	653.911	0.1996	0.1369	0.0128	0.0622	0.2124
2	RINGDENS6	246.303	54.690	61.064	2.272	0.000	39.891	12.278	0.000	0.000	0.000	457.310	1816.91	1087.56	0.01	0.00	201.909	0.000	572.815	0.3525	0.1579	0.0000	0.0000	0.3525
2	RINGDENS7	0.000	50.120	34.311	5.494	23.405	52.276	25.062	0.000	4.515	0.000	401.017	774.20	2030.46	0.47	70.24	173.173	18.062	546.079	0.3171	0.1676	0.0331	0.0614	0.3502
2	RINGDENS8	4618.200	70.569	63.743	1.342	40.126	61.511	48.510	3.188	0.000	2.419	516.674	2100.67	3665.61	-3.43	0.00	250.508	0.000	737.513	0.3397	0.1776	0.0000	0.0000	0.3397
2	RINGDENS9	8940.600	86.286	49.926	0.959	3.138	84.973	34.379	4.230	0.000	30.331	644.364	1443.39	5198.86	0.15	0.00	269.798	0.000	852.299	0.3166	0.1654	0.0000	0.0000	0.3166
2	RINGDENS10	12167.400	142.093	63.415	4.293	0.000	107.706	55.614	0.000	0.000	21.479	649.622	2253.84	8770.88	-5.23	0.00	342.243	0.000	902.129	0.3794	0.1950	0.0000	0.0000	0.3794

taxon	trait	Var(S)	Var(R(S))	Var(F)	Var(S*F)	Var(R*F(S)	Var(M)	Var(S*M)	Var(R*M(S)	Var(F*M)	Var(S*F*M	Var(Error)	Var(Var(F))	Var(Var(M))	cov(Var(F) ,Var(M))	Var(Var(FM))	var(add)	var(dom)	var(phen)	h^2_i	se(h^2_i)	d^2	se(d^2)	H^2_i
3	RINGDENS1	0.000	260.992	106.024	2.940	0.000	104.874	1.263	31.199	8.770	0.000	843.616	3537.94	2869.93	-112.32	313.52	421.795	35.081	1098.685	0.3839	0.1190	0.0319	0.0645	0.4158
3	RINGDENS2	343.155	522.972	108.799	17.602	0.000	72.070	0.000	47.967	0.000	0.000	1075.400	3797.37	1635.68	-97.02	0.00	361.736	0.000	1321.837	0.2737	0.0968	0.0000	0.0000	0.2737
3	RINGDENS3	5317.900	586.237	143.601	34.850	0.000	66.562	0.000	17.737	14.720	22.482	1078.600	7147.51	1634.59	-146.18	963.16	420.325	58.879	1378.551	0.3049	0.1168	0.0427	0.0901	0.3476
3	RINGDENS4	5177.700	101.067	20.702	27.353	2.817	7.352	13.957	25.862	16.806	2.917	494.510	570.94	249.08	-8.48	272.39	56.108	67.223	612.275	0.0916	0.0908	0.1098	0.1078	0.2014
3	RINGDENS5	900.269	115.308	69.756	7.333	0.000	59.424	0.000	15.638	0.000	12.812	546.100	1457.31	937.33	-64.90	0.00	258.359	0.000	711.062	0.3633	0.1124	0.0000	0.0000	0.3633
3	RINGDENS6	1474.000	235.487	63.368	0.000	11.788	55.901	21.382	15.420	12.809	0.000	625.131	1258.34	1400.57	-196.50	192.10	238.538	51.238	805.799	0.2960	0.1039	0.0636	0.0688	0.3596
3	RINGDENS7	947.129	99.322	46.291	0.000	0.000	37.063	11.089	5.715	3.182	0.000	463.193	604.80	532.86	-20.75	76.90	166.708	12.728	566.533	0.2943	0.1027	0.0225	0.0619	0.3167
3	RINGDENS8	7533.300	112.915	63.996	33.672	4.649	80.936	9.291	40.287	0.000	4.148	535.294	1630.18	1778.71	-39.04	0.00	289.863	0.000	772.272	0.3753	0.1270	0.0000	0.0000	0.3753
3	RINGDENS9	564.593	116.624	37.424	0.000	24.553	52.362	0.000	14.117	16.838	0.000	475.153	551.59	802.70	-6.96	168.67	179.571	67.351	620.446	0.2894	0.1037	0.1086	0.0837	0.3980
3	RINGDENS10	163.972	157.607	52.246	2.700	3.149	70.942	1.905	7.450	0.000	29.844	521.766	913.80	1409.62	-44.87	0.00	246.377	0.000	690.002	0.3571	0.1167	0.0000	0.0000	0.3571
1	PILMN	52330.500	2311.100	1746.400	273.469	762.487	4411.100	389.462	1.577	153.390	0.000	8421.900	1710706.36	8952583.35	-813.47	35046.76	12315.000	613.558	16159.784	0.7621	0.2561	0.0380	0.0463	0.8000
2	PILMN	24113.500	135.797	885.393	0.000	0.000	576.732	101.913	248.834	120.094	0.000	4216.300	359013.51	201254.65	468.69	11235.96	2924.251	480.376	6149.266	0.4755	0.1887	0.0781	0.0690	0.5537
3	PILMN	21913.700	967.772	1413.000	72.523	35.316	1924.900	0.000	268.069	168.608	150.772	5486.700	501901.83	812276.46	-26016.63	32355.47	6675.800	674.432	9519.888	0.7012	0.1586	0.0708	0.0756	0.7721
1	PILNTH	6776.100	1047.900	1122.800	59.830	509.681	2960.000	199.505	76.590	124.122	0.000	6714.900	657186.44	3999688.13	-246.34	22412.83	8165.600	496.488	11767.428	0.6939	0.2438	0.0422	0.0509	0.7361
2	PILNTH	4470.500	93.391	620.766	0.000	0.000	407.305	51.729	279.764	38.677	0.000	3598.100	175802.11	98689.61	259.64	5243.11	2056.143	154.706	4996.341	0.4115	0.1693	0.0310	0.0580	0.4425
3	PILNTH	8926.600	615.925	783.218	38.666	143.411	1270.000	0.000	132.960	102.784	8.418	4494.700	165337.59	349412.14	-8541.31	13668.54	4106.437	411.136	6974.158	0.5888	0.1472	0.0590	0.0671	0.6478
1	PILSTH	14788.000	1759.800	1189.900	168.131	443.426	2862.000	90.457	0.000	37.005	0.000	6735.000	776289.04	3563665.87	-298.63	15744.46	8103.800	148.021	11525.918	0.7031	0.2385	0.0128	0.0435	0.7159
2	PILSTH	20156.600	154.154	728.154	0.000	28.661	467.068	81.549	51.008	104.740	78.146	3858.000	251313.51	133464.05	495.63	15401.38	2390.444	418.961	5397.326	0.4429	0.1826	0.0776	0.0920	0.5205
3	PILSTH	25447.800	774.122	1096.000	76.636	0.000	1330.900	0.000	313.390	87.665	106.343	4668.000	301064.47	398586.33	-16565.67	19041.79	4853.800	350.661	7678.934	0.6321	0.1499	0.0457	0.0719	0.6778
1	PILN1	538.657	714.008	856.835	61.709	295.457	2121.200	0.000	0.000	57.345	0.000	5488.800	382692.20	1909699.28	43.15	12054.77	5956.070	229.381	8881.346	0.6706	0.2295	0.0258	0.0494	0.6965
2	PILN1	1821.200	148.325	449.591	0.000	0.000	270.435	58.704	197.084	26.757	0.000	3057.500	93867.38	49395.25	167.11	3583.81	1440.053	107.026	4060.072	0.3547	0.1560	0.0264	0.0590	0.3810
3	PILN1	1828.700	530.912	651.064	15.661	98.387	909.588	0.000	3.167	141.731	0.000	3804.000	115112.60	186761.09	-4371.08	10638.87	3121.304	566.923	5623.597	0.5550	0.1432	0.1008	0.0734	0.6558
1	PILN2	3135.200	846.911	748.282	14.444	375.452	2186.100	235.470	223.435	115.479	0.000	5895.600	297824.70	2318974.91	-67.73	17781.31	5868.763	461.916	9794.262	0.5992	0.2358	0.0472	0.0545	0.6464
2	PILN2	2267.100	25.186	524.502	0.000	0.000	380.910	5.110	257.364	27.671	0.000	3312.300	126362.38	77351.42	191.19	4169.67	1810.825	110.685	4507.858	0.4017	0.1624	0.0246	0.0573	0.4263
3	PILN2	3256.600	465.694	631.856	0.000	46.102	1095.200	0.000	102.379	46.838	135.953	3957.500	107468.22	266938.47	-8357.23	12963.01	3454.111	187.353	6015.828	0.5742	0.1457	0.0311	0.0757	0.6053
1	PILS1	10962.100	1047.100	805.312	228.078	345.056	1972.700	54.940	13.565	20.400	0.000	5642.400	421384.41	1703286.01	-114.14	10519.04	5556.023	81.600	9082.452	0.6117	0.2277	0.0090	0.0452	0.6207
2	PILS1	12878.100	92.831	592.513	0.000	42.345	329.621	40.413	131.912	63.246	88.736	3350.700	167342.76	68024.47	367.54	10955.73	1844.267	252.985	4639.486	0.3975	0.1707	0.0545	0.0902	0.4520
3	PILS1	13503.300	737.425	812.325	43.190	0.000	971.418	0.000	180.755	116.497	40.496	4022.300	168606.90	218997.78	-9250.38	13742.42	3567.485	465.987	6186.980	0.5766	0.1438	0.0753	0.0758	0.6519
1	PILS2	2919.000	1426.700	837.270	68.400	256.111	2075.700	28.668	0.000	0.000	0.000	5665.300	361471.01	1846995.55	-402.00	0.00	5825.940	0.000	8931.449	0.6523	0.2271	0.0000	0.0000	0.6523
2	PILS2	7751.700	133.514	519.811	0.000	21.186	368.029	52.628	0.000	113.275	11.843	3335.700	131944.36	80982.24	295.59	10843.05	1775.680	453.100	4422.472	0.4015	0.1697	0.1025	0.0942	0.5040
3	PILS2	12110.800	472.671	751.202	70.967	0.000	895.792	82.064	229.659	21.075	97.484	3914.600	149506.52	203069.44	-8706.42	13149.59	3293.988	84.301	6062.843	0.5433	0.1451	0.0139	0.0757	0.5572
3	SG4	35.528	0.872	5.112	1.249	0.000	2.942	2.663	1.466	10.003	0.000	63.966	20.74	16.26	-3.11	15.95	16.107	40.010	87.400	0.1843	0.1196	0.4578	0.1828	0.6421
3	SG5	11.219	4.234	4.105	0.000	0.000	1.343	0.000	7.724	0.000	0.000	82.326	6.15	2.40	0.16	0.00	10.895	0.000	95.497	0.1141	0.0598	0.0000	0.0000	0.1141
3	SG6	11.021	1.096	4.699	0.000	1.896	4.834	0.361	1.658	2.016	0.000	63.790	8.50	9.76	-0.06	3.60	19.067	8.066	79.255	0.2406	0.0977	0.1018	0.0958	0.3423
3	SG7	1.822	4.542	9.192	0.000	0.000	5.946	0.000	5.287	0.000	0.000	75.582	22.16	11.26	0.20	0.00	30.276	0.000	96.007	0.3154	0.1042	0.0000	0.0000	0.3154
3	SG8	15.166	4.159	5.271	0.000	0.545	5.339	0.000	1.848	1.261	3.459	78.446	11.34	12.05	0.37	8.47	21.220	5.043	96.168	0.2207	0.0940	0.0524	0.1211	0.2731
3	SG10	2.605	1.981	1.477	0.277	0.000	3.337	2.730	0.000	4.751	0.000	66.854	4.25	11.21	0.10	7.14	9.629	19.004	79.427	0.1212	0.0963	0.2393	0.1346	0.3605
3	SGMEAN	76.474	11.471	18.799	0.000	0.000	17.410	0.000	0.671	8.870	2.957	137.953	113.10	101.73	0.94	39.08	72.418	35.462	186.660	0.3880	0.1320	0.1901	0.1340	0.5781
3	SGSD	173.709	51.211	10.206	22.142	40.657	54.721	6.450	0.000	9.339	0.000	623.340	437.29	1098.61	-43.97	256.85	129.854	37.354	766.854	0.1693	0.0937	0.0487	0.0836	0.2180
1	PROT	2803.600	1780.700	82.216	269.723	0.000	0.000	24.541	1.747	177.349	0.000	7340.400	56991.18	0.00	0.00	26615.31	164.431	709.396	7895.976	0.0208	0.0602	0.0898	0.0826	0.1107
2	PROT	367.373	544.900	475.236	230.984	0.000	329.331	0.000	295.445	0.000	310.584	5959.300	194976.00	75146.59	62.79	0.00	1609.136	0.000	7600.881	0.2117	0.1249	0.0000	0.0000	0.2117
3	PROT	285.175	1121.800	174.184	0.000	0.000	284.676	27.499	145.346	279.674	0.000	6351.500	24600.44	47601.23	1185.59	32863.96	917.720	1118.696	7262.879	0.1264	0.0721	0.1540	0.0998	0.2804

Appendix 17 A comparison of parental vari ance in individual ring wood density measured based on cambial age and based on tree age

Table 1 Ratio of $4\sigma^2_{GCA}/\sigma^2_P$ for wood density of individual rings in PEE, PCH and F_1 populations, with rings assigned based on both cambial age and tree age

cambial age	tree age	PEE		PCH		F_1	
		cambial age	tree age	cambial age	tree age	cambial age	tree age
1	3	0.35 (0.18)	0.34 (0.23)	0.21 (0.12)	0.19 (0.15)	0.38 (0.12)	0.25 (0.12)
2	4	0.48 (0.23)	0.72 (0.28)	0.19 (0.15)	0.19 (0.14)	0.27 (0.10)	0.37 (0.12)
3	5	0.51 (0.21)	0.65 (0.27)	0.14 (0.12)	0.09 (0.12)	0.30 (0.12)	0.33 (0.14)
4	6	0.22 (0.22)	0.61 (0.24)	0.04 (0.15)	0.13 (0.13)	0.09 (0.09)	0.39 (0.12)
5	7	0.45 (0.23)	0.48 (0.23)	0.20 (0.14)	0.25 (0.19)	0.36 (0.11)	0.41 (0.13)
6	8	0.38 (0.18)	0.60 (0.24)	0.35 (0.16)	0.34 (0.16)	0.30 (0.10)	0.39 (0.12)
7	9	0.47 (0.21)	0.58 (0.22)	0.32 (0.17)	0.34 (0.18)	0.29 (0.10)	0.46 (0.13)
8	10	0.46 (0.20)	0.45 (0.20)	0.34 (0.18)	0.28 (0.19)	0.38 (0.13)	0.31 (0.10)
9	11	0.48 (0.20)	0.46 (0.20)	0.32 (0.17)	0.40 (0.21)	0.29 (0.10)	0.34 (0.11)
10	12	0.36 (0.16)	0.40 (0.17)	0.38 (0.20)	0.37 (0.18)	0.36 (0.12)	0.38 (0.12)
	mean	**0.42**	**0.53**	**0.25**	**0.26**	**0.30**	**0.36**

Note: standard errors of ratios, estimated using a Taylor series expansion, are shown in brackets; $4\sigma^2_{GCA}/\sigma^2_P$, known in pure species populations as the narrow-sense individual tree heritability (h^2_t) is used here only as a familiar measure of the ratio of GCA variance to phenotypic variance, and not as a genetic parameter of application in breeding within the F_1 hybrid population.

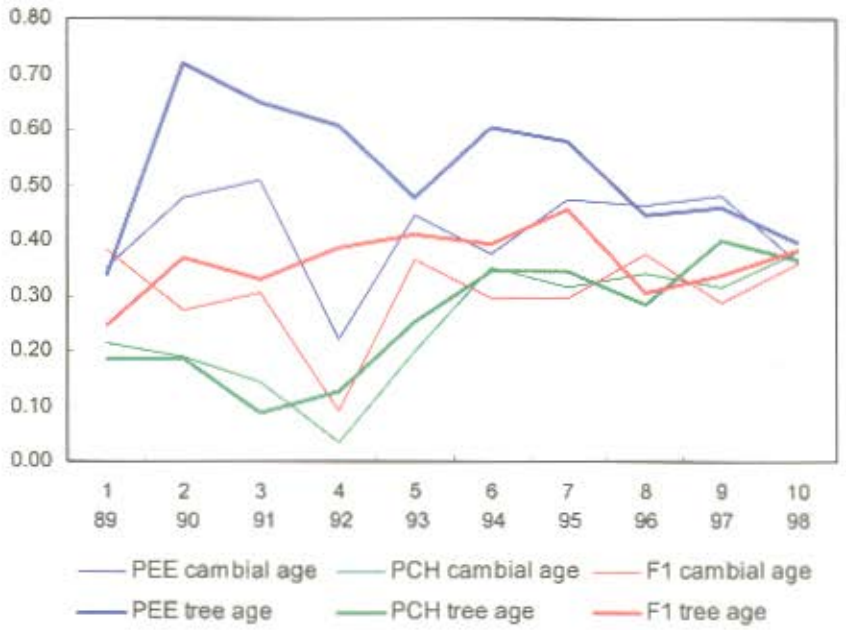


Figure 1 Ratio of $4\sigma^2_{GCA}/\sigma^2_P$ for wood density of individual rings in PEE, PCH and F_1, with rings assigned based on both cambial age and tree age.

THEORETICAL GENETIC MODEL FOR INTERSPECIFIC HYBRIDS

(PART I : single locus)

PEExPCH F_1 HYBRID MODEL

Covariance among full - sibs (F_1 HYBRID)

```
In[1]:= z1 = Expand[1/16 (D - 1/4 (d1 + D + a + d2))^2]
```

$$\text{Out}[1]= \frac{a^2}{256} - \frac{3\,D\,a}{128} + \frac{d_1\,a}{128} + \frac{d_2\,a}{128} + \frac{9\,D^2}{256} + \frac{d_1^2}{256} + \frac{d_2^2}{256} - \frac{3\,D\,d_1}{128} - \frac{3\,D\,d_2}{128} + \frac{d_1\,d_2}{128}$$

$$\frac{a^2}{256} - \frac{3\,D\,a}{128} + \frac{d_1\,a}{128} + \frac{d_2\,a}{128} + \frac{9\,D^2}{256} + \frac{d_1^2}{256} + \frac{d_2^2}{256} - \frac{3\,D\,d_1}{128} - \frac{3\,D\,d_2}{128} + \frac{d_1\,d_2}{128}$$

```
In[2]:= z2 = Expand[1/8 (1/2 (D + d2) - 1/4 (d1 + D + a + d2))^2]
```

$$\text{Out}[2]= \frac{a^2}{128} - \frac{D\,a}{64} + \frac{d_1\,a}{64} - \frac{d_2\,a}{64} + \frac{D^2}{128} + \frac{d_1^2}{128} + \frac{d_2^2}{128} - \frac{D\,d_1}{64} + \frac{D\,d_2}{64} - \frac{d_1\,d_2}{64}$$

$$\frac{a^2}{128} - \frac{D\,a}{64} + \frac{d_1\,a}{64} - \frac{d_2\,a}{64} + \frac{D^2}{128} + \frac{d_1^2}{128} + \frac{d_2^2}{128} - \frac{D\,d_1}{64} + \frac{D\,d_2}{64} - \frac{d_1\,d_2}{64}$$

```
In[3]:= z3 = Expand[1/16 (d2 - 1/4 (d1 + D + a + d2))^2]
```

$$\text{Out}[3]= \frac{a^2}{256} + \frac{D\,a}{128} + \frac{d_1\,a}{128} - \frac{3\,d_2\,a}{128} + \frac{D^2}{256} + \frac{d_1^2}{256} + \frac{9\,d_2^2}{256} + \frac{D\,d_1}{128} - \frac{3\,D\,d_2}{128} - \frac{3\,d_1\,d_2}{128}$$

$$\frac{a^2}{256} + \frac{D\,a}{128} + \frac{d_1\,a}{128} - \frac{3\,d_2\,a}{128} + \frac{D^2}{256} + \frac{d_1^2}{256} + \frac{9\,d_2^2}{256} + \frac{D\,d_1}{128} - \frac{3\,D\,d_2}{128} - \frac{3\,d_1\,d_2}{128}$$

```
In[4]:= z4 = Expand[1/8 ((d1 + D)/2 - 1/4 (d1 + D + a + d2))^2]
```

$$\text{Out}[4]= \frac{a^2}{128} - \frac{D\,a}{64} - \frac{d_1\,a}{64} + \frac{d_2\,a}{64} + \frac{D^2}{128} + \frac{d_1^2}{128} + \frac{d_2^2}{128} + \frac{D\,d_1}{64} - \frac{D\,d_2}{64} - \frac{d_1\,d_2}{64}$$

$$\frac{a^2}{128} - \frac{D\,a}{64} - \frac{d_1\,a}{64} + \frac{d_2\,a}{64} + \frac{D^2}{128} + \frac{d_1^2}{128} + \frac{d_2^2}{128} + \frac{D\,d_1}{64} - \frac{D\,d_2}{64} - \frac{d_1\,d_2}{64}$$


```
In[5]:= z5 = Expand[1/4 (1/4 (d1 + D + a + d2) - 1/4 (d1 + D + a + d2))^2]
```

```
Out[5]= 0

        0
```

```
In[6]:= z6 = Expand[1/8 (1/2 (a + d2) - 1/4 (d1 + D + a + d2))^2]
```

$$\text{Out}[6]= \frac{a^2}{128} - \frac{D\,a}{64} - \frac{d_1\,a}{64} + \frac{d_2\,a}{64} + \frac{D^2}{128} + \frac{d_1^2}{128} + \frac{d_2^2}{128} + \frac{D\,d_1}{64} - \frac{D\,d_2}{64} - \frac{d_1\,d_2}{64}$$

$$\frac{a^2}{128} - \frac{D\,a}{64} - \frac{d_1\,a}{64} + \frac{d_2\,a}{64} + \frac{D^2}{128} + \frac{d_1^2}{128} + \frac{d_2^2}{128} + \frac{D\,d_1}{64} - \frac{D\,d_2}{64} - \frac{d_1\,d_2}{64}$$

```
In[7]:= z7 = Expand[1/16 (d1 - 1/4 (d1 + D + a + d2))^2]
```

$$\text{Out}[7]= \frac{a^2}{256} + \frac{D\,a}{128} - \frac{3\,d_1\,a}{128} + \frac{d_2\,a}{128} + \frac{D^2}{256} + \frac{9\,d_1^2}{256} + \frac{d_2^2}{256} - \frac{3\,D\,d_1}{128} + \frac{D\,d_2}{128} - \frac{3\,d_1\,d_2}{128}$$

$$\frac{a^2}{256} + \frac{D\,a}{128} - \frac{3\,d_1\,a}{128} + \frac{d_1\,a}{128} + \frac{D^2}{256} + \frac{9\,d_1^2}{256} + \frac{d_2^2}{256} - \frac{3\,D\,d_1}{128} + \frac{D\,d_2}{128} - \frac{3\,d_1\,d_2}{128}$$

```
In[8]:= z8 = Expand[1/8 (1/2 (d1 + a) - 1/4 (d1 + D + a + d2))^2]
```

$$\text{Out}[8]= \frac{a^2}{128} - \frac{D\,a}{64} + \frac{d_1\,a}{64} - \frac{d_2\,a}{64} + \frac{D^2}{128} + \frac{d_1^2}{128} + \frac{d_2^2}{128} - \frac{D\,d_1}{64} + \frac{D\,d_2}{64} - \frac{d_1\,d_2}{64}$$

$$\frac{a^2}{128} - \frac{D\,a}{64} + \frac{d_1\,a}{64} - \frac{d_2\,a}{64} + \frac{D^2}{128} + \frac{d_1^2}{128} + \frac{d_2^2}{128} - \frac{D\,d_1}{64} + \frac{D\,d_2}{64} - \frac{d_1\,d_2}{64}$$

```
In[9]:= z9 = Expand[1/16 (a - 1/4 (d1 + D + a + d2))^2]
```

$$\text{Out}[9]= \frac{9\,a^2}{256} - \frac{3\,D\,a}{128} - \frac{3\,d_1\,a}{128} - \frac{3\,d_2\,a}{128} + \frac{D^2}{256} + \frac{d_1^2}{256} + \frac{d_2^2}{256} + \frac{D\,d_1}{128} + \frac{D\,d_2}{128} + \frac{d_1\,d_2}{128}$$

$$\frac{9\,a^2}{256} - \frac{3\,D\,a}{128} - \frac{3\,d_1\,a}{128} - \frac{3\,d_2\,a}{128} + \frac{D^2}{256} + \frac{d_1^2}{256} + \frac{d_2^2}{256} + \frac{D\,d_1}{128} + \frac{D\,d_2}{128} + \frac{d_1\,d_2}{128}$$

$\text{Cov}_{\text{Pee}\,\cdot\,\text{Pch}}$ (FS)

```
In[10]:= z50 = z1 + z2 + z3 + z4 + z5 + z6 + z7 + z8 + z9
```

$$\text{Out}[10]= \frac{5\,a^2}{64} - \frac{3\,D\,a}{32} - \frac{d_1\,a}{32} - \frac{d_2\,a}{32} + \frac{5\,D^2}{64} + \frac{5\,d_1^2}{64} + \frac{5\,d_2^2}{64} - \frac{D\,d_1}{32} - \frac{D\,d_2}{32} - \frac{3\,d_1\,d_2}{32}$$

In[11]:= Together[5 a^2/64 - 3 D a/32 - d1 a/32 - d2 a/32 + 5 D^2/64 + 5 d1^2/64 + 5 d2^2/64 - D d1/32 - D d2/32 - 3 d1 d2/32]

Out[11]= 1/64 (5 a^2 - 6 D a - 2 d1 a - 2 d2 a + 5 D^2 + 5 d1^2 + 5 d2^2 - 2 D d1 - 2 D d2 - 6 d1 d2)

1/64 (5 a^2 - 6 D a - 2 d1 a - 2 d2 a + 5 D^2 + 5 d1^2 + 5 d2^2 - 2 D d1 - 2 D d2 - 6 d1 d2)

Covariance (half - sib) among PEE parents (F_1 HYBRID)

In[12]:= y1 = Expand[1/4 ((d2 + D)/2 - 1/4 (d1 + D + a + d2))^2]

Out[12]= a^2/64 - D a/32 + d1 a/32 - d2 a/32 + D^2/64 + d1^2/64 + d2^2/64 - D d1/32 + D d2/32 - d1 d2/32

In[13]:= y2 = Expand[1/4 (1/2 (a + d1) - 1/4 (d1 + D + a + d2))^2]

Out[13]= a^2/64 - D a/32 + d1 a/32 - d2 a/32 + D^2/64 + d1^2/64 + d2^2/64 - D d1/32 + D d2/32 - d1 d2/32

$Cov_{Pee \times Pch}\ (HS)_{Pee}$

In[14]:= y50 = y1 + y2

Out[14]= a^2/32 - D a/16 + d1 a/16 - d2 a/16 + D^2/32 + d1^2/32 + d2^2/32 - D d1/16 + D d2/16 - d1 d2/16

In[15]:= Together[a^2/32 - D a/16 + d1 a/16 - d2 a/16 + D^2/32 + d1^2/32 + d2^2/32 - D d1/16 + D d2/16 - d1 d2/16]

Out[15]= 1/32 (a^2 - 2 D a + 2 d1 a - 2 d2 a + D^2 + d1^2 + d2^2 - 2 D d1 + 2 D d2 - 2 d1 d2)

1/32 (a^2 - 2 D a + 2 d1 a - 2 d1 a + D^2 + d1^2 + d2^2 - 2 D d1 + 2 D d2 - 2 d1 d2)

Covariance (half - sib) among PCH parents (F_1 HYBRID)

In[16]:= x1 = Expand[1/4 (1/2 (D + d1) - 1/4 (d1 + D + a + d2))^2]

Out[16]= a^2/64 - D a/32 - d1 a/32 + d2 a/32 + D^2/64 + d1^2/64 + d2^2/64 + D d1/32 - D d2/32 - d1 d2/32

In[17]:= x2 = Expand[1/4 (1/2 (d2 + a) - 1/4 (d1 + D + a + d2))^2]

Out[17]= a^2/64 - D a/32 - d1 a/32 + d2 a/32 + D^2/64 + d1^2/64 + d2^2/64 + D d1/32 - D d2/32 - d1 d2/32

$Cov_{Pee \times Pch}\ (HS)_{Pch}$

In[18]:= x50 = x1 + x2

Out[18]= a^2/32 - D a/16 - d1 a/16 + d2 a/16 + D^2/32 + d1^2/32 + d2^2/32 + D d1/16 - D d2/16 - d1 d2/16

In[19]:= Together[a^2/32 - D a/16 - d1 a/16 + d2 a/16 + D^2/32 + d1^2/32 + d2^2/32 + D d1/16 - D d2/16 - d1 d2/16]

Out[19]= 1/32 (a^2 - 2 D a - 2 d1 a + 2 d2 a + D^2 + d1^2 + d2^2 + 2 D d1 - 2 D d2 - 2 d1 d2)

1/32 (a^2 - 2 D a - 2 d1 a + 2 d2 a + D^2 + d1^2 + d2^2 + 2 D d1 - 2 D d2 - 2 d1 d2)

SCA variance (F_1 HYBRID)

$\sigma^2_{SCA\ (Pee \times Pch)}$

In[20]:= w50 = z50 - y50 - x50

Out[20]= a^2/64 + D a/32 - d1 a/32 - d2 a/32 + D^2/64 + d1^2/64 + d2^2/64 - D d1/32 - D d2/32 + d1 d2/32

In[21]:= Together[a^2/64 + D a/32 - d1 a/32 - d2 a/32 + D^2/64 + d1^2/64 + d2^2/64 - D d1/32 - D d2/32 + d1 d2/32]

Out[21]= 1/64 (a^2 + 2 D a - 2 d1 a - 2 d2 a + D^2 + d1^2 + d2^2 - 2 D d1 - 2 D d2 + 2 d1 d2)

1/64 (a^2 + 2 D a - 2 d1 a - 2 d2 a + D^2 + d1^2 + d2^2 - 2 D d1 - 2 D d2 + 2 d1 d2)

PURE PEE MODEL

overall mean

In[22]:= $vv1 = \frac{1}{8}\left(\frac{1}{2}(d+a_1)+\frac{1}{2}(d+a_1)+\frac{1}{2}(d+a_2)+\frac{1}{2}(d+a_2)\right)+\frac{2d+a_1+a_2}{16}+\frac{1}{16}(d+d+a_1+a_2)$

Out[22]= $\frac{1}{4}(2d+a_1+a_2)$

$\frac{1}{4}(2d+a_1+a_2)$

Covariance among full - sibs (PEE)

In[23]:= $v1 = \text{Expand}\left[\frac{1}{16}\left(a_1-\frac{1}{4}(2d+a_1+a_2)\right)^2\right]$

Out[23]= $\frac{d^2}{64}-\frac{3a_1d}{64}+\frac{a_2d}{64}+\frac{9a_1^2}{256}+\frac{a_2^2}{256}-\frac{3a_1a_2}{128}$

In[24]:= $v2 = \text{Expand}\left[\frac{1}{8}\left(\frac{1}{2}(d+a_1)-\frac{1}{4}(2d+a_1+a_2)\right)^2\right]$

Out[24]= $\frac{a_1^2}{128}-\frac{a_2a_1}{64}+\frac{a_2^2}{128}$

In[25]:= $v3 = \text{Expand}\left[\frac{1}{16}\left(d-\frac{1}{4}(2d+a_1+a_2)\right)^2\right]$

Out[25]= $\frac{d^2}{64}-\frac{a_1d}{64}-\frac{a_2d}{64}+\frac{a_1^2}{256}+\frac{a_2^2}{256}+\frac{a_1a_2}{128}$

In[26]:= $v4 = \text{Expand}\left[\frac{1}{8}\left(\frac{1}{2}(d+a_1)-\frac{1}{4}(2d+a_1+a_2)\right)^2\right]$

Out[26]= $\frac{a_1^2}{128}-\frac{a_2a_1}{64}+\frac{a_2^2}{128}$

In[27]:= $v5 = \text{Expand}\left[\frac{1}{4}\left(\frac{1}{4}(2d+a_1+a_2)-\frac{1}{4}(2d+a_1+a_2)\right)^2\right]$

Out[27]= 0

In[28]:= $v6 = \text{Expand}\left[\frac{1}{8}\left(\frac{1}{2}(d+a_2)-\frac{1}{4}(2d+a_1+a_2)\right)^2\right]$

Out[28]= $\frac{a_1^2}{128}-\frac{a_2a_1}{64}+\frac{a_2^2}{128}$

In[29]:= $v7 = \text{Expand}\left[\frac{1}{16}\left(d-\frac{1}{4}(2d+a_1+a_2)\right)^2\right]$

Out[29]= $\frac{d^2}{64}-\frac{a_1d}{64}-\frac{a_2d}{64}+\frac{a_1^2}{256}+\frac{a_2^2}{256}+\frac{a_1a_2}{128}$

In[30]:= $v8 = \text{Expand}\left[\frac{1}{8}\left(\frac{1}{2}(d+a_2)-\frac{1}{4}(2d+a_1+a_2)\right)^2\right]$

Out[30]= $\frac{a_1^2}{128}-\frac{a_2a_1}{64}+\frac{a_2^2}{128}$

In[31]:= $v9 = \text{Expand}\left[\frac{1}{16}\left(a_2-\frac{1}{4}(2d+a_1+a_2)\right)^2\right]$

Out[31]= $\frac{d^2}{64}+\frac{a_1d}{64}-\frac{3a_2d}{64}+\frac{a_1^2}{256}+\frac{9a_2^2}{256}-\frac{3a_1a_2}{128}$

$Cov_{Pee \times Pee}$ (FS)

In[32]:= v50 = v1 + v2 + v3 + v4 + v5 + v6 + v7 + v8 + v9

Out[32]= $\frac{d^2}{16}-\frac{a_1d}{16}-\frac{a_2d}{16}+\frac{5a_1^2}{64}+\frac{5a_2^2}{64}-\frac{3a_1a_2}{32}$

In[33]:= $\text{Together}\left[\frac{d^2}{16}-\frac{a_1d}{16}-\frac{a_2d}{16}+\frac{5a_1^2}{64}+\frac{5a_2^2}{64}-\frac{3a_1a_2}{32}\right]$

Out[33]= $\frac{1}{64}(4d^2-4a_1d-4a_2d+5a_1^2+5a_2^2-6a_1a_2)$

$\frac{1}{64}(4d^2-4a_1d-4a_2d+5a_1^2+5a_2^2-6a_1a_2)$

Covariance (half - sib) among PEE parents (PEE)

In[34]:= $u1 = \text{Expand}\left[\frac{1}{4}\left(\frac{1}{2}(d+a_1)-\frac{1}{4}(2d+a_1+a_2)\right)^2\right]$

Out[34]= $\frac{a_1^2}{64}-\frac{a_2a_1}{32}+\frac{a_2^2}{64}$

In[35]:= $u2 = \text{Expand}\left[\frac{1}{4}\left(\frac{1}{2}(d+a_2)-\frac{1}{4}(2d+a_1+a_2)\right)^2\right]$

Out[35]= $\frac{a_1^2}{64}-\frac{a_2a_1}{32}+\frac{a_2^2}{64}$

$Cov_{Pee \times Pee\ (HS)\ Pee}$

In[36]:= u50 = u1 + u2

Out[36]= $\frac{a_1^2}{32}-\frac{a_2a_1}{16}+\frac{a_2^2}{32}$

In[37]:=
Together[$\frac{a_1^2}{32} - \frac{a_2\,a_1}{16} + \frac{a_2^2}{32}$]

Out[37]= $\frac{1}{32}(a_1^2 - 2\,a_2\,a_1 + a_2^2)$

$\frac{1}{32}(a_1^2 - 2\,a_1\,a_1 + a_2^2)$

SCA variance (PEE)

$\sigma^2_{SCA\ (Pee\times Pee)}$

In[39]:= t50 = v50 - u50 - u50

Out[39]= $\frac{d^2}{16} - \frac{a_1\,d}{16} - \frac{a_2\,d}{16} + \frac{a_1^2}{64} + \frac{a_2^2}{64} + \frac{a_1\,a_2}{32}$

In[40]:= Together[$\frac{d^2}{16} - \frac{a_1\,d}{16} - \frac{a_2\,d}{16} + \frac{a_1^2}{64} + \frac{a_2^2}{64} + \frac{a_1\,a_2}{32}$]

Out[40]= $\frac{1}{64}(4\,d^2 - 4\,a_1\,d - 4\,a_2\,d + a_1^2 + a_2^2 + 2\,a_1\,a_2)$

$\frac{1}{64}(4\,d^2 - 4\,a_1\,d - 4\,a_1\,d + a_1^2 + a_1^2 + 2\,a_1\,a_2)$

PURE PCH MODEL

Overall mean

In[41]:= w2 =
$\frac{1}{8}\left(\frac{1}{2}(a_2' + d') + \frac{1}{2}(a_2' + d') + \frac{1}{2}(d' + a_1') + \frac{1}{2}(d' + a_1')\right) + \frac{a_2' + 2\,d' + a_1'}{16} + \frac{1}{16}(a_2' + d' + d' + a_1')$

Out[41]= $\frac{1}{4}(2\,d' + a_1' + a_2')$

$\frac{1}{4}(2\,d' + a_1' + a_2')$

Covariance among full - sibs (PCH)

In[42]:= s1 = Expand[$\frac{1}{16}\left(a_1' - \frac{1}{4}(a_2' + 2\,d' + a_1')\right)^2$]

Out[42]= $\frac{(d')^2}{64} - \frac{3}{64}a_1'\,d' + \frac{1}{64}a_2'\,d' + \frac{9}{256}(a_1')^2 + \frac{1}{256}(a_2')^2 - \frac{3}{128}a_1'\,a_2'$

In[43]:= s2 = Expand[$\frac{1}{8}\left(\frac{1}{2}(d' + a_1') - \frac{1}{4}(a_2' + 2\,d' + a_1')\right)^2$]

Out[43]= $\frac{1}{128}(a_1')^2 - \frac{1}{64}a_2'\,a_1' + \frac{1}{128}(a_2')^2$

In[44]:= s3 = Expand[$\frac{1}{16}\left(d' - \frac{1}{4}(a_2' + 2\,d' + a_1')\right)^2$]

Out[44]= $\frac{(d')^2}{64} - \frac{1}{64}a_1'\,d' - \frac{1}{64}a_2'\,d' + \frac{1}{256}(a_1')^2 + \frac{1}{256}(a_2')^2 + \frac{1}{128}a_1'\,a_2'$

In[45]:= s4 = Expand[$\frac{1}{8}\left(\frac{1}{2}(d' + a_1') - \frac{1}{4}(a_2' + 2\,d' + a_1')\right)^2$]

Out[45]= $\frac{1}{128}(a_1')^2 - \frac{1}{64}a_2'\,a_1' + \frac{1}{128}(a_2')^2$

In[46]:= s5 = Expand[$\frac{1}{4}\left(\frac{1}{4}(a_2' + 2\,d' + a_1') - \frac{1}{4}(a_2' + 2\,d' + a_1')\right)^2$]

Out[46]= 0

In[47]:= s6 = Expand[$\frac{1}{8}\left(\frac{1}{2}(a_2' + d') - \frac{1}{4}(a_2' + 2\,d' + a_1')\right)^2$]

Out[47]= $\frac{1}{128}(a_1')^2 - \frac{1}{64}a_2'\,a_1' + \frac{1}{128}(a_2')^2$

In[48]:= s7 = Expand[$\frac{1}{16}\left(d' - \frac{1}{4}(a_2' + 2\,d' + a_1')\right)^2$]

Out[48]= $\frac{(d')^2}{64} - \frac{1}{64}a_1'\,d' - \frac{1}{64}a_2'\,d' + \frac{1}{256}(a_1')^2 + \frac{1}{256}(a_2')^2 + \frac{1}{128}a_1'\,a_2'$

In[49]:= s8 = Expand[$\frac{1}{8}\left(\frac{1}{2}(a_2' + d') - \frac{1}{4}(a_2' + 2\,d' + a_1')\right)^2$]

Out[49]= $\frac{1}{128}(a_1')^2 - \frac{1}{64}a_2'\,a_1' + \frac{1}{128}(a_2')^2$

In[50]:= s9 = Expand[$\frac{1}{16}\left(a_2' - \frac{1}{4}(a_2' + 2\,d' + a_1')\right)^2$]

Out[50]= $\frac{(d')^2}{64} + \frac{1}{64}a_1'\,d' - \frac{3}{64}a_2'\,d' + \frac{1}{256}(a_1')^2 + \frac{9}{256}(a_2')^2 - \frac{3}{128}a_1'\,a_2'$

$Cov_{Pch\times Pch}$ (FS)

In[51]:= s50 = s1 + s2 + s3 + s4 + s5 + s6 + s7 + s8 + s9

Out[51]= $\frac{(d')^2}{16} - \frac{1}{16}a_1'\,d' - \frac{1}{16}a_2'\,d' + \frac{5}{64}(a_1')^2 + \frac{5}{64}(a_2')^2 - \frac{3}{32}a_1'\,a_2'$

In[52]:= Together $\left[\frac{(d')^2}{16} - \frac{1}{16} a_1' d' - \frac{1}{16} a_2' d' + \frac{5}{64} (a_1')^2 + \frac{5}{64} (a_2')^2 - \frac{3}{32} a_1' a_2'\right]$

Out[52]= $\frac{1}{64}(4(d')^2 - 4a_1' d' - 4a_2' d' + 5(a_1')^2 + 5(a_2')^2 - 6a_1' a_2')$

$\frac{1}{64}(4(d')^2 - 4a_1' d' - 4a_2' d' + 5(a_1')^2 + 5(a_2')^2 - 6a_1' a_2')$

Covariance (half - sib) among PCH parents (PCH)

In[53]:= r1 = Expand$\left[\frac{1}{4}\left(\frac{1}{2}(d' + a_1') - \frac{1}{4}(a_2' + 2d' + a_1')\right)^2\right]$

Out[53]= $\frac{1}{64}(a_1')^2 - \frac{1}{32}a_2' a_1' + \frac{1}{64}(a_2')^2$

In[54]:= r2 = Expand$\left[\frac{1}{4}\left(\frac{1}{2}(a_2' + d') - \frac{1}{4}(a_2' + 2d' + a_1')\right)^2\right]$

Out[54]= $\frac{1}{64}(a_1')^2 - \frac{1}{32}a_2' a_1' + \frac{1}{64}(a_2')^2$

$\mathrm{Cov}_{\mathrm{Pch}\,\times\,\mathrm{Pch}}\,(\mathrm{HS})_{\mathrm{Pch}}$

In[55]:= r50 = r1 + r2

Out[55]= $\frac{1}{32}(a_1')^2 - \frac{1}{16}a_2' a_1' + \frac{1}{32}(a_2')^2$

In[56]:= Together$\left[\frac{1}{32}(a_1')^2 - \frac{1}{16}a_2' a_1' + \frac{1}{32}(a_2')^2\right]$

Out[56]= $\frac{1}{32}((a_1')^2 - 2a_2' a_1' + (a_2')^2)$

$\frac{1}{32}((a_1')^2 - 2a_2' a_1' + (a_2')^2)$

SCA variance (PCH)

$\sigma^2_{\mathrm{SCA}\,(\mathrm{Pch}\,\times\,\mathrm{Pch})}$

In[57]:= q50 = s50 - r50 - r50

Out[57]= $\frac{(d')^2}{16} - \frac{1}{16}a_1' d' - \frac{1}{16}a_2' d' + \frac{1}{64}(a_1')^2 + \frac{1}{64}(a_2')^2 + \frac{1}{32}a_1' a_2'$

In[58]:= Together $\left[\frac{(d')^2}{16} - \frac{1}{16} a_1' d' - \frac{1}{16} a_2' d' + \frac{1}{64} (a_1')^2 + \frac{1}{64} (a_2')^2 + \frac{1}{32} a_1' a_2'\right]$

Out[58]= $\frac{1}{64}(4(d')^2 - 4a_1' d' - 4a_2' d' + (a_1')^2 + (a_2')^2 + 2a_1' a_2')$

$\frac{1}{64}(4(d')^2 - 4a_1' d' - 4a_2' d' + (a_1')^2 + (a_2')^2 + 2a_1' a_2')$

PURE SPECIES - HYBRID COVARIANCE MODEL

PEE parental (pure cross performance - hybrid cross performance) covariance)

In[59]:= p1 = Expand$\left[\frac{1}{4}\left(\frac{d_2 + D}{2} - \frac{1}{4}(d_1 + D + a + d_2)\right)\left(\frac{1}{2}(d + a_1) - \frac{1}{4}(2d + a_1 + a_2)\right)\right]$

Out[59]= $-\frac{a a_1}{64} + \frac{D a_1}{64} - \frac{d_1 a_1}{64} + \frac{d_2 a_1}{64} + \frac{a a_2}{64} - \frac{D a_2}{64} + \frac{a_2 d_1}{64} - \frac{a_2 d_2}{64}$

In[60]:= p2 = Expand$\left[\frac{1}{4}\left(\frac{1}{2}(a + d_1) - \frac{1}{4}(d_1 + D + a + d_2)\right)\left(\frac{1}{2}(d + a_2) - \frac{1}{4}(2d + a_1 + a_2)\right)\right]$

Out[60]= $-\frac{a a_1}{64} + \frac{D a_1}{64} - \frac{d_1 a_1}{64} + \frac{d_2 a_1}{64} + \frac{a a_2}{64} - \frac{D a_2}{64} + \frac{a_2 d_1}{64} - \frac{a_2 d_2}{64}$

$\mathrm{Cov}\,(\mathrm{PeexPee}, \mathrm{PeexPch})\,(\mathrm{HS})$

In[61]:= p50 = p1 + p2

Out[61]= $-\frac{a a_1}{32} + \frac{D a_1}{32} - \frac{d_1 a_1}{32} + \frac{d_2 a_1}{32} + \frac{a a_2}{32} - \frac{D a_2}{32} + \frac{a_2 d_1}{32} - \frac{a_2 d_2}{32}$

In[62]:= Together$\left[-\frac{a a_1}{32} + \frac{D a_1}{32} - \frac{d_1 a_1}{32} + \frac{d_2 a_1}{32} + \frac{a a_2}{32} - \frac{D a_2}{32} + \frac{a_2 d_1}{32} - \frac{a_2 d_2}{32}\right]$

Out[62]= $\frac{1}{32}(-a a_1 + D a_1 - d_1 a_1 + d_2 a_1 + a a_2 - D a_2 + a_2 d_1 - a_2 d_2)$

$\frac{1}{32}(-a a_1 + D a_1 - d_1 a_1 + d_2 a_1 + a a_1 - D a_1 + a_2 d_1 - a_2 d_2)$

PCH parental (pure cross performance - hybrid cross performance) covariance

```
In[63]:= o1 = Expand[1/4 (1/2 (D + d2) - 1/4 (d1 + D + a + d2)) (1/2 (d' + a1') - 1/4 (a2' + 2 d' + a1'))]
```

$$\text{Out[63]= } -\frac{1}{64} a a_1' + \frac{D a_1'}{64} - \frac{1}{64} d_1 a_1' + \frac{1}{64} d_2 a_1' + \frac{a a_2'}{64} - \frac{D a_2'}{64} + \frac{1}{64} d_1 a_2' - \frac{1}{64} d_2 a_2'$$

```
In[64]:= o2 = Expand[1/4 (1/2 (d1 + a) - 1/4 (d1 + D + a + d2)) (1/2 (a2' + d') - 1/4 (a2' + 2 d' + a1'))]
```

$$\text{Out[64]= } -\frac{1}{64} a a_1' + \frac{D a_1'}{64} - \frac{1}{64} d_1 a_1' + \frac{1}{64} d_2 a_1' + \frac{a a_2'}{64} - \frac{D a_2'}{64} + \frac{1}{64} d_1 a_2' - \frac{1}{64} d_2 a_2'$$

$\text{Cov}_{(\text{Pch}\times\text{Pch},\ \text{Pee}\times\text{Pch})}$ (HS)

```
In[65]:= o50 = o1 + o2
```

$$\text{Out[65]= } -\frac{1}{32} a a_1' + \frac{D a_1'}{32} - \frac{1}{32} d_1 a_1' + \frac{1}{32} d_2 a_1' + \frac{a a_2'}{32} - \frac{D a_2'}{32} + \frac{1}{32} d_1 a_2' - \frac{1}{32} d_2 a_2'$$

```
In[66]:= Together[-1/32 a a1' + D a1'/32 - 1/32 d1 a1' + 1/32 d2 a1' + a a2'/32 - D a2'/32 + 1/32 d1 a2' - 1/32 d2 a2']
```

$$\text{Out[66]= } \frac{1}{32}(-a a_1' + D a_1' - d_1 a_1' + d_2 a_1' + a a_2' - D a_2' + d_1 a_2' - d_2 a_2')$$

$$\frac{1}{32}(-a a_1' + D a_1' - d_1 a_1' + d_2 a_1' + a a_2' - D a_2' + d_1 a_2' - d_2 a_2')$$

TAXA MEANS MODEL

Difference between PEExPCH hybrid population mean and PEE population mean

$\Delta_1 = \mu_{\text{Pee x Pch}} - \mu_{\text{Pee x Pee}}$

```
In[67]:=
e1 = 1/4 (d1 + D + a + d2) - 1/4 (2 d + a1 + a2)
```

$$\text{Out[67]= } \frac{1}{4}(-2d - a_1 - a_2) + \frac{1}{4}(a + D + d_1 + d_2)$$


```
In[68]:=
Together[1/4 (-2 d - a1 - a2) + 1/4 (a + D + d1 + d2)]
```

$$\text{Out[68]= } \frac{1}{4}(a - 2d + D - a_1 - a_2 + d_1 + d_2)$$

$$\frac{1}{4}(a - 2d + D - a_1 - a_1 + d_1 + d_2)$$

Difference between PEExPCH hybrid population mean and PCH population mean

$\Delta_2 = \mu_{\text{Pee x Pch}} - \mu_{\text{Pch x Pch}}$

```
In[69]:=
e2 = 1/4 (d1 + D + a + d2) - 1/4 (a2' + 2 d' + a1')
```

$$\text{Out[69]= } \frac{1}{4}(a + D + d_1 + d_2) + \frac{1}{4}(-2d' - a_1' - a_2')$$

```
In[70]:=
Together[1/4 (a + D + d1 + d2) + 1/4 (-2 d' - a1' - a2')]
```

$$\text{Out[70]= } \frac{1}{4}(a + D + d_1 + d_2 - 2d' - a_1' - a_2')$$

$$\frac{1}{4}(a + D + d_1 + d_2 - 2d' - a_1' - a_2')$$

THEORETICAL GENETIC MODEL FOR INTERSPECIFIC HYBRIDS

(PART II : multiple loci)

SINGLE-LOCUS - MULTIPLE-LOCI TERMINOLOGY SUBSTITUTIONS

$d^2 = H_{dd}$

$(d')^2 = H_{d'd'}$

$D^2 = H_{DD}$

$d\,a_2 = \Pi_{da_2}$

$Dd_1 = \Pi_{Dd_1}$

$Dd_2 = \Pi_{Dd_2}$

$D\,a_2 = \Pi_{Da_2}$

$a_1^2 = H_{a_1a_1}$

$a_1\,a_2 = \Pi_{a_1a_2}$

$a_1\,d = \Pi_{a_1d}$

$a_1\,D = \Pi_{a_1D}$

$d_1^2 = H_{d_1d_1}$

$d_2^2 = H_{d_2d_2}$

$a^2 = H_{aa}$

$Da = \Pi_{Da}$

$d_1\,d_2 = \Pi_{d_1d_2}$

$d_1\,a = \Pi_{d_1a}$

$d_2\,a = \Pi_{d_2a}$

$a_2^2 = H_{a_2a_2}$

$(a_1')^2 = H_{a_1'a_1'}$

$(a_2')^2 = H_{a_2'a_2'}$

$a_1'\,d' = \Pi_{a_1'd'}$

$a_2'\,d' = \Pi_{a_2'd'}$

$a_1'\,a_2' = \Pi_{a_1'a_2'}$

$d_1\,a_1 = \Pi_{d_1a_1}$

$d_2\,a_1 = \Pi_{d_2a_1}$

$d_1\,a_2 = \Pi_{d_1a_2}$

$d_2\,a_2 = \Pi_{d_2a_2}$

$aa_1 = \Pi_{aa_1}$

$aa_2 = \Pi_{aa_2}$

$Da_1' = \Pi_{Da_1'}$

$Da_2' = \Pi_{Da_2'}$

$d_1\,a_1' = \Pi_{d_1a_1'}$

$d_2\,a_1' = \Pi_{d_2a_1'}$

$d_1\,a_2' = \Pi_{d_1a_2'}$

$d_2\,a_2' = \Pi_{d_2a_2'}$

$aa_1' = \Pi_{aa_1'}$

$aa_2' = \Pi_{aa_2'}$

TERMS EXPRESSING SUMMATION OF GENOTYPIC VALUES ACROSS LOCI

$$In[71]:= H_{DD} = \frac{((w^{n-1}+1)\,(1-w^{n-1}))\,D^2}{(w+1)\,(1-w)}$$

$$Out[71]= \frac{D^2(1-w^{n-1})(w^{n-1}+1)}{(1-w)(w+1)}$$

$$In[72]:= H_{d'd'} = \frac{(((v')^{n-1}+1)\,(1-(v')^{n-1}))\,(d')^2}{(v'+1)\,(1-v')}$$

$$Out[72]= \frac{(d')^2(1-(v')^{n-1})((v')^{n-1}+1)}{(1-v')(v'+1)}$$

$$In[73]:= H_{dd} = \frac{((v^{n-1}+1)\,(1-v^{n-1}))\,d^2}{(v+1)\,(1-v)}$$

$$Out[73]= \frac{d^2(1-v^{n-1})(v^{n-1}+1)}{(1-v)(v+1)}$$

In[74]:= $H_{a_1 a_1} = \frac{((u^{n-1}+1)\,(1-u^{n-1}))\,a_1^2}{(u+1)\,(1-u)}$

Out[74]= $\frac{(1-u^{n-1})(u^{n-1}+1)\,a_1^2}{(1-u)(u+1)}$

In[75]:= $\Pi_{a_2} = \frac{(1-(s\,v)^{n-1})\,d\,a_2}{1-s\,v}$

Out[75]= $\frac{d\,(1-(s\,v)^{n-1})\,a_2}{1-s\,v}$

In[76]:= $\Pi_{D a_2} = \frac{(1-(s\,w)^{n-1})\,D\,a_2}{1-s\,w}$

Out[76]= $\frac{D(1-(s\,w)^{n-1})\,a_2}{1-s\,w}$

In[77]:= $\Pi_{a_1 a_2} = \frac{(1-(u\,s)^{n-1})\,a_1\,a_2}{1-u\,s}$

Out[77]= $\frac{(1-(s\,u)^{n-1})\,a_1\,a_2}{1-s\,u}$

In[78]:= $\Pi_{a_1 d} = \frac{(1-(u\,v)^{n-1})\,a_1\,d}{1-u\,v}$

Out[78]= $\frac{d\,(1-(u\,v)^{n-1})\,a_1}{1-u\,v}$

In[79]:= $\Pi_{a_1 D} = \frac{(1-(u\,w)^{n-1})\,a_1\,D}{1-u\,w}$

Out[79]= $\frac{D(1-(u\,w)^{n-1})\,a_1}{1-u\,w}$

In[80]:= $\Pi_{a_1' a_2'} = \frac{(1-(u'\,s')^{n-1})\,a_1'\,a_2'}{1-(u'\,s')}$

Out[80]= $\frac{(1-(s'\,u')^{n-1})\,a_1'\,a_2'}{1-s'\,u'}$

In[81]:= $H_{a_1' a_1'} = \frac{(((u')^{n-1}+1)\,(1-(u')^{n-1}))\,(a_1')^2}{(u'+1)\,(1-u')}$

Out[81]= $\frac{(1-(u')^{n-1})((u')^{n-1}+1)\,(a_1')^2}{(1-u')(u'+1)}$

In[82]:= $\Pi_{a_1' d'} = \frac{(1-(u'\,v')^{n-1})\,a_1'\,d'}{1-u'\,v'}$

Out[82]= $\frac{d'\,(1-(u'\,v')^{n-1})\,a_1'}{1-u'\,v'}$

In[83]:= $\Pi_{a_2' d'} = \frac{(1-(s'\,v')^{n-1})\,a_2'\,d'}{1-(s'\,v')}$

Out[83]= $\frac{d'\,(1-(s'\,v')^{n-1})\,a_2'}{1-s'\,v'}$

In[84]:= $\Pi_{D a_1'} = \frac{(1-(u'\,w)^{n-1})\,a_1'\,D}{1-u'\,w}$

Out[84]= $\frac{D(1-(w\,u')^{n-1})\,a_1'}{1-w\,u'}$

In[85]:= $H_{d_1 d_1} = \frac{((k^{n-1}+1)\,(1-k^{n-1}))\,d_1^2}{(k+1)\,(1-k)}$

Out[85]= $\frac{(1-k^{n-1})(k^{n-1}+1)\,d_1^2}{(1-k)(k+1)}$

In[86]:= $H_{d_2 d_2} = \frac{((l^{n-1}+1)\,(1-l^{n-1}))\,d_2^2}{(l+1)\,(1-l)}$

Out[86]= $\frac{(1-l^{n-1})(l^{n-1}+1)\,d_2^2}{(1-l)(l+1)}$

In[87]:= $H_{aa} = \frac{((m^{n-1}+1)\,(1-m^{n-1}))\,a^2}{(m+1)\,(1-m)}$

Out[87]= $\frac{a^2(1-m^{n-1})(m^{n-1}+1)}{(1-m)(m+1)}$

In[88]:= $\Pi_{D d_1} = \frac{(1-(k\,w)^{n-1})\,d_1\,D}{1-k\,w}$

Out[88]= $\frac{D(1-(k\,w)^{n-1})\,d_1}{1-k\,w}$

In[89]:= $\Pi_{Dd_2} = \frac{(1 - (1\,w)^{n-1})\ d_2\ D}{1 - 1\,w}$

Out[89]= $\frac{D(1-(lw)^{n-1})d_2}{1-lw}$

In[90]:= $\Pi_{Da} = \frac{(1 - (m\,w)^{n-1})\ D\,a}{1 - m\,w}$

Out[90]= $\frac{aD(1-(mw)^{n-1})}{1-mw}$

In[91]:= $\Pi_{d_1 d_2} = \frac{(1 - (k\,l)^{n-1})\ d_1\ d_2}{1 - k\,l}$

Out[91]= $\frac{(1-(kl)^{n-1})d_1 d_2}{1-kl}$

In[92]:= $\Pi_{d_1 a} = \frac{(1 - (k\,m)^{n-1})\ d_1\ a}{1 - k\,m}$

Out[92]= $\frac{a(1-(km)^{n-1})d_1}{1-km}$

In[93]:= $\Pi_{d_2 a} = \frac{(1 - (1\,m)^{n-1})\ d_2\ a}{1 - 1\,m}$

Out[93]= $\frac{a(1-(lm)^{n-1})d_2}{1-lm}$

In[94]:= $\Pi_{a_2', a_2'} = \frac{(((s')^{n-1} + 1)\ (1 - (s')^{n-1}))\ (a_2')^2}{(s' + 1)\ (1 - s')}$

Out[94]= $\frac{(1-(s')^{n-1})((s')^{n-1}+1)(a_2')^2}{(1-s')(s'+1)}$

In[95]:=
$\Pi_{a_2 a_2} = \frac{((s^{n-1} + 1)\ (1 - s^{n-1}))\ a_2^2}{(s + 1)\ (1 - s)}$

Out[95]= $\frac{(1-s^{n-1})(s^{n-1}+1)a_2^2}{(1-s)(s+1)}$

In[96]:= $\Pi_{d_1 a_1} = \frac{(1 - (k\,u)^{n-1})\ d_1\ a_1}{1 - k\,u}$

Out[96]= $\frac{(1-(ku)^{n-1})a_1 d_1}{1-ku}$

In[97]:= $\Pi_{d_2 a_1} = \frac{(1 - (1\,u)^{n-1})\ d_2\ a_1}{1 - 1\,u}$

Out[97]= $\frac{(1-(lu)^{n-1})a_1 d_2}{1-lu}$

In[98]:= $\Pi_{d_1 a_2} = \frac{(1 - (k\,s)^{n-1})\ d_1\ a_2}{1 - k\,s}$

Out[98]= $\frac{(1-(ks)^{n-1})a_2 d_1}{1-ks}$

In[99]:= $\Pi_{d_2 a_2} = \frac{(1 - (1\,s)^{n-1})\ d_2\ a_2}{1 - 1\,s}$

Out[99]= $\frac{(1-(ls)^{n-1})a_2 d_2}{1-ls}$

In[100]:= $\Pi_{a_1 a} = \frac{(1 - (m\,u)^{n-1})\ a\ a_1}{1 - m\,u}$

Out[100]= $\frac{a(1-(mu)^{n-1})a_1}{1-mu}$

In[101]:= $\Pi_{a_2 a} = \frac{(1 - (m\,s)^{n-1})\ a\ a_2}{1 - m\,s}$

Out[101]= $\frac{a(1-(ms)^{n-1})a_2}{1-ms}$

In[102]:= $\Pi_{Da_1'} = \frac{(1 - (w\,u')^{n-1})\ D\,a_1'}{1 - w\,u'}$

Out[102]= $\frac{D(1-(wu')^{n-1})a_1'}{1-wu'}$

$$In[103]:= \Pi_{a_2',D} = \frac{(1-(ws')^{n-1})\,D a_2'}{1-ws'}$$

$$Out[103]= \frac{D(1-(ws')^{n-1})a_2'}{1-ws'}$$

$$In[104]:= \Pi_{d_1 a_1'} = \frac{(1-(ku')^{n-1})\,d_1 a_1'}{1-ku'}$$

$$Out[104]= \frac{d_1(1-(ku')^{n-1})a_1'}{1-ku'}$$

$$In[105]:= \Pi_{d_2 a_1'} = \frac{(1-(lu')^{n-1})\,d_2 a_1'}{1-lu'}$$

$$Out[105]= \frac{d_2(1-(lu')^{n-1})a_1'}{1-lu'}$$

$$In[106]:= \Pi_{d_1 a_2'} = \frac{(1-(ks')^{n-1})\,d_1 a_2'}{1-ks'}$$

$$Out[106]= \frac{d_1(1-(ks')^{n-1})a_2'}{1-ks'}$$

$$In[107]:= \Pi_{d_2 a_2'} = \frac{(1-(ls')^{n-1})\,d_2 a_2'}{1-ls'}$$

$$Out[107]= \frac{d_2(1-(ls')^{n-1})a_2'}{1-ls'}$$

$$In[108]:= \Pi_{aa_1'} = \frac{(1-(mu')^{n-1})\,a a_1'}{1-mu'}$$

$$Out[108]= \frac{a(1-(mu')^{n-1})a_1'}{1-mu'}$$

$$In[109]:= \Pi_{aa_2'} = \frac{(1-(ms')^{n-1})\,a a_2'}{1-ms'}$$

$$Out[109]= \frac{a(1-(ms')^{n-1})a_2'}{1-ms'}$$

$$In[110]:= H_D = \frac{(1-w^{n-1})\,D}{1-w}$$

$$Out[110]= \frac{D(1-w^{n-1})}{1-w}$$

$$In[111]:= H_d = \frac{(1-v^{n-1})\,d}{1-v}$$

$$Out[111]= \frac{d(1-v^{n-1})}{1-v}$$

$$In[112]:= H_{d'} = \frac{(1-v'^{n-1})\,d'}{1-v'}$$

$$Out[112]= \frac{d'(1-(v')^{n-1})}{1-v'}$$

$$In[113]:= H_{a_1} = \frac{(1-u^{n-1})\,a_1}{1-u}$$

$$Out[113]= \frac{(1-u^{n-1})a_1}{1-u}$$

$$In[114]:= H_{a_1'} = \frac{(1-u'^{n-1})\,a_1'}{1-u'}$$

$$Out[114]= \frac{(1-(u')^{n-1})a_1'}{1-u'}$$

$$In[115]:= H_{a_2} = \frac{(1-s^{n-1})\,a_2}{1-s}$$

$$Out[115]= \frac{(1-s^{n-1})a_2}{1-s}$$

$$In[116]:= H_{a_2'} = \frac{(1-s'^{n-1})\,a_2'}{1-s'}$$

$$Out[116]= \frac{(1-(s')^{n-1})a_2'}{1-s'}$$

$$In[117]:= H_{d_1} = \frac{(1-k^{n-1})\,d_1}{1-k}$$

$$Out[117]= \frac{(1-k^{n-1})d_1}{1-k}$$

In[118]:= $H_{d_2} = \frac{(1 - l^{n-1})\, d_2}{1 - l}$

Out[118]= $\frac{(1 - l^{n-1})\, d_2}{1 - l}$

In[119]:= $H_a = \frac{(1 - m^{n-1})\, a}{1 - m}$

Out[119]= $\frac{a(1 - m^{n-1})}{1 - m}$

EQUATIONS: FOR SINGLE-LOCUS AND FOR MULTIPLE-LOCI

1. $\mathrm{Cov}_{\mathrm{Pee} \times \mathrm{Pch}}\ (\mathrm{HS})_{\mathrm{Pee}}$

$$g1 = \frac{1}{32}\left(a^2 - 2Da + 2d_1 a - 2d_2 a + D^2 + d_1^2 + d_2^2 - 2Dd_1 + 2Dd_2 - 2d_1 d_2\right)$$

In[120]:= $g1a = \frac{1}{32}\left(H_{aa} - 2\Pi_{Da} + 2\Pi_{d_1 a} - 2\Pi_{d_2 a} + H_{DD} + H_{d_1 d_1} + H_{d_2 d_2} - 2\Pi_{Dd_1} + 2\Pi_{Dd_2} - 2\Pi_{d_1 d_2}\right)$

Out[120]= $\frac{1}{32}\left(\frac{(1 - m^{n-1})(m^{n-1} + 1)a^2}{(1 - m)(m + 1)} - \frac{2D(1 - (mw)^{n-1})a}{1 - mw} + \frac{2(1 - (km)^{n-1})d_1 a}{1 - km} - \frac{2(1 - (lm)^{n-1})d_2 a}{1 - lm} + \frac{(1 - k^{n-1})(k^{n-1} + 1)d_1^2}{(1 - k)(k + 1)} + \frac{(1 - l^{n-1})(l^{n-1} + 1)d_2^2}{(1 - l)(l + 1)} + \frac{D^2(1 - w^{n-1})(w^{n-1} + 1)}{(1 - w)(w + 1)} - \frac{2D(1 - (kw)^{n-1})d_1}{1 - kw} + \frac{2D(1 - (lw)^{n-1})d_2}{1 - lw} - \frac{2(1 - (kl)^{n-1})d_1 d_2}{1 - kl}\right)$

2. $\mathrm{Cov}_{\mathrm{Pee} \times \mathrm{Pch}}\ (\mathrm{HS})_{\mathrm{Pch}}$

$$g2 = \frac{1}{32}\left(a^2 - 2Da - 2d_1 a + 2d_2 a + D^2 + d_1^2 + d_2^2 + 2Dd_1 - 2Dd_2 - 2d_1 d_2\right)$$

In[121]:= $g2a = \frac{1}{32}\left(H_{aa} - 2\Pi_{Da} - 2\Pi_{d_1 a} + 2\Pi_{d_2 a} + H_{DD} + H_{d_1 d_1} + H_{d_2 d_2} + 2\Pi_{Dd_1} - 2\Pi_{Dd_2} - 2\Pi_{d_1 d_2}\right)$

Out[121]= $\frac{1}{32}\left(\frac{(1 - m^{n-1})(m^{n-1} + 1)a^2}{(1 - m)(m + 1)} - \frac{2D(1 - (mw)^{n-1})a}{1 - mw} - \frac{2(1 - (km)^{n-1})d_1 a}{1 - km} + \frac{2(1 - (lm)^{n-1})d_2 a}{1 - lm} + \frac{(1 - k^{n-1})(k^{n-1} + 1)d_1^2}{(1 - k)(k + 1)} + \frac{(1 - l^{n-1})(l^{n-1} + 1)d_2^2}{(1 - l)(l + 1)} + \frac{D^2(1 - w^{n-1})(w^{n-1} + 1)}{(1 - w)(w + 1)} + \frac{2D(1 - (kw)^{n-1})d_1}{1 - kw} - \frac{2D(1 - (lw)^{n-1})d_2}{1 - lw} - \frac{2(1 - (kl)^{n-1})d_1 d_2}{1 - kl}\right)$

3. $\sigma^2_{\mathrm{SCA}\ (\mathrm{Pee} \times \mathrm{Pch})}$

$$g3 = \frac{1}{64}\left(a^2 + 2Da - 2d_1 a - 2d_2 a + D^2 + d_1^2 + d_2^2 - 2Dd_1 - 2Dd_2 + 2d_1 d_2\right)$$

In[122]:= $g3a = \frac{1}{64}\left(H_{aa} + 2\Pi_{Da} - 2\Pi_{d_1 a} - 2\Pi_{d_2 a} + H_{DD} + H_{d_1 d_1} + H_{d_2 d_2} - 2\Pi_{Dd_1} - 2\Pi_{Dd_2} + 2\Pi_{d_1 d_2}\right)$

Out[122]= $\frac{1}{64}\left(\frac{(1 - m^{n-1})(m^{n-1} + 1)a^2}{(1 - m)(m + 1)} + \frac{2D(1 - (mw)^{n-1})a}{1 - mw} - \frac{2(1 - (km)^{n-1})d_1 a}{1 - km} - \frac{2(1 - (lm)^{n-1})d_2 a}{1 - lm} + \frac{(1 - k^{n-1})(k^{n-1} + 1)d_1^2}{(1 - k)(k + 1)} + \frac{(1 - l^{n-1})(l^{n-1} + 1)d_2^2}{(1 - l)(l + 1)} + \frac{D^2(1 - w^{n-1})(w^{n-1} + 1)}{(1 - w)(w + 1)} - \frac{2D(1 - (kw)^{n-1})d_1}{1 - kw} - \frac{2D(1 - (lw)^{n-1})d_2}{1 - lw} + \frac{2(1 - (kl)^{n-1})d_1 d_2}{1 - kl}\right)$

4. $\mathrm{Cov}_{\mathrm{Pee} \times \mathrm{Pee}}\ (\mathrm{HS})_{\mathrm{Pee}}$

$$g4 = \frac{1}{32}\left(a_1^2 - 2a_2 a_1 + a_2^2\right)$$

In[123]:= $g4a = \frac{1}{32}\left(H_{a_1 a_1} - 2\Pi_{a_1 a_2} + H_{a_2 a_2}\right)$

Out[123]= $\frac{1}{32}\left(\frac{(1 - u^{n-1})(u^{n-1} + 1)a_1^2}{(1 - u)(u + 1)} - \frac{2(1 - (su)^{n-1})a_2 a_1}{1 - su} + \frac{(1 - s^{n-1})(s^{n-1} + 1)a_2^2}{(1 - s)(s + 1)}\right)$

5. $\sigma^2_{\mathrm{SCA}\ (\mathrm{Pee} \times \mathrm{Pee})}$

$$g5 = \frac{1}{64}\left(4d^2 - 4a_1 d - 4a_2 d + a_1^2 + a_2^2 + 2a_1 a_2\right)$$

In[124]:= $g5a = \frac{1}{64}\left(4H_{dd} - 4\Pi_{a_1 d} + H_{a_1 a_1} - 4\Pi_{da_2} + 2\Pi_{a_1 a_2} + H_{a_2 a_2}\right)$

Out[124]= $\frac{1}{64}\left(\frac{4(1 - v^{n-1})(v^{n-1} + 1)d^2}{(1 - v)(v + 1)} - \frac{4(1 - (uv)^{n-1})a_1 d}{1 - uv} - \frac{4(1 - (sv)^{n-1})a_2 d}{1 - sv} + \frac{(1 - u^{n-1})(u^{n-1} + 1)a_1^2}{(1 - u)(u + 1)} + \frac{(1 - s^{n-1})(s^{n-1} + 1)a_2^2}{(1 - s)(s + 1)} + \frac{2(1 - (su)^{n-1})a_1 a_2}{1 - su}\right)$

6. $\mathrm{Cov}_{\mathrm{Pch} \times \mathrm{Pch}}\ (\mathrm{HS})_{\mathrm{Pch}}$

$$g6 = \frac{1}{32}\left((a_1')^2 - 2a_2' a_1' + (a_2')^2\right)$$

In[125]:= $g6a = \frac{1}{32}\left(H_{a_1' a_1'} - 2\Pi_{a_1' a_2'} + H_{a_2' a_2'}\right)$

Out[125]= $\frac{1}{32}\left(\frac{\mathrm{Null}(1 - (u')^{n-1})((u')^{n-1} + 1)(a_1')^2}{(1 - u')(u' + 1)} - \frac{2(1 - (s'u')^{n-1})a_2' a_1'}{1 - s'u'} + \frac{(1 - (s')^{n-1})((s')^{n-1} + 1)(a_2')^2}{(1 - s')(s' + 1)}\right)$

7. $\sigma^2_{SCA\ (Pch \times Pch)}$

$$g7 = \frac{1}{64}\left(4\,(d')^2 - 4\,a'_1\,d' - 4\,a'_2\,d' + (a'_1)^2 + (a'_2)^2 + 2\,a'_1\,a'_2\right)$$

In[126]:=
```
g7a = 1/64 (4 H_d',d' - 4 Π_a1',d' - 4 Π_a2',d' + H_a1',a1' + H_a2',a2' + 2 Π_a1',a2')
```

Out[126]=
$$\frac{1}{64}\left(\frac{4\,(1-(\nu')^{n-1})\,((\nu')^{n-1}+1)\,(d')^2}{(1-\nu')\,(\nu'+1)} - \frac{4\,(1-(u'\nu')^{n-1})\,a'_1\,d'}{1-u'\nu'} - \frac{4\,(1-(s'\nu')^{n-1})\,a'_2\,d'}{1-s'\nu'} + \frac{(1-(u')^{n-1})\,((u')^{n-1}+1)\,(a'_1)^2}{(1-u')\,(u'+1)} + \frac{(1-(s')^{n-1})\,((s')^{n-1}+1)\,(a'_2)^2}{(1-s')\,(s'+1)} + \frac{2\,(1-(s'u')^{n-1})\,a'_1\,a'_2}{1-s'u'}\right)$$

8. $Cov_{(Pea \times Pea,\ Pea \times Pch)}$ (HS)

$$g8 = \frac{1}{32}\left(-a\,a_1 + D\,a_1 - d_1\,a_1 + d_2\,a_1 + a\,a_2 - D\,a_2 + a_2\,d_1 - a_2\,d_2\right)$$

In[127]:=
```
g8a = 1/32 (-Π_a1,a + Π_a1,D - Π_d1,a1 + Π_d2,a1 + Π_a2,a - Π_Da2 + Π_a2,d1 - Π_a2,d2)
```

Out[127]=
$$\frac{1}{32}\left(-\frac{a\,(1-(m\,u)^{n-1})\,a_1}{1-m\,u} + \frac{D\,(1-(u\,w)^{n-1})\,a_1}{1-u\,w} - \frac{(1-(k\,u)^{n-1})\,d_1\,a_1}{1-k\,u} + \frac{(1-(l\,u)^{n-1})\,d_2\,a_1}{1-l\,u} + \frac{a\,(1-(m\,s)^{n-1})\,a_2}{1-m\,s} - \frac{D\,(1-(s\,w)^{n-1})\,a_2}{1-s\,w} + \frac{(1-(k\,s)^{n-1})\,a_2\,d_1}{1-k\,s} - \frac{(1-(l\,s)^{n-1})\,a_2\,d_2}{1-l\,s}\right)$$

9. $Cov_{(Pch \times Pch,\ Pea \times Pch)}$ (HS)

$$g9 = \frac{1}{32}\left(-a\,a'_1 + D\,a'_1 - d_1\,a'_1 + d_2\,a'_1 + a\,a'_2 - D\,a'_2 + d_1\,a'_2 - d_2\,a'_2\right)$$

In[128]:=
```
g9a = 1/32 (-Π_aa2',1 + Π_Da2',1 - Π_d1,a1' + Π_d2,a1' + Π_aa2',2 - Π_a2',D + Π_d1,a2' - Π_d2,a2')
```

Out[128]=
$$\frac{1}{32}\left(-\frac{d_1\,(1-(k\,u')^{n-1})\,a'_1}{1-k\,u'} + \frac{d_2\,(1-(l\,u')^{n-1})\,a'_1}{1-l\,u'} - \frac{a\,(1-(m\,u')^{n-1})\,a'_1}{1-m\,u'} + \frac{D\,(1-(w\,u')^{n-1})\,a'_1}{1-w\,u'} + \frac{d_1\,(1-(k\,s')^{n-1})\,a'_2}{1-k\,s'} - \frac{d_2\,(1-(l\,s')^{n-1})\,a'_2}{1-l\,s'} + \frac{a\,(1-(m\,s')^{n-1})\,a'_2}{1-m\,s'} - \frac{D\,(1-(w\,s')^{n-1})\,a'_2}{1-w\,s'}\right)$$

10. $\mu_{Pea \times Pch} - \mu_{Pea \times Pea}$ $(= \Delta_1)$

$$g14 = \frac{1}{4}\left(a - 2\,d + D - a_1 - a_2 + d_1 + d_2\right)$$

In[129]:=
```
g14a = (1 / 4) * (H_D - 2 H_d + H_a - H_a1 - H_a2 + H_d1 + H_d2)
```

Out[129]=
$$\frac{1}{4}\left(\frac{a\,(1-m^{n-1})}{1-m} - \frac{2\,d\,(1-\nu^{n-1})}{1-\nu} + \frac{D\,(1-w^{n-1})}{1-w} - \frac{(1-u^{n-1})\,a_1}{1-u} - \frac{(1-s^{n-1})\,a_2}{1-s} + \frac{(1-k^{n-1})\,d_1}{1-k} + \frac{(1-l^{n-1})\,d_2}{1-l}\right)$$

11. $\mu_{Pea \times Pch} - \mu_{Pch \times Pch}$ $(= \Delta_2)$

$$g15 = \frac{1}{4}\left(a + D + d_1 + d_2 - 2\,d' - a'_1 - a'_2\right)$$

In[130]:=
```
g15a = (1 / 4) * (H_D + H_a + H_d1 + H_d2 - 2 H_d',1 - H_a2',1)
```

Out[130]=
$$\frac{1}{4}\left(\frac{a\,(1-m^{n-1})}{1-m} + \frac{D\,(1-w^{n-1})}{1-w} + \frac{(1-k^{n-1})\,d_1}{1-k} + \frac{(1-l^{n-1})\,d_2}{1-l} - \frac{2\,d'\,(1-(\nu')^{n-1})}{1-\nu'} - \frac{(1-(u')^{n-1})\,a'_1}{1-u'} - \frac{(1-(s')^{n-1})\,a'_2}{1-s'}\right)$$

GLOBALOPTIMIZATION 4.3 :: AN ADD - ON FOR MATHEMATICA

ITERATIVE SEARCH FOR SOLUTIONS FOR n = 3... 12

SCENARIO 1 (LI AND WU 1996 MODEL)

TRAIT : ubvol

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GlobalSearch[fa3, , , range, .00001, Starts → 20]

{{{h → 6.97209, ae → 3.41526, d → 5.98297, ap → 7.82753, dp → 7.39692, ar → 5.9992,
   w → 1.34449, vp → 0.598329, u → 0.349647, v → 0.666472, up → 0.421203}, 5.47156},
 {{h → 7.91932, ae → -0.107125, d → 4.35749, ap → 6.70121, dp → 6.65594, ar → 5.62509,
   w → 1.09359, vp → 0.596177, u → -6.64304, v → 0.617839, up → 0.437991}, 4.96718},
 {{h → 7.98948, ae → 0.0444546, d → 2.72865, ap → 5.28756, dp → 3.73143, ar → 4.61773,
   w → 0.80069, vp → 0.898387, u → 0.422963, v → 0.576023, up → 0.55725}, 4.69188},
 {{h → 10.9266, ae → 2.9525, d → 5.34086, ap → 6.38527, dp → 6.4429, ar → 6.02553,
   w → 0.788693, vp → 0.860761, u → 0.613645, v → 0.624671, up → 1.01455}, 5.53947},
 {{h → 9.07934, ae → 4.46086, d → 7.0294, ap → 8.98264, dp → 7.86451, ar → 5.82338,
   w → 0.927094, vp → 0.476627, u → 0.127301, v → 0.369753, up → 0.351839}, 4.92163},
 {{h → 11.3048, ae → 3.16405, d → 5.95859, ap → 6.3686, dp → 7.53299, ar → 6.07057,
   w → 0.804712, vp → 0.722511, u → 0.377824, v → 0.515421, up → 1.05488}, 6.00629},
 {{h → 8.92818, ae → 4.38054, d → 6.35114, ap → 8.96532, dp → 7.52112, ar → 5.96185,
   w → 1.09124, vp → 0.639311, u → 0.211699, v → 0.499799, up → 0.394072}, 5.04756},
 {{h → 11.8447, ae → 2.56183, d → 6.5045, ap → 8.96836, dp → 8.65017, ar → 6.09444,
   w → 0.75378, vp → 0.602146, u → 0.416064, v → 0.407528, up → 0.416113}, 6.08375},
 {{h → 7.64897, ae → 6.44836, d → 6.38561, ap → 8.03833, dp → 7.36719, ar → 4.74918,
   w → 0.885481, vp → 0.307287, u → -0.218798, v → 0.122731, up → 0.0687574}, 4.66658},
 {{h → 7.47096, ae → 6.37725, d → 6.3819, ap → 8.9697, dp → 6.786, ar → 3.28997,
   w → 0.88878, vp → 0.141653, u → -0.512763, v → 0.00741272, up → 0.0534226}, 4.7713},
 {{h → 9.68164, ae → 4.15645, d → 7.11433, ap → 9.20066, dp → 8.80137, ar → 6.15617,
   w → 1.03046, vp → 0.566721, u → 0.365771, v → 0.503747, up → 0.43444}, 5.50305},
 {{h → 12.2305, ae → 2.6015, d → 4.77944, ap → 6.62949, dp → 7.15822, ar → 5.95307,
   w → 0.637699, vp → 0.80681, u → 0.715465, v → 0.788933, up → 0.851899}, 5.99927},
 {{h → 11.3172, ae → 2.14659, d → 4.84401, ap → 7.79771, dp → 7.11764, ar → 6.08504,
   w → 0.783694, vp → 0.827045, u → 0.751145, v → 0.749201, up → 0.575592}, 5.52079},
 {{h → 6.64999, ae → 2.55197, d → 4.85254, ap → 4.31487, dp → 5.72598, ar → 5.65203,
   w → 1.30403, vp → 0.706807, u → 0.221192, v → 0.5576, up → 1.25678}, 5.24359},
 {{h → 11.4373, ae → 2.41153, d → 5.38899, ap → 8.15102, dp → 8.27971, ar → 5.82426,
   w → 0.756573, vp → 0.601378, u → 0.340276, v → 0.458761, up → 0.389221}, 5.40498},
 {{h → 4.35196, ae → -1.50946, d → -0.641839, ap → 0.0685117, dp → 2.77795, ar → 3.57958,
   w → 1.28935, vp → 0.693713, u → 0.919928, v → -0.321216, up → 20.2102}, 4.50154},
 {{h → 7.1475, ae → -1.10672, d → 2.78988, ap → 8.53068, dp → 6.11832, ar → 4.0229,
   w → 1.012, vp → 0.233704, u → 0.495033, v → 0.419854, up → 0.0255133}, 3.66168},
 {{h → 8.67845, ae → 5.74918, d → 5.9808, ap → 8.2143, dp → 7.69337, ar → 3.87303,
   w → 0.647597, vp → 0.11834, u → -0.491441, v → -0.0599698, up → -0.032461}, 4.30137},
 {{h → 9.1631, ae → 4.51038, d → 7.94609, ap → 9.45719, dp → 10.1451, ar → 6.22892,
   w → 1.11146, vp → 0.501256, u → 0.34975, v → 0.534919, up → 0.368731}, 6.21618},
 {{h → 9.03636, ae → 4.07613, d → 7.19552, ap → 7.8494, dp → 7.86552, ar → 6.14286,
   w → 1.15064, vp → 0.702326, u → 0.325461, v → 0.468398, up → 0.686878},
  5.77661}}


ClearAll[GlobalSearch]

<< go41.mx
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GlobalSearch[fa4, , , range, .00001, Starts → 20]

{{{h → 11.2602, ae → 2.14225, d → 5.95883, ap → 8.8116, dp → 7.03916, ar → 5.50813,
   w → 0.670684, vp → 0.702013, u → 0.606176, v → 0.549209, up → 0.537143}, 4.5765},
 {{h → 11.1388, ae → 4.53071, d → 5.93816, ap → 9.4354, dp → 8.60886, ar → 5.76606,
   w → 0.831094, vp → 0.708829, u → 0.568699, v → 0.725398, up → 0.626708}, 4.86093},
 {{h → 11.348, ae → 4.62892, d → 8.80252, ap → 9.05126, dp → 10.3977, ar → 6.14882,
   w → 0.857574, vp → 0.67927, u → 0.620542, v → 0.598102, up → 0.753668}, 6.59659},
 {{h → 8.25129, ae → 3.64266, d → 5.91386, ap → 9.21144, dp → 7.39368, ar → 4.73671,
   w → 0.939381, vp → 0.65002, u → 0.136882, v → 0.525297, up → 0.451213}, 3.09522},
 {{h → 12.1533, ae → 6.05272, d → 8.22825, ap → 8.63771, dp → 9.80971, ar → 6.56488,
   w → 0.859768, vp → 0.756301, u → 0.515885, v → 0.721896, up → 0.917456}, 7.58395},
 {{h → 0.787908, ae → -1.54855, d → 3.41975, ap → -1.6164, dp → 2.49523, ar → 3.11337,
   w → -2.3764, vp → 0.883314, u → 0.677898, v → 0.36273, up → -0.0495111}, 7.30021},
 {{h → 7.94134, ae → 1.24054, d → 4.30839, ap → 1.91769, dp → 6.12471, ar → 4.45602,
   w → 0.79766, vp → 0.634338, u → 0.0035982, v → 0.339512, up → 1.58223}, 4.67274},
 {{h → 5.50614, ae → 0.354034, d → 3.18693, ap → 5.97005, dp → 4.56505, ar → 4.06516,
   w → 0.963928, vp → 0.993854, u → -0.0140068, v → 0.850951, up → 0.169799}, 4.55719},
 {{h → 7.26401, ae → 1.6544, d → 4.47125, ap → 8.15769, dp → 7.76436, ar → 5.07924,
   w → 1.03672, vp → 0.660187, u → 0.838622, v → 0.730014, up → 0.423567}, 3.12916},
 {{h → 13.217, ae → 6.88313, d → 8.59244, ap → 9.52404, dp → 10.5707, ar → 6.13402,
   w → 0.758814, vp → 0.63486, u → 0.364305, v → 0.603678, up → 0.784454}, 8.50673},
 {{h → 6.12291, ae → 0.590539, d → 4.06197, ap → 8.57933, dp → 6.70927, ar → 4.15572,
   w → 1.02915, vp → 0.495105, u → 0.195339, v → 0.601191, up → 0.293505}, 2.56102},
 {{h → 9.36257, ae → 3.55602, d → 5.89008, ap → 9.71768, dp → 7.31862, ar → 5.20528,
   w → 0.86021, vp → 0.690184, u → 0.441494, v → 0.580827, up → 0.469236}, 3.33175},
 {{h → 8.66018, ae → 0.927392, d → 3.88244, ap → 8.80931, dp → 5.50287, ar → 4.2125,
   w → 0.758598, vp → 0.618387, u → 0.0765539, v → 0.508221, up → 0.331147}, 2.53526},
 {{h → 9.7182, ae → 4.81062, d → 7.61355, ap → 10.5741, dp → 8.40548, ar → 5.38188,
   w → 0.868637, vp → 0.680252, u → 0.379591, v → 0.500015, up → 0.448036}, 4.31887},
 {{h → 4.88694, ae → -1.89117, d → -0.620697, ap → 5.45555, dp → 2.78683, ar → 3.07674,
   w → 0.888291, vp → 0.712288, u → 0.883861, v → -0.683912, up → -0.482528}, 3.07481},
 {{h → 9.66766, ae → 4.75029, d → 7.18538, ap → 6.7852, dp → 8.0543, ar → 5.66708,
   w → 0.90819, vp → 0.739642, u → 0.491598, v → 0.586139, up → 0.905899}, 4.68871},
 {{h → 8.12534, ae → 2.82753, d → 5.72539, ap → 7.44234, dp → 8.99749, ar → 5.48912,
   w → 0.931284, vp → 0.584088, u → 0.632266, v → 0.701595, up → 0.601298}, 4.1837},
 {{h → 12.7257, ae → 4.86325, d → 7.39075, ap → 5.74141, dp → 9.34701, ar → 5.43094,
   w → 0.685057, vp → 0.593613, u → 0.403242, v → 0.491325, up → 1.08135}, 7.37914},
 {{h → 8.45139, ae → 4.55656, d → 7.08858, ap → 8.95692, dp → 8.62163, ar → 5.65516,
   w → 0.950234, vp → 0.651042, u → 0.522192, v → 0.617576, up → 0.572737}, 3.79704},
 {{h → 10.7651, ae → 4.59356, d → 7.75379, ap → 9.25576, dp → 10.2986, ar → 5.79823,
   w → 0.835038, vp → 0.613031, u → 0.49736, v → 0.591071, up → 0.615295},
  5.3776}}


ClearAll[GlobalSearch]

<< go41.mx

GlobalSearch[fa5, , , range, .00001, Starts → 50]

{{{h → 10.3316, ae → 6.15807, d → 8.27141, ap → 10.6796, dp → 10.2223, ar → 4.89181,
   w → 0.797979, vp → 0.621493, u → 0.432656, v → 0.589819, up → 0.556856}, 5.43387},
 {{h → 7.35704, ae → 1.38124, d → 3.97538, ap → 8.25244, dp → 5.84128, ar → 3.81038,
   w → 0.716474, vp → 0.539985, u → -0.143509, v → 0.363118, up → 0.196587}, 2.29357},
 {{h → 7.95267, ae → 4.69428, d → 6.46072, ap → 12.2523, dp → 7.59007, ar → 5.20337,
   w → 0.978466, vp → 0.782978, u → 0.595535, v → 0.73623, up → 0.497726}, 3.96088},
 {{h → 10.9522, ae → 9.91787, d → 9.37025, ap → 11.0503, dp → 10.5776, ar → 5.37045,
```

<pages removed to conserve space>

{{h → 6.79836, ae → 0.33857, d → 6.94438, ap → 6.48465, dp → 6.96226, ar → 2.67441,
w → 0.714431, vp → 0.659121, u → 0.823808, v → 0.563771, up → 0.575358},
4.54492}}

```
ClearAll[GlobalSearch]

<< go41.mx

GlobalSearch[fall, , , range, .00001, Starts → 50]
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{{{h → 2.38583, ae → 8.15755, d → 1.391, ap → 6.34168, dp → 3.07567, ar → 0.299559,
w → 1.01, vp → 0.76146, u → -0.0767816, v → 0.679637, up → 0.541244}, 3.60816},
{{h → 4.7339, ae → 0.735943, d → 0.281347, ap → 7.1011, dp → 2.07076, ar → 1.7887,
w → 0.831661, vp → 0.724971, u → 0.657674, v → 1.05345, up → 0.575711}, 3.32362},
{{h → 6.23305, ae → 4.39879, d → 6.27312, ap → 2.82637, dp → 7.53722, ar → 2.35036,
w → 0.734216, vp → 0.578288, u → -0.186627, v → 0.44461, up → 0.797574}, 6.0991},
{{h → 8.09569, ae → 2.71804, d → 3.31491, ap → 2.90231, dp → 6.11289, ar → 2.76933,
w → 0.701457, vp → 0.68579, u → 0.515575, v → 0.795313, up → 0.894849}, 6.98013},
{{h → 4.86323, ae → 1.3381, d → 5.06585, ap → 6.71488, dp → 7.3149, ar → 2.53542,
w → 0.787785, vp → 0.687008, u → 0.266848, v → 0.704389, up → 0.402424}, 3.74764},
{{h → 6.33043, ae → 6.06837, d → 5.19942, ap → 8.75505, dp → 4.27829, ar → 2.23341,
w → 0.844372, vp → 0.764726, u → 0.54754, v → 0.551421, up → 0.646241}, 3.1021},
{{h → 8.88265, ae → 1.84562, d → 7.39915, ap → 4.37418, dp → 7.70045, ar → 2.82531,
w → 0.658449, vp → 0.606425, u → 0.663822, v → 0.488694, up → 0.763759}, 8.81616},
{{h → 8.36248, ae → 5.99697, d → 7.5535, ap → 4.55308, dp → 6.42603, ar → 2.94239,
w → 0.740427, vp → 0.809801, u → 0.603247, v → 0.627911, up → 0.758588}, 8.67802},
{{h → 6.38022, ae → -0.347187, d → 4.15595, ap → 3.418, dp → 4.36105, ar → 1.97425,
w → 0.678683, vp → 0.551945, u → 1.06276, v → 0.517697, up → 0.794635}, 4.81985},
{{h → 4.95335, ae → 7.40495, d → 6.3171, ap → 7.96659, dp → 6.99154, ar → 1.63043,
w → 0.804591, vp → 0.592978, u → -0.12219, v → 0.365, up → 0.333915}, 3.05977},
{{h → 8.28294, ae → 6.83394, d → 6.09265, ap → 9.5317, dp → 9.04349, ar → 3.22703,
w → 0.81663, vp → 0.761892, u → 0.698772, v → 0.802683, up → 0.662936}, 8.22892},
{{h → 4.56714, ae → -0.771972, d → 4.21969, ap → 6.12901, dp → 8.48303, ar → 2.28712,
w → 0.785969, vp → 0.718514, u → 0.318861, v → 0.870049, up → 0.463491}, 7.03883},
{{h → 8.78514, ae → 2.46077, d → 8.12266, ap → 3.92815, dp → 8.69033, ar → 2.69892,
w → 0.690266, vp → 0.589961, u → 0.455302, v → 0.575379, up → 0.8649}, 10.2692},
{{h → 6.02303, ae → -4.01801, d → 0.00341384,
ap → 5.16541, dp → 0.999931, ar → 0.917892, w → 0.217503, vp → 0.218629,
u → 0.770556, v → 0.750783, up → -0.660656}, 3.08131}, {{h → 7.87885,
ae → 1.25296, d → 2.99162, ap → 4.25395, dp → 4.66396, ar → 2.50712, w → 0.646297,
vp → 0.603817, u → 0.579454, v → 0.460057, up → 0.664446}, 4.63522}, {{h → 5.81341,
ae → 0.401684, d → 5.03959, ap → 3.25834, dp → 4.71883, ar → 2.48781, w → 0.701339,
vp → 0.782761, u → 0.598109, v → 0.601676, up → 0.608387}, 5.78517}, {{h → 4.97622,
ae → 8.37966, d → 6.50533, ap → 7.4377, dp → 3.67806, ar → 2.52409, w → 0.952845,
vp → 0.929694, u → 0.523913, v → 0.752431, up → 0.812769}, 4.26244}, {{h → 6.26343,
ae → 6.34142, d → 3.75613, ap → 7.52904, dp → 4.6146, ar → 1.46998, w → 0.70835,
vp → 0.584842, u → -0.479397, v → 0.085858, up → 0.280848}, 2.76426}, {{h → 10.395,
ae → 9.76681, d → 6.42473, ap → 8.187, dp → 10.6702, ar → 3.74553, w → 0.799104,
vp → 0.777753, u → 0.61763, v → 0.887854, up → 0.815555}, 15.4283}, {{h → 4.84306,
ae → 7.69161, d → 4.93967, ap → 7.97554, dp → 7.89489, ar → 3.08023, w → 0.89261,
vp → 0.752261, u → 0.431437, v → 0.798449, up → 0.58566}, 3.83844}, {{h → 5.30843,
ae → 5.89596, d → 5.50251, ap → 7.25468, dp → 6.46704, ar → 2.15001, w → 0.810593,
vp → 0.609458, u → -0.116762, v → 0.47992, up → 0.528372}, 1.65553}, {{h → 6.67876,
ae → 4.67968, d → 6.37062, ap → 6.70171, dp → 8.36664, ar → 1.84072, w → 0.683617,
vp → 0.711723, u → -0.633252, v → 0.700654, up → 0.322385}, 6.97966}, {{h → 10.4664,
ae → 5.47954, d → 6.48895, ap → 5.25921, dp → 3.9342, ar → 2.92062, w → 0.734429,
vp → 0.862692, u → 0.577986, v → 0.709392, up → 0.896261}, 9.77763}, {{h → 5.88195,

ae → 4.01671, d → 1.47179, ap → 1.95393, dp → 1.97213, ar → 1.90751, w → 0.742329,
vp → 0.771692, u → -0.705318, v → 0.32838, up → 0.895528}, 3.80051}, {{h → 7.49218,
ae → 0.44319, d → 6.66262, ap → 5.8051, dp → 5.66242, ar → 2.6507, w → 0.729576,
vp → 0.666571, u → 0.890994, v → 0.564324, up → 0.74704}, 5.71063}, {{h → 13.6552,
ae → 5.19305, d → 8.18843, ap → 3.85485, dp → 10.0411, ar → 4.80582, w → 0.730051,
vp → 0.860352, u → 0.881546, v → 0.872137, up → 0.989947}, 20.1364}, {{h → 8.94165,
ae → 5.6426, d → 6.35402, ap → 4.73523, dp → 7.82424, ar → 2.59859, w → 0.720997,
vp → 0.600576, u → 0.398305, v → 0.598722, up → 0.832323}, 7.71822}, {{h → 6.33627,
ae → 5.07258, d → 3.15869, ap → 7.30346, dp → 4.63045, ar → 1.94018, w → 0.711297,
vp → 0.721103, u → -0.513918, v → 0.639489, up → 0.307106}, 2.81124}, {{h → 8.0581,
ae → 7.94914, d → 7.6651, ap → 9.54988, dp → 8.32356, ar → 3.21614, w → 0.859071,
vp → 0.793375, u → 0.760131, v → 0.699259, up → 0.686612}, 7.53351}, {{h → 7.58746,
ae → -0.666087, d → 2.87539, ap → 1.63013, dp → 2.92543, ar → 2.19613, w → 0.569321,
vp → 0.870216, u → 0.811533, v → 0.789965, up → 0.876112}, 5.31409}, {{h → 6.51107,
ae → 7.26484, d → 6.88891, ap → 7.87398, dp → 7.93787, ar → 2.17667, w → 0.801392,
vp → 0.647544, u → 0.427013, v → 0.492825, up → 0.542537}, 3.92479}, {{h → 5.11906,
ae → 7.65817, d → 8.41945, ap → 2.66307, dp → 6.11941, ar → 1.97114, w → 0.837774,
vp → 0.817282, u → 0.335722, v → 0.546134, up → 0.809264}, 8.02274}, {{h → 6.03972,
ae → 8.00829, d → 8.41694, ap → 9.51349, dp → 8.43704, ar → 2.46772, w → 0.859552,
vp → 0.731962, u → 0.443596, v → 0.655138, up → 0.608489}, 5.34039}, {{h → 5.78668,
ae → 4.36168, d → 3.12607, ap → 2.13319, dp → 5.73917, ar → 2.49195, w → 0.760902,
vp → 0.583387, u → 0.0990797, v → 0.505556, up → 0.859909}, 4.81857}, {{h → 6.33763,
ae → 3.51274, d → 3.22198, ap → 6.51894, dp → 5.00098, ar → 1.87047, w → 0.683248,
vp → 0.742881, u → -0.782863, v → 0.718782, up → 0.25722}, 3.33787}, {{h → 5.19802,
ae → 8.06036, d → 6.64488, ap → 7.04623, dp → 6.31496, ar → 1.60999, w → 0.871272,
vp → 0.655429, u → 0.231517, v → 0.4724, up → 0.676776}, 1.51468}, {{h → 9.56192,
ae → 6.60041, d → 8.79484, ap → 7.29509, dp → 4.95977, ar → 2.87276, w → 0.765574,
vp → 0.80386, u → 0.612222, v → 0.520847, up → 0.780905}, 9.40388}, {{h → 9.11346,
ae → 4.37286, d → 5.5189, ap → 1.18373, dp → 3.31967, ar → 3.15636, w → 0.664848,
vp → 0.895057, u → 0.661133, v → 0.450797, up → 1.00696}, 10.6013}, {{h → 6.72967,
ae → 2.6652, d → 3.5925, ap → 5.93393, dp → 1.88332, ar → 1.93732, w → 0.787269,
vp → 0.947927, u → 0.772046, v → 0.535918, up → 0.679334}, 5.42726}, {{h → 8.62781,
ae → 2.14081, d → 5.69075, ap → 1.6387, dp → 6.06899, ar → 2.62279, w → 0.628539,
vp → 0.669042, u → 0.360022, v → 0.545167, up → 0.966233}, 9.39957}, {{h → 10.9651,
ae → 8.32602, d → 11.2716, ap → 9.73072, dp → 10.4761, ar → 3.40429, w → 0.776927,
vp → 0.703862, u → 0.541402, v → 0.69741, up → 0.802185}, 17.8324}, {{h → 9.48809,
ae → 7.33068, d → 10.4812, ap → 9.52249, dp → 7.98287, ar → 5.01316, w → 0.900585,
vp → 0.929598, u → 0.837032, v → 0.859206, up → 0.883046}, 10.0716}, {{h → 7.12603,
ae → 1.35346, d → 4.93558, ap → 3.83758, dp → 5.68895, ar → 2.9702, w → 0.741327,
vp → 0.677277, u → 0.826214, v → 0.576991, up → 0.800344}, 5.12594}, {{h → 6.83006,
ae → 4.08283, d → 6.0797, ap → 6.40058, dp → 7.92823, ar → 2.54669, w → 0.762669,
vp → 0.531453, u → 0.172666, v → 0.555336, up → 0.691645}, 4.39102}, {{h → 7.11858,
ae → 0.735392, d → 3.98515, ap → 6.45699, dp → 2.87827, ar → 2.39114, w → 0.710673,
vp → 0.761302, u → 0.793145, v → 0.403181, up → 0.594435}, 3.42579}, {{h → 10.2682,
ae → 2.34581, d → 3.50528, ap → 3.78813, dp → 3.4128, ar → 2.47798, w → 0.488742,
vp → 0.778077, u → -0.180874, v → 0.501613, up → 0.608041}, 7.14353}, {{h → 10.6628,
ae → 7.16324, d → 5.42245, ap → 9.13609, dp → 9.51038, ar → 3.59178, w → 0.782375,
vp → 0.780597, u → 0.665906, v → 0.919353, up → 0.794091}, 14.7526}, {{h → 3.31779,
ae → 2.16174, d → 4.47543, ap → 6.08947, dp → 8.69332, ar → 2.5258, w → 0.898156,
vp → 0.582249, u → 0.0485152, v → 0.70498, up → 0.496063}, 3.40883}, {{h → 5.26643,
ae → 3.42438, d → 2.69617, ap → 8.47195, dp → 2.82144, ar → 1.89593, w → 0.830033,
vp → 0.75334, u → 0.535066, v → 0.388103, up → 0.485265}, 3.15106},
{{h → 7.8715, ae → 7.13514, d → 6.47738, ap → 6.78865, dp → 4.31178, ar → 2.19706,
w → 0.731704, vp → 0.857621, u → 0.331709, v → 0.596283, up → 0.599953},
6.80382}}

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TRAIT : dens

ClearAll[GlobalSearch]

<< go41.mx

GlobalSearch[fb3, , , range, .00001, Starts → 20]

{{{h → 10.0705, ae → 12.4362, d → 11.3481, ap → 11.8543, dp → 9.78891, ar → 5.60198,
   w → 0.356908, vp → 0.542913, u → 0.778266, v → 0.609182, up → 0.579727}, 3.94264},
 {{h → 8.42105, ae → 13.386, d → 10.3468, ap → 9.02969, dp → 8.22452, ar → 6.17648,
   w → 0.364501, vp → 0.675897, u → 0.621361, v → 0.601123, up → 0.791606}, 2.92277},
 {{h → 8.67552, ae → 10.3659, d → 8.73041, ap → 10.5309, dp → 7.8904, ar → 5.33315,
   w → 0.572551, vp → 0.62329, u → 1.13172, v → 0.988662, up → 0.604467}, 3.34005},
 {{h → 2.72874, ae → 8.40938, d → 4.99365, ap → 3.51845, dp → 3.62842, ar → 5.23135,
   w → 0.170573, vp → 0.975371, u → -0.277602, v → 0.486269, up → 0.521297}, 4.11509},
 {{h → 9.11655, ae → 13.0953, d → 11.9593, ap → 11.1826, dp → 10.0647, ar → 6.60849,
   w → 0.546238, vp → 0.663466, u → 0.774401, v → 0.663235, up → 0.712425}, 4.25143},
 {{h → 9.94485, ae → 10.9267, d → 8.17908, ap → 10.7821, dp → 7.49773, ar → 4.97696,
   w → 0.455005, vp → 0.677587, u → 0.993344, v → 0.937026, up → 0.621882}, 3.13417},
 {{h → 9.44895, ae → 11.8932, d → 9.18743, ap → 10.6308, dp → 7.87598, ar → 3.81775,
   w → 0.138303, vp → 0.37291, u → 0.645794, v → 0.522373, up → 0.417705}, 2.46433},
 {{h → 8.61262, ae → 13.2677, d → 11.4726, ap → 11.0553, dp → 9.10175, ar → 6.5937,
   w → 0.554841, vp → 0.649856, u → 0.706799, v → 0.615324, up → 0.701505}, 3.75533},
 {{h → 4.51736, ae → 13.4093, d → 9.33366, ap → 5.13743, dp → 6.6969, ar → 6.15588,
   w → 0.426887, vp → 0.735674, u → 0.306222, v → 0.452577, up → 1.00177}, 3.30158},
 {{h → 8.46168, ae → 10.9976, d → 6.70955, ap → 8.98981, dp → 5.4421, ar → 2.26852,
   w → 0.465188, vp → 0.86134, u → 0.538689, v → 0.571109, up → 0.636653}, 3.54158},
 {{h → 4.0121, ae → 12.6835, d → 7.33302, ap → 6.32062, dp → 4.74686, ar → 4.99504,
   w → -0.0887471, vp → 0.744523, u → 0.136585, v → 0.397157, up → 0.190345}, 2.43889},
 {{h → 5.77089, ae → 8.70991, d → 5.55879, ap → 7.4105, dp → 4.39757, ar → 0.606723,
   w → 0.936549, vp → 0.755132, u → 0.684502, v → 0.382087, up → 0.517852}, 3.91036},
 {{h → 8.93816, ae → 13.194, d → 10.1582, ap → 10.3237, dp → 8.16835, ar → 5.41656,
   w → 0.24728, vp → 0.531478, u → 0.57832, v → 0.559341, up → 0.56712}, 2.64532},
 {{h → 8.3852, ae → 12.4078, d → 9.97816, ap → 9.67246, dp → 7.53134, ar → 6.77303,
   w → 0.63305, vp → 0.808806, u → 0.878976, v → 0.704745, up → 0.845374}, 3.5667},
 {{h → 8.10529, ae → 12.2605, d → 8.31469, ap → 8.95719, dp → 7.28726, ar → 4.78155,
   w → 1.06725, vp → 0.841135, u → 0.715414, v → 0.739259, up → 0.954669}, 4.4682},
 {{h → 9.37833, ae → 13.1701, d → 12.2085, ap → 11.6516, dp → 10.3379, ar → 6.52129,
   w → 0.4889, vp → 0.62095, u → 0.753745, v → 0.611024, up → 0.611643}, 4.46855},
 {{h → 8.42534, ae → 10.8454, d → 7.17286, ap → 8.07769, dp → 6.35668, ar → 2.40234,
   w → 0.530544, vp → 0.838607, u → 0.626761, v → 0.689469, up → 0.88534}, 3.79487},
 {{h → 1.56554, ae → 9.81034, d → 5.98631, ap → 3.87559, dp → 1.06874, ar → 1.20929,
   w → 4.27695, vp → 3.02413, u → 0.570708, v → 0.540031, up → 1.78334}, 2.65857},
 {{h → 7.4782, ae → 12.479, d → 11.9164, ap → 10.1724, dp → 8.97215, ar → 6.79529,
   w → 0.907709, vp → 0.766842, u → 0.867349, v → 0.663581, up → 0.900405}, 4.48093},
 {{h → 5.65281, ae → 11.6264, d → 9.0183, ap → 6.30521, dp → 4.7788, ar → 4.31119,
   w → 1.42207, vp → 1.4255, u → 0.779795, v → 0.610121, up → 1.63676},
  3.26779}}


ClearAll[GlobalSearch]

<< go41.mx
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GlobalSearch[fb4, , , range, .00001, Starts → 20]

{{{h → 7.40697, ae → 10.7231, d → 9.03869, ap → 9.33054, dp → 5.42125, ar → 3.59488,
   w → 0.850268, vp → 0.989392, u → 0.778242, v → 0.498975, up → 0.710548}, 4.76549},
 {{h → 6.92412, ae → 9.05296, d → 7.92351, ap → 8.62578, dp → 5.22453, ar → 2.62177,
   w → 0.644602, vp → 0.819344, u → 0.874217, v → 0.648758, up → 0.729999}, 3.74082},
 {{h → 8.77638, ae → 10.8957, d → 9.47584, ap → 10.7153, dp → 7.52592, ar → 4.40904,
   w → 0.605035, vp → 0.712409, u → 0.839737, v → 0.633692, up → 0.6326}, 3.71071},
 {{h → 4.83117, ae → 7.90849, d → 3.67429, ap → 4.64936, dp → 5.33193, ar → 0.4628,
   w → 0.945857, vp → 0.490947, u → 0.763089, v → 0.91655, up → 0.966882}, 3.7888},
 {{h → 4.53285, ae → 8.50891, d → 5.54817, ap → 8.11513, dp → 5.83516, ar → 2.14186,
   w → 1.0975, vp → 0.677239, u → 0.918266, v → 0.961158, up → 0.814628}, 3.89608},
 {{h → 6.87015, ae → 10.6968, d → 11.6407, ap → 10.6309, dp → 7.94523, ar → 5.41558,
   w → 1.01329, vp → 0.866168, u → 0.938749, v → 0.66452, up → 0.820761}, 5.29459},
 {{h → 3.49105, ae → 12.0944, d → 7.78801, ap → 6.70213, dp → 3.84997, ar → 4.71631,
   w → 0.484279, vp → 0.881032, u → 0.255899, v → 0.475849, up → 0.438633}, 2.59759},
 {{h → 3.96762, ae → 11.1784, d → 7.06846, ap → 5.47686, dp → 5.36461, ar → 5.00049,
   w → 0.41436, vp → 0.650316, u → 0.169547, v → 0.469459, up → 0.447011}, 3.24067},
 {{h → 11.5453, ae → 9.98646, d → 13.6896, ap → 13.3857, dp → 9.91547, ar → 6.9802,
   w → 0.653897, vp → 0.857481, u → 1.08243, v → 0.708208, up → 0.735672}, 8.91788},
 {{h → 8.07616, ae → 11.3212, d → 7.26319, ap → 8.49893, dp → 5.56553, ar → 3.99936,
   w → 0.663297, vp → 0.868355, u → 0.75089, v → 0.834572, up → 0.861292}, 3.16932},
 {{h → 9.43797, ae → 11.6258, d → 8.42417, ap → 9.22808, dp → 7.08357, ar → 4.57594,
   w → 0.560587, vp → 0.74324, u → 0.767559, v → 0.754014, up → 0.816006}, 2.40356},
 {{h → 6.83612, ae → 9.35856, d → 7.905, ap → 7.3768, dp → 6.36613, ar → 5.04127,
   w → 0.297649, vp → 0.725519, u → 0.701785, v → 0.644594, up → 0.528093}, 4.23912},
 {{h → 9.1902, ae → 11.1298, d → 9.42548, ap → 10.5109, dp → 9.25111, ar → 3.61385,
   w → 0.496105, vp → 0.411181, u → 0.736375, v → 0.590505, up → 0.613081}, 3.55858},
 {{h → 8.9679, ae → 12.5183, d → 8.67222, ap → 11.1902, dp → 8.84714, ar → 5.35132,
   w → 0.746604, vp → 0.676819, u → 0.767437, v → 0.881686, up → 0.749643}, 3.35257},
 {{h → 9.10376, ae → 8.4331, d → 7.2012, ap → 9.25181, dp → 6.64316, ar → 2.10587,
   w → 0.285167, vp → 0.465229, u → 0.890712, v → 0.591781, up → 0.550939}, 2.01403},
 {{h → 2.3733, ae → -0.140668, d → 3.28353, ap → 2.40083, dp → 3.67513, ar → 4.21535,
   w → 0.132119, vp → 0.47525, u → 3.54072, v → 0.513706, up → 0.503306}, 6.05499},
 {{h → -0.343729, ae → -3.01359, d → 1.66643, ap → 0.811751, dp → 1.78672, ar → 3.41968,
   w → -2.06575, vp → 0.746791, u → 0.496854, v → 0.755376, up → -0.132459}, 5.27249},
 {{h → 10.2862, ae → 8.98235, d → 8.55215, ap → 9.68063, dp → 7.85094, ar → 3.8083,
   w → 0.394325, vp → 0.602788, u → 0.999617, v → 0.635919, up → 0.640785}, 3.16533},
 {{h → 3.52341, ae → 8.76644, d → 5.67448, ap → 2.13567, dp → 1.46407, ar → 0.385066,
   w → 0.938712, vp → 1.71177, u → 0.568298, v → 0.357403, up → 1.70727}, 2.22331},
 {{h → 4.92975, ae → 10.5073, d → 9.18919, ap → 8.04262, dp → 5.99412, ar → 6.67436,
   w → 0.834967, vp → 0.979473, u → 0.636102, v → 0.767891, up → 0.741837},
  5.28882}}


ClearAll[GlobalSearch]

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GlobalSearch[fb5, , , range, .00001, Starts → 50]

{{{h → 5.77696, ae → 12.0879, d → 8.67334, ap → 3.76159, dp → 6.24046, ar → 5.1403,
   w → 0.59317, vp → 0.824207, u → 0.526287, v → 0.670652, up → 1.05097}, 2.88078},
 {{h → 9.19729, ae → 5.52234, d → 7.28626, ap → 7.87995, dp → 6.54523, ar → 4.74432,
   w → 0.688685, vp → 0.901848, u → 1.28179, v → 0.903064, up → 0.907352}, 4.42814},
 {{h → 10.3211, ae → 12.6457, d → 10.5883, ap → 8.84862, dp → 10.268, ar → 5.22634,
   w → 0.563173, vp → 0.728355, u → 0.693251, v → 0.767019, up → 0.789648}, 4.21408},
 {{h → 3.05597, ae → 9.43645, d → 5.37971, ap → 5.02738, dp → 2.88885, ar → 0.916685,
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<pages removed to conserve space>

{{h → 6.67699, ae → 7.18864, d → 5.53541, ap → 5.7585, dp → 6.13496, ar → 1.11499,
w → 0.650348, vp → 0.633947, u → 0.843016, v → 0.800013, up → 0.872832}, 2.51672},
{{h → 8.10666, ae → 7.00416, d → 3.99364, ap → 2.49865, dp → 3.11789, ar → 0.0113966,
w → 0.11317, vp → 0.716013, u → 0.732919, v → 0.66563, up → 1.00088}, 2.6797},
{{h → 7.17495, ae → 5.34038, d → 7.57686, ap → 10.044, dp → 6.41799, ar → 3.48834,
w → 0.402585, vp → 0.725228, u → 0.899658, v → 0.717195, up → 0.40988}, 7.52386},
{{h → 1.08588, ae → 10.9176, d → 7.8008, ap → 6.03148, dp → 6.45787, ar → 4.59951,
w → 1.2175, vp → 0.769576, u → 0.469987, v → 0.701787, up → 0.491026}, 5.74487},
{{h → 8.96071, ae → 11.7459, d → 10.9702, ap → 9.01942, dp → 10.2544, ar → 4.10544,
w → 0.588718, vp → 0.583927, u → 0.68061, v → 0.58951, up → 0.67805}, 4.69631},
{{h → 3.86308, ae → 10.4777, d → 6.84589, ap → 7.34974, dp → 3.92029, ar → 2.26936,
w → 1.07944, vp → 0.88268, u → 0.707874, v → 0.705162, up → 0.867222}, 4.7108},
{{h → 9.67824, ae → 10.9661, d → 8.9972, ap → 6.28019, dp → 8.24961, ar → 3.94214,
w → 0.670279, vp → 0.737864, u → 0.778017, v → 0.753963, up → 0.983092}, 3.72458},
{{h → 8.65755, ae → 11.7233, d → 12.763, ap → 13.2882, dp → 11.2787, ar → 5.82258,
w → 0.829898, vp → 0.755206, u → 0.849432, v → 0.697037, up → 0.6442}, 8.76259},
{{h → 10.3898, ae → 12.5079, d → 14.9021, ap → 14.8306, dp → 14.7034, ar → 7.36261,
w → 0.868672, vp → 0.73584, u → 0.881712, v → 0.769952, up → 0.752713}, 14.4472},
{{h → 7.93625, ae → 12.2177, d → 8.26795, ap → 11.3087, dp → 7.19823, ar → 4.59022,
w → 0.615907, vp → 0.764039, u → 0.620587, v → 0.748789, up → 0.53706}, 3.34797},
{{h → 7.66657, ae → 11.7833, d → 6.8273, ap → 6.5143, dp → 5.6215, ar → 4.21683,
w → 0.525383, vp → 0.795533, u → 0.581746, v → 0.753075, up → 0.743582}, 1.65795},
{{h → 8.56527, ae → 11.8826, d → 9.68264, ap → 7.8238, dp → 8.8319, ar → 4.21839,
w → 0.574532, vp → 0.602262, u → 0.64745, v → 0.60324, up → 0.725751}, 3.29213},
{{h → 10.8937, ae → 11.3721, d → 9.42522, ap → 8.96135, dp → 10.1196, ar → 3.64889,
w → 0.446916, vp → 0.644151, u → 0.688768, v → 0.712471, up → 0.652246}, 5.85026},
{{h → 5.64762, ae → 11.6185, d → 8.24848, ap → 8.71178, dp → 6.79673, ar → 4.42597,
w → 0.616382, vp → 0.685535, u → 0.53392, v → 0.652131, up → 0.534219},
2.95449}}

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ClearAll[GlobalSearch]

<< go41.mx

GlobalSearch[fb7, , , range, .00001, Starts → 50]
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{{{h → 7.75318, ae → 8.41484, d → 4.89291, ap → 4.87726, dp → 3.67803, ar → 1.63145,
w → 0.605268, vp → 0.827287, u → 0.802224, v → 0.717173, up → 0.866243}, 2.57143},
{{h → 4.14752, ae → 7.24596, d → 3.50733, ap → 6.91501, dp → 3.85784, ar → 0.305055,
w → 0.792783, vp → 0.455021, u → 0.726881, v → 0.780341, up → 0.741336}, 3.09427},
{{h → 8.09906, ae → 11.2211, d → 9.54406, ap → 5.78893, dp → 8.46422, ar → 3.4948,
w → 0.583853, vp → 0.623699, u → 0.616525, v → 0.650028, up → 0.860316}, 5.12815},
{{h → 4.1151, ae → 9.9631, d → 6.48921, ap → 8.7828, dp → 6.26436, ar → 3.96234,
w → 0.758663, vp → 0.748535, u → 0.598469, v → 0.795034, up → 0.54618}, 4.92735},
{{h → 7.49915, ae → 7.69497, d → 5.06571, ap → 6.76539, dp → 4.66596, ar → 0.894329,
w → 0.504463, vp → 0.60748, u → 0.761441, v → 0.643927, up → 0.671599}, 0.888263},
{{h → -1.39867, ae → 2.63814, d → 3.03184, ap → -0.992833, dp → 2.13484, ar → 2.25917,
w → 0.53579, vp → 0.797533, u → 0.811477, v → 0.643406, up → -0.0245365}, 5.89926},
{{h → 10.9198, ae → 11.2925, d → 13.8722, ap → 12.8494, dp → 12.8269, ar → 4.81517,
w → 0.692465, vp → 0.630709, u → 0.818477, v → 0.608592, up → 0.658932}, 14.9877},
{{h → 3.94717, ae → 4.63898, d → 3.92296, ap → 5.34319, dp → 7.04208, ar → 0.57908,
w → 0.884173, vp → 0.441937, u → 0.991766, v → 0.844118, up → 0.853867}, 3.30944},
{{h → 7.15714, ae → 10.1998, d → 5.792, ap → 7.66528, dp → 6.57563, ar → 1.95689,
w → 0.709645, vp → 0.57672, u → 0.683666, v → 0.782602, up → 0.810208}, 2.90153},
{{h → 8.05506, ae → 12.2944, d → 11.0953, ap → 13.13, dp → 9.33989, ar → 5.22401,
w → 0.790439, vp → 0.753391, u → 0.704529, v → 0.750186, up → 0.67421}, 6.54702},
{{h → 8.03984, ae → 10.5551, d → 6.0996, ap → 8.29469, dp → 5.30759, ar → 2.53325,

w → 0.481808, vp → 0.727877, u → 0.64304, v → 0.687406, up → 0.554434}, 1.2688},
{{h → 8.10977, ae → 10.7443, d → 7.58946, ap → 7.27716, dp → 6.61095, ar → 2.86466,
w → 0.42417, vp → 0.68419, u → 0.574218, v → 0.682027, up → 0.633846}, 1.56547},
{{h → 7.82861, ae → 6.60218, d → 6.12923, ap → 6.59673, dp → 5.7163, ar → 1.10942,
w → 0.524467, vp → 0.637773, u → 0.879855, v → 0.592486, up → 0.657215}, 2.07364},
{{h → 4.01994, ae → 6.44355, d → 2.79012, ap → 6.44441, dp → 3.32523, ar → 0.304556,
w → 0.825939, vp → 0.477237, u → 0.812733, v → 0.793543, up → 0.75683}, 2.95376},
{{h → 5.20863, ae → 11.1153, d → 8.53164, ap → 6.9687, dp → 6.6949, ar → 4.59796,
w → 0.736172, vp → 0.782097, u → 0.617087, v → 0.713947, up → 0.704218}, 2.49325},
{{h → 9.22155, ae → 11.3134, d → 10.299, ap → 8.42369, dp → 10.3176, ar → 3.31406,
w → 0.484241, vp → 0.634283, u → 0.655687, v → 0.642556, up → 0.597175}, 6.40336},
{{h → 8.86081, ae → 10.8369, d → 8.85461, ap → 7.51521, dp → 7.95238, ar → 2.83828,
w → 0.500725, vp → 0.578101, u → 0.687192, v → 0.506035, up → 0.625122}, 3.65207},
{{h → 2.19564, ae → 5.64888, d → 3.57998, ap → 4.50298, dp → 1.38521, ar → -1.02172,
w → 0.743905, vp → 0.657776, u → 0.665452, v → 0.410621, up → 0.627466}, 3.44855},
{{h → 4.34868, ae → 10.744, d → 7.51196, ap → 7.28701, dp → 5.41332, ar → 3.7266,
w → 0.565574, vp → 0.708494, u → 0.484406, v → 0.611989, up → 0.474485}, 2.35777},
{{h → 6.6538, ae → 11.0403, d → 9.9565, ap → 8.91252, dp → 7.24399, ar → 4.14788,
w → 0.696136, vp → 0.677971, u → 0.573693, v → 0.675196, up → 0.741519}, 4.25379},
{{h → 2.30258, ae → 11.0654, d → 9.71658, ap → 6.82668, dp → 4.04791, ar → 3.04117,
w → 0.953555, vp → 0.871723, u → 0.562213, v → 0.482731, up → 0.560423}, 5.19097},
{{h → 6.61037, ae → 6.18662, d → 3.20199, ap → 4.39293, dp → 2.79227, ar → 0.164133,
w → 0.51734, vp → 0.691895, u → 0.846668, v → 0.680385, up → 0.802275}, 1.18696},
{{h → 6.41106, ae → 2.33432, d → 6.35214, ap → 5.52902, dp → 6.67446, ar → 4.04931,
w → 0.543308, vp → 0.778964, u → 1.24139, v → 0.817455, up → 0.707869}, 8.42472},
{{h → 5.69423, ae → 4.58087, d → 3.95864, ap → 8.31253, dp → 4.34453, ar → 2.43549,
w → 0.442833, vp → 0.718131, u → 0.866011, v → 0.856201, up → 0.466899}, 6.51155},
{{h → 9.03635, ae → 9.79845, d → 9.86693, ap → 8.94388, dp → 8.57786, ar → 3.12057,
w → 0.647198, vp → 0.735505, u → 0.81173, v → 0.664529, up → 0.680568}, 4.93349},
{{h → 5.95141, ae → 11.4099, d → 13.1024, ap → 11.5902, dp → 10.794, ar → 4.83101,
w → 0.774766, vp → 0.630598, u → 0.639985, v → 0.605626, up → 0.585088}, 10.2082},
{{h → 6.93802, ae → 11.1876, d → 9.93962, ap → 5.18072, dp → 4.62823, ar → 4.47805,
w → 0.586037, vp → 0.909253, u → 0.588447, v → 0.630598, up → 0.840282}, 7.41514},
{{h → 7.33463, ae → 7.79047, d → 4.30109, ap → 6.92931, dp → 4.73086, ar → 1.76781,
w → 0.718584, vp → 0.647701, u → 0.839554, v → 0.81324, up → 0.84321}, 2.12451},
{{h → 8.69723, ae → 10.42, d → 8.8074, ap → 9.80031, dp → 8.34072, ar → 2.87349,
w → 0.58172, vp → 0.671708, u → 0.7195, v → 0.666105, up → 0.589934}, 3.46772},
{{h → 8.33109, ae → 10.2562, d → 6.43383, ap → 8.25428, dp → 6.68873, ar → 3.16512,
w → 0.743574, vp → 0.735308, u → 0.781503, v → 0.822684, up → 0.829756}, 2.07363},
{{h → 8.23713, ae → 8.80948, d → 7.56345, ap → 6.61388, dp → 6.85489, ar → 1.80399,
w → 0.629366, vp → 0.672504, u → 0.804439, v → 0.598443, up → 0.749518}, 3.0579},
{{h → 10.4858, ae → 11.9397, d → 10.0021, ap → 8.37447, dp → 10.5776, ar → 5.2902,
w → 0.74791, vp → 0.751949, u → 0.795257, v → 0.820206, up → 0.907642}, 5.6798},
{{h → 3.40324, ae → 10.0627, d → 7.27915, ap → 8.31202, dp → 9.28728, ar → 3.724,
w → 0.971318, vp → 0.504799, u → 0.60015, v → 0.793843, up → 0.775062}, 10.1281},
{{h → 3.9221, ae → 5.79033, d → 6.76578, ap → 9.13085, dp → 8.02274, ar → 4.27099,
w → 0.880197, vp → 0.800768, u → 0.912032, v → 0.906803, up → 0.605375}, 9.20078},
{{h → 5.87718, ae → 11.0075, d → 7.66715, ap → 7.72566, dp → 4.43687, ar → 3.20022,
w → 0.7495, vp → 0.812688, u → 0.658414, v → 0.633659, up → 0.723214}, 3.80976},
{{h → 8.70008, ae → 6.09621, d → 5.73171, ap → 5.84091, dp → 4.32642, ar → 0.728041,
w → 0.407942, vp → 0.626385, u → 0.883266, v → 0.490348, up → 0.688139}, 2.7876},
{{h → 3.63802, ae → 9.03908, d → 4.00017,
ap → 5.86421, dp → 2.70942, ar → -0.449537, w → -0.90969, vp → -0.0200145,
u → 0.153944, v → 0.311665, up → 0.00214312}, 2.60537}, {{h → 7.24148,
ae → 6.67453, d → 6.48773, ap → 6.20304, dp → 6.90332, ar → 1.26472, w → 0.67106,
vp → 0.44064, u → 0.887015, v → 0.583495, up → 0.831029}, 3.55521}, {{h → 9.60836,
ae → 10.3912, d → 9.72713, ap → 7.80184, dp → 9.33556, ar → 3.73296, w → 0.686703,
vp → 0.739479, u → 0.81395, v → 0.733645, up → 0.820563}, 3.83123}, {{h → 6.50387,

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ae → 13.0771, d → 12.2818, ap → 12.2579, dp → 10.7887, ar → 4.81537, w → 0.790492,
 vp → 0.606329, u → 0.611444, v → 0.622218, up → 0.612334}, 10.1894}, {{h → 8.78835,
 ae → 6.68271, d → 8.65919, ap → 8.09629, dp → 7.7988, ar → 2.89957, w → 0.713445,
 vp → 0.717388, u → 1.00056, v → 0.659001, up → 0.772239}, 5.88267}, {{h → 6.80398,
 ae → 8.18359, d → 4.88778, ap → 4.57369, dp → 3.9797, ar → 3.97603, w → 0.484191,
 vp → 0.899664, u → 0.672246, v → 0.88341, up → 0.834202}, 4.21557}, {{h → 9.87629,
 ae → 9.62696, d → 8.15327, ap → 9.45439, dp → 7.99256, ar → 3.30524, w → 0.629122,
 vp → 0.679871, u → 0.795683, v → 0.724718, up → 0.729865}, 4.3593}, {{h → 5.18461,
 ae → 12.5145, d → 9.77105, ap → 11.1808, dp → 11.0495, ar → 5.78435, w → 0.947795,
 vp → 0.70923, u → 0.731348, v → 0.775259, up → 0.658902}, 10.0572}, {{h → 7.4748,
 ae → 7.84286, d → 5.37503, ap → 6.66243, dp → 5.13951, ar → 0.950825, w → 0.522137,
 vp → 0.474244, u → 0.754426, v → 0.56476, up → 0.698095}, 1.3664}, {{h → 7.43427,
 ae → 11.3474, d → 11.4326, ap → 7.39935, dp → 7.97371, ar → 4.66743, w → 0.796079,
 vp → 0.808327, u → 0.799544, v → 0.619752, up → 0.802334}, 7.78888}, {{h → 9.03392,
 ae → 11.7337, d → 12.4978, ap → 13.2628, dp → 11.1788, ar → 5.52699, w → 0.810766,
 vp → 0.706833, u → 0.782815, v → 0.726417, up → 0.729891}, 9.20592}, {{h → 5.87754,
 ae → 10.6117, d → 7.24543, ap → 5.63691, dp → 5.13404, ar → 3.66744, w → 0.450491,
 vp → 0.792859, u → 0.511256, v → 0.691503, up → 0.647112}, 1.95064}, {{h → 4.28494,
 ae → 12.8465, d → 11.487, ap → 6.05239, dp → 8.28173, ar → 4.82336, w → 0.865165,
 vp → 0.727085, u → 0.583459, v → 0.605768, up → 0.797361}, 7.06472},
{{h → 8.54365, ae → 10.653, d → 5.51939, ap → 8.1116, dp → 4.84415, ar → 2.71096,
  w → 0.564478, vp → 0.755599, u → 0.654459, v → 0.786108, up → 0.711512},
 1.0454}}
```

SCENARIO 2 : TOTALLY DIFFERENT ALLELES BETWEEN THE SPECIES

TRAIT : ubvol

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<< go41.mx
```



```
GlobalSearch[fa2, , , range, .00001, Starts → 20]
```

```
{{{h → 20.6398, ae → 9.63908, de → 15.4693, ap → 23.9119, dp → 19.2401, ah → 25.5345,
   dhe → 18.1828, are → 16.7786, u → 0.78361, v → 1.35553, s → 0.541249}, 3.74114},
 {{h → 12.9164, ae → 11.8021, de → 11.7799, ap → 13.6529, dp → 18.8174, ah → 19.3898,
   dhe → 21.0573, are → 19.7638, u → 1.00501, v → 0.494452, s → 0.540735}, 4.32139},
 {{h → 15.396, ae → 8.99408, de → 15.3247, ap → 21.595, dp → 19.9314, ah → 20.3977,
   dhe → 22.8012, are → 16.569, u → 0.393325, v → 2.46979, s → 0.883591}, 4.22601},
 {{h → 18.4821, ae → 10.3646, de → 10.361, ap → 11.1862, dp → 18.7548, ah → 23.716,
   dhe → 16.1947, are → 18.3264, u → 1.06916, v → 0.962602, s → 1.0548}, 3.94627},
 {{h → 27.3105, ae → 18.852, de → 13.931, ap → 22.4624, dp → 22.8979, ah → 21.2034,
   dhe → 19.3527, are → 15.322, u → 0.652091, v → 1.05697, s → 0.474387}, 3.7089},
 {{h → 22.6274, ae → 14.8504, de → 14.8244, ap → 15.6719, dp → 23.2387, ah → 27.5265,
   dhe → 20.1726, are → 22.8121, u → 1.25535, v → 0.805871, s → 0.405699}, 3.93765},
 {{h → 6.32786, ae → 2.42666, de → 3.56025, ap → 8.59301, dp → 11.3842, ah → 11.3274,
   dhe → 13.7319, are → 10.3884, u → 0.490555, v → 0.757732, s → 1.02473}, 3.95569},
 {{h → 10.9932, ae → 8.51886, de → 8.49107, ap → 10.0271, dp → 17.2557, ah → 17.1228,
   dhe → 18.9623, are → 16.4806, u → 0.705247, v → 1.01513, s → 0.790073}, 4.04914},
 {{h → 23.6339, ae → 13.5068, de → 17.447, ap → 26.2593, dp → 21.9779, ah → 28.7967,
   dhe → 21.311, are → 21.4684, u → 1.47043, v → 0.776762, s → 1.08553}, 4.56273},
 {{h → 13.5326, ae → 9.30768, de → 4.74352, ap → 14.3266, dp → 13.1411, ah → 7.14533,
   dhe → 15.2433, are → 7.18628, u → 0.510186, v → 1.00578, s → 0.834776}, 3.7001},
 {{h → 21.7818, ae → 14.7659, de → 14.7429, ap → 16.3126, dp → 23.5274, ah → 27.9482,
   dhe → 19.9607, are → 22.7276, u → 0.801732, v → 0.627738, s → 0.733787}, 4.05452},
 {{h → 23.2774, ae → 12.3574, de → 17.3646, ap → 27.4594, dp → 20.7208, ah → 18.2269,
   dhe → 25.5425, are → 20.3191, u → 1.83361, v → 1.09462, s → 0.557366}, 3.60613},
 {{h → 11.7232, ae → 4.76595, de → 4.74774, ap → 5.58736, dp → 12.6062, ah → 16.6295,
   dhe → 9.27203, are → 12.7276, u → 1.49985, v → 0.744609, s → 0.705048}, 3.95682},
 {{h → 11.2906, ae → -0.0528613, de → 6.10808, ap → 14.7062, dp → 9.63578, ah → 6.26146,
   dhe → 13.6804, are → 7.56589, u → 0.966684, v → 0.561531, s → 0.997531}, 2.93626},
 {{h → 14.2146, ae → 7.85346, de → 11.6733, ap → 22.288, dp → 15.3633, ah → 16.9805,
   dhe → 20.5019, are → 15.8151, u → 0.953624, v → 1.08619, s → 0.95391}, 4.87109},
 {{h → 13.8882, ae → 0.898531, de → 1.34206, ap → 13.4232, dp → 5.98688, ah → 8.54073,
   dhe → 6.31014, are → 6.28295, u → 1.42374, v → 0.738383, s → 0.57818}, 4.2455},
 {{h → 2.3362, ae → 1.19903, de → 1.18736, ap → 2.02045, dp → 7.56997, ah → 7.60468,
   dhe → 9.87476, are → 9.16073, u → 0.788515, v → 0.526212, s → 0.633552}, 4.2023},
 {{h → 12.292, ae → 1.05885, de → 6.24669, ap → 12.0898, dp → 11.6384, ah → 16.4905,
   dhe → 9.48692, are → 9.02054, u → 0.552402, v → 0.516358, s → 0.559287}, 4.53331},
 {{h → 17.7646, ae → 0.521783, de → 8.05861, ap → 15.4922, dp → 11.4806, ah → 12.227,
   dhe → 10.0915, are → 8.35194, u → 1.15707, v → 0.600537, s → 0.765026}, 3.3364},
 {{h → 11.9748, ae → 7.85232, de → 10.2606, ap → 9.03087, dp → 16.4179, ah → 17.8065,
   dhe → 19.7949, are → 15.814, u → 0.910178, v → 1.12584, s → 0.434123},
  4.70078}}
```

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ClearAll[GlobalSearch]
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<< go41.mx
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GlobalSearch[fa7, , , range, .00001, Starts → 20]
```

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{{{h → 18.2891, ae → 15.8613, de → 14.291, ap → 11.1752, dp → 20.6125, ah → 21.2915,
   dhe → 15.7677, are → 24.5773, u → 0.616962, v → 0.649644, s → 0.456405}, 7.47722},
 {{h → 15.0587, ae → 3.98683, de → 4.81382, ap → 8.40331, dp → 10.2921, ah → 13.5571,
   dhe → 9.29343, are → 9.84433, u → -0.0409544, v → 0.378288, s → 0.557117}, 1.90384},
 {{h → 12.2715, ae → 8.773, de → 9.85395, ap → 15.2267, dp → 13.6969, ah → 14.6166,
   dhe → 17.6975, are → 13.7323, u → 0.304785, v → 0.389151, s → 0.543051}, 2.74241},
 {{h → 19.6638, ae → 15.2323, de → 11.6569, ap → 16.2623, dp → 16.0144, ah → 14.9828,
   dhe → 12.814, are → 8.11952, u → 0.495551, v → 0.575983, s → 0.678166}, 4.67815},
 {{h → 20.4761, ae → 17.9869, de → 18.628, ap → 21.9595, dp → 22.7482, ah → 21.2629,
   dhe → 24.1612, are → 17.1461, u → 0.335999, v → 0.486698, s → 0.59805}, 4.73982},
 {{h → 7.92829, ae → 1.60338, de → 3.5563, ap → 9.03433, dp → 7.64034, ah → 6.79329,
   dhe → 9.50396, are → 7.51694, u → -0.277721, v → 0.49725, s → 0.554264}, 1.51833},
 {{h → 8.63653, ae → 9.14734, de → 2.62851, ap → 9.08156, dp → 7.86316, ah → 6.0153,
   dhe → 9.40675, are → 4.40719, u → -0.11924, v → 0.532243, s → 0.772364}, 2.94672},
 {{h → 14.5491, ae → 15.5368, de → 11.6929, ap → 17.3167, dp → 15.459, ah → 11.3991,
   dhe → 17.2135, are → 11.4715, u → 0.625717, v → 0.582724, s → 0.533163}, 1.70773},
 {{h → 10.1894, ae → 6.44541, de → 10.7678, ap → 7.82367, dp → 15.6389, ah → 11.8778,
   dhe → 15.4807, are → 14.6465, u → 0.732019, v → 0.446526, s → 0.412893}, 2.95326},
 {{h → 17.3273, ae → 14.687, de → 15.4089, ap → 18.8977, dp → 19.7991, ah → 19.5864,
   dhe → 22.0563, are → 14.1392, u → 0.310837, v → 0.445464, s → 0.651582}, 4.74388},
 {{h → 5.13315, ae → 1.74433, de → 1.64114, ap → 8.25137, dp → 3.25362, ah → 0.662238,
   dhe → 7.42682, are → 3.02724, u → 0.609092, v → 0.469913, s → 0.491834}, 4.41833},
 {{h → 21.218, ae → 20.8357, de → 16.1774, ap → 18.9451, dp → 22.0299, ah → 18.1477,
   dhe → 23.437, are → 15.906, u → 0.44377, v → 0.547845, s → 0.690198}, 6.80116},
 {{h → 4.96241, ae → 7.15112, de → 3.89154, ap → 6.64384, dp → 8.03539, ah → 7.21263,
   dhe → 10.4292, are → 13.779, u → 0.409441, v → 0.666437, s → 0.489519}, 5.6974},
 {{h → 12.7491, ae → 10.2177, de → 10.6179, ap → 11.7659, dp → 13.9458, ah → 14.8875,
   dhe → 10.0814, are → 8.79665, u → 0.784528, v → 0.613563, s → 0.510928}, 3.62715},
 {{h → 16.1369, ae → 14.0096, de → 19.028, ap → 16.0688, dp → 23.4867, ah → 22.4998,
   dhe → 24.0088, are → 20.1783, u → 0.576733, v → 0.486262, s → 0.530351}, 4.09906},
 {{h → 11.9722, ae → 8.0818, de → 7.61977, ap → 6.00856, dp → 10.9945, ah → 12.0917,
   dhe → 8.33806, are → 15.7238, u → 0.74543, v → 0.857896, s → 0.684627}, 5.6183},
 {{h → 16.4675, ae → 7.26066, de → 9.06177, ap → 13.992, dp → 11.7341, ah → 14.6771,
   dhe → 10.6986, are → 10.2709, u → 0.305768, v → 0.575207, s → 0.677931}, 1.77136},
 {{h → 19.2026, ae → 15.8786, de → 12.0166, ap → 17.997, dp → 16.7804, ah → 21.5794,
   dhe → 15.1515, are → 15.2464, u → 0.31933, v → 0.498471, s → 0.571951}, 3.29607},
 {{h → 13.7987, ae → 8.39458, de → 9.7932, ap → 15.864, dp → 11.979, ah → 11.1652,
   dhe → 16.8293, are → 12.895, u → 0.447485, v → 0.486726, s → 0.635316}, 5.35679},
 {{h → 21.0204, ae → 12.712, de → 12.7523, ap → 17.4946, dp → 16.912, ah → 19.3952,
   dhe → 15.979, are → 17.2435, u → 0.264304, v → 0.46209, s → 0.495801},
  2.00757}}
```

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ClearAll[GlobalSearch]
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<< go41.mx
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GlobalSearch[fa11, , , range, .00001, Starts → 20]
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{{{h → 14.1843, ae → 14.7688, de → 12.2109, ap → 13.7134, dp → 16.2298, ah → 14.463,
   dhe → 16.5728, are → 6.49435, u → 0.521653, v → 0.671581, s → 0.903356}, 12.0622},
 {{h → 14.4485, ae → 12.443, de → 12.8691, ap → 18.0788, dp → 15.1176, ah → 16.2637,
   dhe → 18.935, are → 16.9058, u → 0.504125, v → 0.571711, s → 0.627098}, 2.9422},
 {{h → 17.6261, ae → 12.7248, de → 11.4684, ap → 16.1215, dp → 17.1998, ah → 23.2906,
   dhe → 17.2045, are → 18.1621, u → 0.277321, v → 0.330229, s → 0.458071}, 3.84716},
 {{h → 17.4006, ae → 11.5033, de → 9.35528, ap → 13.9985, dp → 13.5451, ah → 14.8974,
   dhe → 11.3179, are → 5.9473, u → 0.317078, v → 0.539553, s → 0.773512}, 4.61091},
 {{h → 16.5725, ae → 14.7948, de → 17.534, ap → 22.5573, dp → 16.4418, ah → 15.221,
   dhe → 20.0083, are → 16.8501, u → 0.740208, v → 0.675015, s → 0.602919}, 4.21063},
 {{h → 21.435, ae → 15.0836, de → 16.4925, ap → 17.4451, dp → 21.1576, ah → 25.4095,
   dhe → 18.9503, are → 21.1041, u → 0.444995, v → 0.468958, s → 0.513595}, 1.87457},
 {{h → 12.9838, ae → 5.83615, de → 11.992, ap → 13.0748, dp → 11.3991, ah → 15.7705,
   dhe → 11.2824, are → 13.3154, u → 0.708875, v → 0.473981, s → 0.485241}, 2.67606},
 {{h → 16.838, ae → 17.0871, de → 16.3764, ap → 19.7705, dp → 19.1921, ah → 13.8094,
   dhe → 19.9605, are → 13.049, u → 0.639915, v → 0.613159, s → 0.534068}, 3.07609},
 {{h → 17.3838, ae → 7.3452, de → 9.94653, ap → 13.1675, dp → 13.7971, ah → 15.0085,
   dhe → 12.0353, are → 12.7951, u → 0.138118, v → 0.489006, s → 0.466705}, 2.8503},
 {{h → 9.06258, ae → 6.7129, de → 10.3508, ap → 10.1708, dp → 13.3557, ah → 14.3782,
   dhe → 15.6591, are → 6.77455, u → 0.555018, v → 0.574377, s → 0.866103}, 7.38434},
 {{h → 15.1351, ae → 12.082, de → 17.1879, ap → 13.4314, dp → 19.6873, ah → 16.8312,
   dhe → 20.0409, are → 18.9673, u → 0.80796, v → 0.68754, s → 0.687453}, 2.27799},
 {{h → 13.9903, ae → 11.0542, de → 13.8059, ap → 15.1741, dp → 18.1658, ah → 20.4179,
   dhe → 21.8761, are → 14.8184, u → 0.448505, v → 0.392248, s → 0.636166}, 5.52171},
 {{h → 24.1147, ae → 17.2296, de → 16.0011, ap → 18.3142, dp → 21.0798, ah → 23.4909,
   dhe → 18.9727, are → 22.4825, u → 0.349162, v → 0.496313, s → 0.486844}, 2.38866},
 {{h → 19.3419, ae → 12.8551, de → 12.1559, ap → 12.1197, dp → 17.7239, ah → 16.5798,
   dhe → 14.3814, are → 20.5069, u → 0.592717, v → 0.529153, s → 0.418294}, 6.53498},
 {{h → 10.3083, ae → 7.41486, de → 8.16174, ap → 10.5858, dp → 11.5467, ah → 5.75192,
   dhe → 12.4878, are → 5.30966, u → 0.593291, v → 0.519173, s → 0.55144}, 3.58001},
 {{h → 13.2488, ae → 10.2352, de → 7.77441, ap → 15.5718, dp → 11.7244, ah → 8.09036,
   dhe → 15.4677, are → 10.0339, u → 0.446432, v → 0.351245, s → 0.389912}, 3.6501},
 {{h → 11.6768, ae → 8.65145, de → 10.0294, ap → 11.6453, dp → 12.464, ah → 7.84348,
   dhe → 14.1335, are → 7.83892, u → 0.694917, v → 0.605425, s → 0.69304}, 4.24764},
 {{h → 8.36263, ae → 9.47675, de → 6.6391, ap → 8.94872, dp → 11.5195, ah → 6.3706,
   dhe → 11.7068, are → 3.94155, u → 0.690708, v → 0.586275, s → 0.646501}, 4.17796},
 {{h → 9.35327, ae → 3.87765, de → 1.49628, ap → 7.13371, dp → 3.479, ah → 4.43706,
   dhe → 1.02725, are → 1.34458, u → 0.620491, v → 0.711983, s → -0.551188}, 4.65378},
 {{h → 19.2147, ae → 19.7958, de → 21.4125, ap → 23.6519, dp → 24.8277, ah → 24.7514,
   dhe → 28.4978, are → 23.9206, u → 0.502555, v → 0.515197, s → 0.556884},
  5.31868}}
```

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TRAIT : dens
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ClearAll[GlobalSearch]
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<< go41.mx
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GlobalSearch[fb2, , , range, .00001, Starts → 30]
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{{{h → 11.0466, ae → 14.1732, de → 10.6757, ap → 10.8547, dp → 6.78302, ah → 3.76013,
   dhe → 6.07568, are → 4.44145, u → 1.50028, v → 0.55122, s → 0.938656}, 0.484372},
 {{h → -1.99497, ae → 0.809653, de → 7.47911, ap → 4.09498, dp → 3.32584, ah → 5.29141,
   dhe → 5.00245, are → 10.5414, u → 0.654139, v → 0.761819, s → 0.663638}, 3.60005},
```

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{{h → 16.9905, ae → 15.7726, de → 24.6181, ap → 19.0443, dp → 18.6662, ah → 24.3071,
  dhe → 19.3196, are → 25.4641, u → 0.885004, v → 0.764176, s → 0.818443}, 2.7233},
 {{h → 13.1201, ae → 18.7379, de → 15.3486, ap → 15.4161, dp → 11.4575, ah → 5.79298,
  dhe → 13.26, are → 9.00614, u → 1.8506, v → 1.01805, s → 0.570261}, 1.31197},
 {{h → 17.3019, ae → 15.8119, de → 24.6742, ap → 19.095, dp → 19.2021, ah → 24.5933,
  dhe → 19.6184, are → 25.537, u → 1.69084, v → 0.41698, s → 0.76878}, 2.75603},
 {{h → 19.1394, ae → 19.4199, de → 28.2829, ap → 22.7052, dp → 21.9303, ah → 26.4258,
  dhe → 24.1119, are → 29.1517, u → 0.98091, v → 0.551693, s → 0.46553}, 2.70578},
 {{h → 15.5561, ae → 18.7721, de → 15.0942, ap → 15.4512, dp → 11.2027, ah → 8.26962,
  dhe → 10.5836, are → 9.0403, u → 0.74057, v → 1.16604, s → 0.952833}, 0.43713},
 {{h → 14.0281, ae → 13.8189, de → 22.4202, ap → 16.6086, dp → 15.8113, ah → 21.7359,
  dhe → 16.5528, are → 23.0185, u → 1.22994, v → 0.793237, s → 0.996514}, 2.8342},
 {{h → 12.3401, ae → 14.025, de → 21.3221, ap → 17.302, dp → 16.5184, ah → 19.6448,
  dhe → 17.7043, are → 23.7322, u → 0.922876, v → 0.442963, s → 0.965751}, 2.93413},
 {{h → 12.0524, ae → 21.6344, de → 12.7723, ap → 7.36476, dp → 10.6977, ah → 4.76613,
  dhe → 10.9701, are → 11.9026, u → -2.54149, v → 0.703117, s → 0.731803}, 6.61094},
 {{h → 23.0284, ae → 24.467, de → 22.9496, ap → 21.145, dp → 19.0586, ah → 15.7144,
  dhe → 16.6753, are → 14.7351, u → 2.27928, v → 0.521192, s → 0.984622}, 1.40648},
 {{h → 8.529, ae → 13.7951, de → 8.72424, ap → 10.4732, dp → 4.83322, ah → 1.24232,
  dhe → 6.26379, are → 4.06328, u → 1.40556, v → 0.721784, s → 1.02171}, 0.662265},
 {{h → 14.6944, ae → 19.3944, de → 16.8944, ap → 16.0783, dp → 13.0005, ah → 7.40504,
  dhe → 13.8692, are → 9.66266, u → 0.831596, v → 0.479095, s → 0.966876}, 1.14977},
 {{h → 11.9494, ae → 14.0577, de → 21.8074, ap → 17.3216, dp → 16.4678, ah → 19.2764,
  dhe → 18.5855, are → 23.7323, u → 1.5759, v → 0.656648, s → 0.65961}, 3.23208},
 {{h → 14.3155, ae → 15.7762, de → 23.4254, ap → 18.8484, dp → 18.0536, ah → 21.7937,
  dhe → 19.384, are → 25.2584, u → 0.803825, v → 1.02756, s → 0.660503}, 2.83909},
 {{h → 10.3852, ae → 11.1745, de → 19.8557, ap → 14.4581, dp → 13.6742, ah → 17.6753,
  dhe → 15.3594, are → 20.9012, u → 0.732789, v → 0.412589, s → 1.24095}, 2.70872},
 {{h → 15.658, ae → 19.5872, de → 17.1582, ap → 16.2653, dp → 13.2672, ah → 8.36978,
  dhe → 13.3616, are → 9.85538, u → 1.34569, v → 0.732139, s → 0.68461}, 0.785021},
 {{h → 17.7884, ae → 22.4467, de → 18.8364, ap → 19.1248, dp → 14.9454, ah → 10.4921,
  dhe → 15.773, are → 12.7149, u → 0.876485, v → 0.873897, s → 0.59293}, 0.509634},
 {{h → 2.85884, ae → 1.74604, de → 10.6103, ap → 5.02629, dp → 4.39374, ah → 10.1564,
  dhe → 5.17849, are → 11.4628, u → 0.55137, v → 0.918098, s → 0.619177}, 2.70976},
 {{h → 14.2813, ae → 15.4115, de → 23.4314, ap → 18.6896, dp → 17.9128, ah → 21.5837,
  dhe → 19.2617, are → 25.1219, u → 0.621478, v → 1.07367, s → 0.628227}, 2.75305},
 {{h → 19.442, ae → 28.0005, de → 22.996, ap → 16.7355, dp → 23.0765, ah → 26.6803,
  dhe → 19.0038, are → 23.1454, u → 0.999667, v → 0.347299, s → 0.618441}, 7.77559},
 {{h → 3.65671, ae → 5.74315, de → 12.0719, ap → 9.02845, dp → 8.26023, ah → 10.943,
  dhe → 8.8771, are → 15.4749, u → 1.72284, v → 0.876563, s → 0.832967}, 3.15314},
 {{h → 14.2764, ae → 20.4684, de → 13.6292, ap → 17.1464, dp → 9.94177, ah → 6.99001,
  dhe → 12.0944, are → 10.7365, u → 0.509357, v → 1.95376, s → 0.498015}, 1.64878},
 {{h → 25.8982, ae → 31.4613, de → 25.8502, ap → 28.1394, dp → 21.9591, ah → 18.6067,
  dhe → 23.689, are → 21.7295, u → 0.900528, v → 0.995814, s → 0.739373}, 0.887847},
 {{h → 3.81262, ae → 3.51, de → 12.12, ap → 6.5102, dp → 5.70712, ah → 11.3481,
  dhe → 6.25108, are → 12.9201, u → 0.769789, v → 0.973081, s → 0.547817}, 2.78308},
 {{h → 17.989, ae → 23.1069, de → 19.5306, ap → 19.8179, dp → 15.623, ah → 10.7024,
  dhe → 16.9218, are → 13.375, u → 0.75087, v → 0.985283, s → 0.934941}, 0.768076},
 {{h → 1.38152, ae → 2.18556, de → 10.8971, ap → 5.19638, dp → 4.39913, ah → 8.90848,
  dhe → 6.47426, are → 11.6063, u → 0.510556, v → 1.59103, s → 0.69624}, 2.77987},
 {{h → 3.70039, ae → 15.5332, de → 11.4933,
  ap → -0.608216, dp → 6.59562, ah → 10.9365, dhe → 8.33821, are → 5.80147,
  u → -0.000303265, v → 0.669526, s → 0.785298}, 9.50325}, {{h → 12.4672,
  ae → 18.1363, de → 13.6337, ap → 14.8144, dp → 9.7427, ah → 5.15861, dhe → 11.5872,
  are → 8.40452, u → 0.776152, v → 1.36201, s → 0.991829}, 0.879717},
 {{h → 19.5003, ae → 25.3934, de → 19.1647, ap → 22.0714, dp → 15.2737, ah → 12.214,
  dhe → 17.3311, are → 15.6616, u → 1.00577, v → 0.849724, s → 0.973795},
 1.22889}}
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ClearAll[GlobalSearch]

<< go41.mx

GlobalSearch[fb3, , , range, .00001, Starts → 30]

{{{h → 15.0733, ae → 18.1911, de → 15.3397, ap → 15.4747, dp → 13.3516, ah → 10.3756,
   dhe → 13.6667, are → 11.7855, u → 0.775825, v → 0.579445, s → 0.57602}, 0.674751},
 {{h → 8.46125, ae → 8.83028, de → 16.2007, ap → 9.14242, dp → 12.7146, ah → 15.5377,
   dhe → 13.2474, are → 18.4575, u → 0.991188, v → 0.681778, s → 0.542503}, 1.64581},
 {{h → 13.7888, ae → 19.4867, de → 17.2596, ap → 14.9877, dp → 15.3813, ah → 16.5062,
   dhe → 14.7877, are → 13.3387, u → 0.173125, v → 0.550919, s → 0.818486}, 4.04077},
 {{h → 24.9857, ae → 28.4064, de → 21.2375, ap → 21.4666, dp → 20.5527, ah → 17.6717,
   dhe → 19.4108, are → 18.7306, u → 0.315334, v → 0.442546, s → 0.533887}, 1.70881},
 {{h → 3.52182, ae → 4.59115, de → 11.7865, ap → 7.82594, dp → 6.16371, ah → 10.741,
   dhe → 8.56193, are → 12.5546, u → 0.0616629, v → 0.292787, s → 0.387626}, 2.45927},
 {{h → 15.2532, ae → 21.2059, de → 13.5956, ap → 18.1452, dp → 11.3366, ah → 8.25572,
   dhe → 13.8391, are → 11.85, u → 0.406496, v → 0.504873, s → 0.501451}, 2.07775},
 {{h → 17.3835, ae → 19.724, de → 15.7943, ap → 16.4055, dp → 13.9778, ah → 11.066,
   dhe → 13.0507, are → 11.1632, u → 0.592339, v → 0.601946, s → 0.631974}, 0.541806},
 {{h → 11.8263, ae → 14.9039, de → 16.9351, ap → 9.5054, dp → 16.3136, ah → 18.229,
   dhe → 13.232, are → 16.1568, u → 0.68212, v → 0.62747, s → 0.574877}, 6.87459},
 {{h → 16.2412, ae → 17.8302, de → 18.4992, ap → 16.5542, dp → 16.2149, ah → 13.756,
   dhe → 15.8698, are → 14.0581, u → 1.12931, v → 0.835753, s → 0.794191}, 1.30208},
 {{h → 2.56978, ae → 3.5075, de → 9.02516, ap → 5.87443, dp → 4.40085, ah → 8.81229,
   dhe → 6.81747, are → 12.2472, u → 0.591991, v → 0.608019, s → 0.517522}, 2.24923},
 {{h → 19.0672, ae → 21.9648, de → 14.2866, ap → 15.9037, dp → 13.0505, ah → 12.2813,
   dhe → 11.9888, are → 13.0049, u → 0.205565, v → 0.535826, s → 0.639273}, 2.52823},
 {{h → 9.88993, ae → 8.65119, de → 14.8734, ap → 11.5075, dp → 10.0703, ah → 15.9927,
   dhe → 10.6809, are → 16.7662, u → 0.614527, v → 0.635977, s → 0.637472}, 2.45541},
 {{h → 27.1082, ae → 29.9665, de → 26.8683, ap → 29.6038, dp → 23.9036, ah → 20.244,
   dhe → 24.702, are → 21.2632, u → 0.66031, v → 0.771084, s → 0.713867}, 2.25014},
 {{h → 11.7056, ae → 12.4791, de → 11.4947, ap → 9.99638, dp → 9.51092, ah → 7.60783,
   dhe → 7.25098, are → 6.31999, u → 0.908702, v → 0.60433, s → 0.60136}, 1.62743},
 {{h → 9.11526, ae → 13.3408, de → 10.199, ap → 11.3014, dp → 7.65712, ah → 3.25481,
   dhe → 9.31979, are → 6.02189, u → 0.651907, v → 0.521532, s → 0.379074}, 1.16689},
 {{h → 6.93487, ae → 8.76361, de → 11.8506, ap → 6.30782, dp → 9.36891, ah → 11.0075,
   dhe → 6.99489, are → 10.2495, u → 1.13994, v → 0.178383, s → 0.0363233}, 3.10963},
 {{h → 13.1676, ae → 16.3538, de → 13.4919, ap → 13.6927, dp → 11.7543, ah → 9.67476,
   dhe → 12.3432, are → 11.3036, u → 0.982975, v → 0.676817, s → 0.686198}, 1.37157},
 {{h → 17.1889, ae → 27.4129, de → 18.8416, ap → 17.454, dp → 19.9675, ah → 19.8778,
   dhe → 18.7193, are → 17.8969, u → 0.525258, v → 0.814551, s → 0.846077}, 6.12836},
 {{h → 16.765, ae → 12.8001, de → 21.6189, ap → 12.8901, dp → 18.4038, ah → 17.3205,
   dhe → 17.1239, are → 21.3753, u → 1.25658, v → 0.758434, s → 0.712434}, 6.4054},
 {{h → 22.0259, ae → 28.1011, de → 23.8775, ap → 24.6954, dp → 22.1282, ah → 18.7393,
   dhe → 25.3623, are → 23.363, u → 0.720298, v → 0.499234, s → 0.502529}, 4.15269},
 {{h → 8.43524, ae → 6.71562, de → 15.573, ap → 9.41923, dp → 10.7214, ah → 14.968,
   dhe → 10.6827, are → 15.0088, u → 0.659984, v → 0.606896, s → 0.612276}, 2.42802},
 {{h → 13.7703, ae → 12.8044, de → 20.2355, ap → 15.5608, dp → 15.2387, ah → 20.3039,
   dhe → 15.7686, are → 20.7896, u → 0.480732, v → 0.519498, s → 0.525538}, 2.17563},
 {{h → 1.55994, ae → -0.129473, de → 7.39014, ap → 3.30396, dp → 2.71683, ah → 7.37954,
   dhe → 3.21791, are → 7.33075, u → 0.261915, v → 0.651547, s → 0.847837}, 2.17327},
 {{h → 22.6022, ae → 24.0329, de → 19.2039, ap → 21.6528, dp → 17.2059, ah → 16.3206,
   dhe → 18.5664, are → 20.7674, u → 0.455877, v → 0.911705, s → 0.911079}, 5.9161},
 {{h → 19.3857, ae → 21.5826, de → 16.9163, ap → 16.4684, dp → 15.7827, ah → 12.3921,
   dhe → 14.1666, are → 12.3743, u → 0.503339, v → 0.50649, s → 0.623453}, 1.18993},
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<pages removed to conserve space>

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ClearAll[GlobalSearch]

<< go41.mx

GlobalSearch[fb8, , , range, .00001, Starts → 30]
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   dhe → 19.4696, are → 15.3175, u → 0.449937, v → 0.544302, s → 0.732795}, 9.68017},
 {{h → 20.1164, ae → 22.8596, de → 22.1561, ap → 19.8277, dp → 21.2924, ah → 17.7795,
   dhe → 20.9801, are → 18.6037, u → 0.626691, v → 0.478065, s → 0.476333}, 1.84359},
 {{h → 19.8733, ae → 20.2769, de → 23.9288, ap → 16.0151, dp → 24.6231, ah → 22.1767,
   dhe → 21.8027, are → 24.8182, u → 0.738108, v → 0.579078, s → 0.540703}, 3.4826},
 {{h → 15.0964, ae → 15.942, de → 17.0797, ap → 16.9316, dp → 14.3708, ah → 16.8092,
   dhe → 14.9087, are → 11.8374, u → 0.333198, v → 0.57897, s → 0.746906}, 5.65572},
 {{h → 17.2096, ae → 18.5864, de → 17.5586, ap → 15.2337, dp → 16.5434, ah → 20.845,
   dhe → 15.6417, are → 15.068, u → 0.459324, v → 0.599598, s → 0.746599}, 6.77901},
 {{h → 20.9698, ae → 18.1214, de → 18.8489, ap → 15.754, dp → 17.036, ah → 13.3087,
   dhe → 16.0506, are → 9.52042, u → 0.411475, v → 0.492132, s → 0.749038}, 6.5864},
 {{h → 8.21511, ae → 11.0611, de → 17.644, ap → 11.2581, dp → 15.1347, ah → 14.5826,
   dhe → 17.1307, are → 15.4866, u → 0.838933, v → 0.591293, s → 0.534226}, 6.0632},
 {{h → 12.3418, ae → 12.9111, de → 12.1487, ap → 9.50709, dp → 8.76885, ah → 4.92306,
   dhe → 7.30925, are → 3.30573, u → 0.0547037, v → 0.0990789, s → 0.542586}, 1.779},
 {{h → 17.3587, ae → 19.4886, de → 16.2614, ap → 16.6316, dp → 15.4791, ah → 11.1064,
   dhe → 15.1429, are → 11.6965, u → 0.612381, v → 0.619889, s → 0.627593}, 0.707173},
 {{h → 14.0378, ae → 13.9551, de → 19.334, ap → 12.1473, dp → 17.9326, ah → 20.51,
   dhe → 15.3773, are → 23.927, u → 0.627193, v → 0.573667, s → 0.434172}, 2.98117},
 {{h → 9.68266, ae → 11.3966, de → 9.07076, ap → 6.70729, dp → 7.65165, ah → 11.3025,
   dhe → 5.48076, are → 10.2727, u → 0.0329894, v → 0.553444, s → 0.498326}, 5.86776},
 {{h → 7.06523, ae → 6.71054, de → 12.2857, ap → 9.7584, dp → 8.016, ah → 13.0213,
   dhe → 9.28269, are → 14.9625, u → 0.30921, v → 0.451712, s → 0.431969}, 1.98572},
 {{h → 15.5176, ae → 22.5462, de → 16.9989, ap → 19.1179, dp → 16.2178, ah → 16.0373,
   dhe → 16.0398, are → 13.9577, u → 0.477976, v → 0.681836, s → 0.682786}, 5.78758},
 {{h → 6.14655, ae → 5.17732, de → 8.82598, ap → 7.26589, dp → 5.95097, ah → 9.75623,
   dhe → 6.80167, are → 10.7903, u → 0.143742, v → 0.585433, s → 0.623068}, 2.60496},
 {{h → 12.302, ae → 14.7914, de → 9.2003, ap → 10.9633, dp → 7.77524, ah → 4.68086,
   dhe → 10.1927, are → 7.97148, u → 0.127266, v → 0.585772, s → 0.723939}, 3.84676},
 {{h → 10.9795, ae → 14.8213, de → 12.6731, ap → 13.9593, dp → 10.7893, ah → 6.59529,
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 {{h → 11.4683, ae → 10.1688, de → 15.8944, ap → 11.0423, dp → 13.2232, ah → 16.6816,
   dhe → 12.0867, are → 18.5436, u → 0.509739, v → 0.595961, s → 0.509583}, 2.17267},
 {{h → 15.0899, ae → 13.8326, de → 12.0632, ap → 15.7445, dp → 9.93605, ah → 9.99858,
   dhe → 11.4405, are → 14.21, u → 0.444116, v → 0.744284, s → 0.71558}, 6.0447},
 {{h → 20.3132, ae → 21.0274, de → 22.0385, ap → 22.5756, dp → 18.4231, ah → 16.4033,
   dhe → 18.3094, are → 17.0702, u → 0.617502, v → 0.523557, s → 0.428239}, 2.56188},
 {{h → 5.83591, ae → 7.7749, de → 9.48379, ap → 8.05578, dp → 7.17842, ah → 10.6269,
   dhe → 8.48408, are → 7.89984, u → 0.332581, v → 0.612924, s → 0.805367}, 3.59097},
 {{h → 8.63793, ae → 12.5524, de → 5.43049, ap → 8.16959, dp → 4.71379, ah → 1.84238,
   dhe → 6.30068, are → 3.42942, u → 0.455506, v → 0.542114, s → 0.800381}, 1.54844},
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   dhe → 17.4982, are → 14.8959, u → 0.622182, v → 0.5717, s → 0.527517}, 2.37813},
 {{h → 18.5562, ae → 14.9872, de → 11.6726, ap → 12.2432, dp → 9.36937, ah → 11.0637,
   dhe → 8.7828, are → 7.80071, u → 0.167663, v → 0.41116, s → 0.738424}, 4.26282},
 {{h → 16.8009, ae → 13.6769, de → 20.5444, ap → 16.6898, dp → 16.3745, ah → 22.4889,
   dhe → 15.6068, are → 20.1197, u → 0.412707, v → 0.489402, s → 0.536516}, 3.62813},
 {{h → 21.0425, ae → 19.9827, de → 19.5675, ap → 15.2144, dp → 18.069, ah → 18.6176,
   dhe → 17.3813, are → 14.5795, u → 0.19327, v → 0.424353, s → 0.643266}, 7.09307},
 {{h → 18.1366, ae → 19.2839, de → 17.5296, ap → 16.9539, dp → 16.4174, ah → 12.0586,
   dhe → 16.3265, are → 10.4888, u → 0.592895, v → 0.610308, s → 0.726458}, 3.90712},
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 {{h → 9.99829, ae → 14.1416, de → 21.5538, ap → 19.4736, dp → 14.9954, ah → 16.4742,
   dhe → 20.8782, are → 19.1098, u → 0.824598, v → 0.624295, s → 0.444352}, 13.9957},
 {{h → 17.2986, ae → 14.4853, de → 11.1545, ap → 9.55306, dp → 10.6644, ah → 10.7681,
   dhe → 6.64065, are → 5.52966, u → 0.415055, v → 0.654333, s → 0.81227}, 6.78491},
 {{h → 21.3033, ae → 16.0932, de → 25.1251, ap → 18.7509, dp → 21.2477, ah → 27.6479,
   dhe → 18.0472, are → 23.4588, u → 0.546752, v → 0.54741, s → 0.571954}, 7.22067},
 {{h → 16.7986, ae → 12.555, de → 10.4207, ap → 8.54322, dp → 8.7996, ah → 9.48759,
   dhe → 7.39584, are → 5.73944, u → 0.153461, v → 0.494287, s → 0.832509},
  4.22825}}
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ClearAll[GlobalSearch]

<< go41.mx

GlobalSearch[fb9, , , range, .00001, Starts → 30]
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   dhe → 14.5447, are → 23.2518, u → 0.394066, v → 0.440236, s → 0.3937}, 3.31186},
 {{h → 13.4673, ae → 16.1782, de → 7.59659, ap → 10.8023, dp → 6.14993, ah → 6.13604,
   dhe → 6.69802, are → 7.2036, u → 0.119256, v → 0.421939, s → 0.592995}, 3.07228},
 {{h → 3.48372, ae → 3.52112, de → 8.06483, ap → 5.63983, dp → 4.80188, ah → 9.4629,
   dhe → 5.89967, are → 11.0142, u → 0.495171, v → 0.578419, s → 0.563121}, 2.05356},
 {{h → 10.9236, ae → 13.9045, de → 5.11122, ap → 10.5916, dp → 3.48137, ah → 3.77868,
   dhe → 2.8077, are → 4.20227, u → 0.133263, v → 0.556461, s → 0.456573}, 3.63327},
 {{h → 15.1306, ae → 15.7165, de → 15.1415, ap → 12.4908, dp → 13.9598, ah → 8.34154,
   dhe → 13.8387, are → 6.64793, u → 0.502302, v → 0.493405, s → 0.737645}, 4.53575},
 {{h → 8.75987, ae → 12.3615, de → 4.77572, ap → 3.55429, dp → 3.90806, ah → 4.25223,
   dhe → 3.59347, are → 6.7364, u → -0.319413, v → 0.616412, s → 0.557993}, 4.31755},
 {{h → 10.826, ae → 12.0431, de → 15.7676, ap → 10.1137, dp → 13.0174, ah → 16.586,
   dhe → 11.9966, are → 12.9819, u → 0.157571, v → 0.376184, s → 0.503827}, 4.75465},
 {{h → 18.6824, ae → 24.988, de → 17.842, ap → 19.0796, dp → 16.9209, ah → 11.1709,
   dhe → 20.0566, are → 15.341, u → 0.296369, v → 0.319627, s → 0.431942}, 3.38581},
 {{h → 1.47841, ae → 4.6168, de → 8.02166, ap → 4.81346, dp → 5.94235, ah → 7.36866,
   dhe → 7.63973, are → 13.9556, u → 0.63187, v → 0.654269, s → 0.397854}, 3.29589},
 {{h → 13.3514, ae → 14.7322, de → 11.2275, ap → 10.1996, dp → 9.03242, ah → 10.9742,
   dhe → 6.9003, are → 7.7687, u → -0.174764, v → 0.394469, s → 0.506103}, 3.65088},
 {{h → 22.8505, ae → 26.3301, de → 20.0985, ap → 16.5578, dp → 22.9927, ah → 17.5904,
   dhe → 19.9728, are → 21.6635, u → 0.573983, v → 0.501463, s → 0.453605}, 7.13006},
 {{h → 18.4783, ae → 20.0521, de → 15.8714, ap → 17.2536, dp → 14.9012, ah → 11.8868,
   dhe → 13.8407, are → 11.3555, u → 0.550857, v → 0.614071, s → 0.622469}, 0.718689},
 {{h → 11.6473, ae → 10.1352, de → 13.5724, ap → 12.7411, dp → 9.89431, ah → 16.6629,
   dhe → 10.1632, are → 17.6807, u → 0.411785, v → 0.529261, s → 0.516193}, 3.69603},
 {{h → 10.7647, ae → 17.0218, de → 13.6706, ap → 11.5721, dp → 12.4077, ah → 15.3591,
   dhe → 14.1568, are → 11.8418, u → 0.178368, v → 0.435837, s → 0.66857}, 4.22202},
 {{h → 12.5101, ae → 16.5308, de → 6.64749, ap → 11.382, dp → 6.10479, ah → 5.50297,
   dhe → 5.53936, are → 7.58726, u → 0.411544, v → 0.543905, s → 0.431579}, 5.3943},
 {{h → 11.3305, ae → 11.3608, de → 15.8271, ap → 11.0994, dp → 13.7158, ah → 16.6657,
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 {{h → 13.2888, ae → 13.7371, de → 18.2491, ap → 16.7757, dp → 14.1517, ah → 18.6497,
   dhe → 16.4021, are → 21.3728, u → 0.404385, v → 0.496073, s → 0.49072}, 2.17834},
 {{h → 9.57228, ae → 14.9389, de → 8.32498, ap → 12.3119, dp → 7.05318, ah → 3.59153,
   dhe → 9.69735, are → 7.12307, u → 0.553114, v → 0.520595, s → 0.502153}, 2.35993},
 {{h → 10.2823, ae → 11.7074, de → 11.0092, ap → 9.82037, dp → 9.59104, ah → 5.71283,
   dhe → 8.43702, are → 5.87247, u → 0.658988, v → 0.510466, s → 0.421064}, 1.21269},
 {{h → 6.34945, ae → 1.78304, de → 9.46131, ap → 4.45499, dp → 5.89554, ah → 12.1768,
   dhe → 3.37667, are → 9.27406, u → 0.565319, v → 0.591254, s → 0.611814}, 5.08738},
 {{h → 11.2124, ae → 12.0302, de → 12.6164, ap → 9.365, dp → 11.4102, ah → 7.01573,
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dhe → 9.18886, are → 4.54559, u → 0.624725, v → 0.421628, s → 0.599365}, 3.95487},
{{h → 20.1188, ae → 19.3497, de → 21.6862, ap → 21.0276, dp → 19.2327, ah → 22.6542,
dhe → 19.7974, are → 24.3636, u → 0.611502, v → 0.698119, s → 0.686863}, 2.0997},
{{h → 13.3886, ae → 16.7688, de → 17.4792, ap → 15.189, dp → 16.1368, ah → 18.5003,
dhe → 16.9004, are → 19.6302, u → 0.737535, v → 0.524333, s → 0.478075}, 4.23094},
{{h → 13.2321, ae → 15.0182, de → 11.116, ap → 8.933, dp → 9.34437, ah → 6.15269,
dhe → 11.2678, are → 8.88232, u → -0.0868061, v → 0.356515, s → 0.591026}, 2.63655},
{{h → 16.3925, ae → 18.264, de → 14.1541, ap → 10.6931, dp → 16.684, ah → 12.1785,
dhe → 14.7048, are → 18.0793, u → 0.718553, v → 0.646719, s → 0.588163}, 8.91008},
{{h → 9.19776, ae → 9.17616, de → 10.5453, ap → 7.89499, dp → 9.66856, ah → 12.0461,
dhe → 8.86357, are → 16.7336, u → 0.696051, v → 0.791819, s → 0.667452}, 3.36677},
{{h → 18.2852, ae → 20.1115, de → 15.0227, ap → 16.6507, dp → 13.3427, ah → 10.7932,
dhe → 13.6225, are → 11.0631, u → 0.281345, v → 0.466905, s → 0.569722}, 1.32963},
{{h → 19.2223, ae → 21.3828, de → 15.9362, ap → 17.8103, dp → 16.1697, ah → 14.5613,
dhe → 15.6029, are → 14.9348, u → 0.745731, v → 0.732751, s → 0.744899}, 1.98253},
{{h → 21.8004, ae → 22.9493, de → 20.863, ap → 19.3823, dp → 19.6381, ah → 22.5231,
dhe → 17.2125, are → 15.0056, u → 0.364145, v → 0.558478, s → 0.685207}, 7.66041},
{{h → 6.27026, ae → 1.98476, de → 4.98934, ap → 3.18653, dp → 2.95634, ah → 3.15549,
dhe → 4.19267, are → 6.93529, u → -0.627777, v → 0.670122, s → 0.669166},
5.26157}}

```
ClearAll[GlobalSearch]

<< go41.mx

GlobalSearch[fb10, , , range, .00001, Starts → 30]
```

{{{h → 11.6528, ae → 14.3575, de → 12.9479, ap → 11.0549, dp → 11.0116, ah → 4.87178,
dhe → 10.579, are → 5.55074, u → 0.401099, v → 0.307396, s → 0.361066}, 1.65},
{{h → 20.6945, ae → 15.0119, de → 23.114, ap → 16.6609, dp → 19.2894, ah → 17.389,
dhe → 18.7737, are → 22.2341, u → 0.618117, v → 0.503197, s → 0.509058}, 8.40034},
{{h → 15.8265, ae → 13.0475, de → 14.1831, ap → 13.9459, dp → 10.7583, ah → 8.51478,
dhe → 16.3794, are → 13.3237, u → 0.224145, v → 0.441754, s → 0.673992}, 8.98073},
{{h → 18.7345, ae → 20.0363, de → 17.4236, ap → 16.4402, dp → 16.3697, ah → 12.2374,
dhe → 15.5482, are → 10.9217, u → 0.488675, v → 0.484454, s → 0.598011}, 2.26737},
{{h → 21.4314, ae → 23.7675, de → 18.1853, ap → 18.74, dp → 18.2158, ah → 14.6713,
dhe → 18.4101, are → 14.7179, u → 0.5556, v → 0.602515, s → 0.687016}, 2.78331},
{{h → 7.6304, ae → 12.0402, de → 13.053, ap → 10.8844, dp → 11.8188, ah → 13.4562,
dhe → 14.8602, are → 20.793, u → 0.69375, v → 0.679825, s → 0.594554}, 5.59184},
{{h → 12.7592, ae → 15.7078, de → 11.0747, ap → 13.7236, dp → 9.30507, ah → 5.97489,
dhe → 8.98288, are → 6.97047, u → 0.438399, v → 0.534311, s → 0.398928}, 1.07151},
{{h → 11.9274, ae → 11.4453, de → 18.253, ap → 13.0091, dp → 14.8108, ah → 18.6081,
dhe → 17.391, are → 15.6807, u → 0.504692, v → 0.518333, s → 0.691104}, 6.23166},
{{h → 17.7707, ae → 19.7667, de → 18.8063, ap → 16.6508, dp → 17.5754, ah → 20.4343,
dhe → 17.134, are → 14.4071, u → 0.415215, v → 0.576933, s → 0.726484}, 5.80809},
{{h → 2.14109, ae → 6.2408, de → 5.57047, ap → 2.31004, dp → 4.95387, ah → 6.69938,
dhe → 4.19228, are → 6.76646, u → 0.433178, v → 0.719813, s → 0.653871}, 5.09784},
{{h → 8.62304, ae → 13.4216, de → 5.06585, ap → 9.8029, dp → 4.68795, ah → 1.86099,
dhe → 6.66371, are → 4.75326, u → 0.546628, v → 0.788948, s → 0.840864}, 3.91407},
{{h → 6.13334, ae → 8.2084, de → 9.5862, ap → 7.31806, dp → 6.48908, ah → 11.6274,
dhe → 6.96535, are → 8.87367, u → -0.0981956, v → 0.398376, s → 0.595484}, 3.41668},
{{h → 17.9009, ae → 18.3603, de → 12.1297, ap → 11.1309, dp → 11.4078, ah → 13.2597,
dhe → 8.5104, are → 10.4826, u → 0.114608, v → 0.50984, s → 0.579488}, 4.67506},
{{h → 18.9031, ae → 24.102, de → 17.7784, ap → 26.7319, dp → 14.4588, ah → 12.3041,
dhe → 17.7109, are → 16.7562, u → 0.543954, v → 0.610555, s → 0.485748}, 6.86777},
{{h → 10.9332, ae → 13.0197, de → 14.6192, ap → 12.546, dp → 12.3619, ah → 14.9708,
dhe → 13.4444, are → 9.37185, u → 0.325618, v → 0.568673, s → 0.787725}, 6.02831},

{{h → 15.5876, ae → 18.2501, de → 11.1368, ap → 14.1597, dp → 9.28185, ah → 8.10133,
dhe → 10.5291, are → 9.18727, u → 0.183461, v → 0.391397, s → 0.566357}, 1.71821},
{{h → 13.539, ae → 16.5984, de → 19.473, ap → 17.5039, dp → 16.3884, ah → 17.4817,
dhe → 17.3934, are → 17.2486, u → 0.743382, v → 0.574126, s → 0.477722}, 5.11093},
{{h → 9.15474, ae → 9.18646, de → 8.15345, ap → 6.24238, dp → 7.57848, ah → 5.53476,
dhe → 3.26898, are → 2.46244, u → 0.691746, v → 0.394767, s → 0.587109}, 3.96818},
{{h → 20.0146, ae → 21.5508, de → 18.9173, ap → 18.1325, dp → 18.1199, ah → 14.5945,
dhe → 16.5244, are → 13.9431, u → 0.565818, v → 0.514699, s → 0.531343}, 0.935053},
{{h → 17.9509, ae → 17.6279, de → 13.9924, ap → 13.4832, dp → 12.8093, ah → 10.528,
dhe → 10.0278, are → 8.18168, u → 0.385143, v → 0.458289, s → 0.555816}, 2.18418},
{{h → 5.81058, ae → 8.82453, de → 13.0741, ap → 7.16678, dp → 12.141, ah → 10.1523,
dhe → 11.8831, are → 6.68514, u → 0.822126, v → 0.448788, s → 0.48883}, 9.12733},
{{h → 22.0679, ae → 19.0451, de → 18.6026, ap → 15.4437, dp → 17.7824, ah → 14.5716,
dhe → 15.7837, are → 10.6879, u → 0.498047, v → 0.587418, s → 0.757802}, 6.56477},
{{h → 16.6533, ae → 13.7561, de → 11.7044, ap → 10.5135, dp → 9.13546, ah → 9.00638,
dhe → 9.73153, are → 5.94392, u → 0.0650495, v → 0.327172, s → 0.773319}, 2.93347},
{{h → 12.3345, ae → 15.6416, de → 12.9989, ap → 11.8133, dp → 11.6354, ah → 12.4111,
dhe → 11.2814, are → 8.85117, u → 0.191218, v → 0.574875, s → 0.719083}, 4.35322},
{{h → 22.0914, ae → 19.737, de → 27.1979, ap → 22.7035, dp → 23.1306, ah → 27.8189,
dhe → 23.6758, are → 25.3662, u → 0.466973, v → 0.513034, s → 0.58022}, 4.37363},
{{h → 12.3838, ae → 15.2597, de → 10.6815, ap → 11.3991, dp → 8.02072, ah → 5.00902,
dhe → 9.50192, are → 6.50916, u → -0.0145812, v → 0.270925, s → 0.530156}, 0.815172},
{{h → 18.8087, ae → 21.6827, de → 20.5839, ap → 17.9392, dp → 20.0208, ah → 21.8763,
dhe → 19.4702, are → 15.4868, u → 0.535701, v → 0.639793, s → 0.767256}, 8.05401},
{{h → 26.9141, ae → 26.7146, de → 19.9709, ap → 23.1989, dp → 18.4729, ah → 19.6779,
dhe → 15.262, are → 17.12, u → 0.348645, v → 0.475669, s → 0.479671}, 5.14541},
{{h → 19.8104, ae → 20.9011, de → 17.9745, ap → 18.9662, dp → 16.9686, ah → 16.1834,
dhe → 15.4233, are → 12.5074, u → 0.557944, v → 0.716845, s → 0.76017}, 6.71891},
{{h → 16.2647, ae → 16.8941, de → 17.8671, ap → 17.6961, dp → 15.2114, ah → 19.7315,
dhe → 15.9751, are → 24.0049, u → 0.424588, v → 0.578051, s → 0.515689},
3.9092}}

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ClearAll[GlobalSearch]

<< go41.mx

GlobalSearch[fb11, , , range, .00001, Starts → 30]
```

{{{h → 8.55197, ae → 12.7452, de → 8.90645, ap → 7.21776, dp → 6.75949, ah → 11.4079,
dhe → 5.27565, are → 7.6895, u → -0.312305, v → 0.377016, s → 0.53394}, 3.53839},
{{h → 7.02777, ae → 6.33941, de → 11.9561, ap → 7.47317, dp → 9.03628, ah → 13.1474,
dhe → 8.26241, are → 15.3542, u → 0.549633, v → 0.572719, s → 0.451085}, 1.74149},
{{h → 6.67854, ae → 12.0482, de → 6.98797, ap → 8.18691, dp → 6.09097, ah → 8.86433,
dhe → 6.00981, are → 5.16705, u → 0.246792, v → 0.709592, s → 0.861413}, 3.25501},
{{h → 15.0424, ae → 20.0875, de → 20.0227, ap → 14.8002, dp → 20.7696, ah → 21.6609,
dhe → 20.2208, are → 28.3014, u → 0.641645, v → 0.571864, s → 0.438858}, 4.00068},
{{h → 13.2997, ae → 18.7581, de → 13.4441, ap → 11.7274, dp → 14.227, ah → 6.75911,
dhe → 16.3232, are → 9.66157, u → 0.512705, v → 0.52712, s → 0.663631}, 6.04626},
{{h → 12.4735, ae → 10.0969, de → 13.647, ap → 16.0029, dp → 10.2653, ah → 13.3784,
dhe → 11.2718, are → 13.6809, u → 0.46799, v → 0.704518, s → 0.711127}, 3.70024},
{{h → 9.66294, ae → 9.45406, de → 9.70489, ap → 4.5125, dp → 7.75743, ah → 9.46413,
dhe → 7.5793, are → 4.76798, u → -0.303028, v → 0.467546, s → 0.821276}, 4.33038},
{{h → 5.79853, ae → 4.37928, de → 4.4912, ap → 5.07392, dp → 3.27458, ah → 7.12837,
dhe → 2.7313, are → 10.7568, u → 0.635058, v → 0.849166, s → 0.712147}, 5.40343},
{{h → 14.2413, ae → 10.7381, de → 14.8886, ap → 13.3751, dp → 12.0301, ah → 18.2661,
dhe → 10.422, are → 15.4369, u → 0.588658, v → 0.679893, s → 0.700134}, 5.17107},
{{h → 15.5823, ae → 20.4114, de → 16.6743, ap → 17.2585, dp → 15.3022, ah → 9.36016,