Heritability Estimates of Density Characteristics in Juvenile Pinus Radiata Wood

By J. W. P. Nicholls*), J. D. Morris**) and L. A. Pederick**)

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Summary

Densitometric determinations were carried out on wood specimens from replicated progeny trials established at two locations in Victoria. Seventeen families were sampled at each site, the families being chosen to provide five male groups, each containing families derived from a common pollen parent but differing mother trees. This design enables evaluation of both additive and non-additive genetic variance.

Estimates of heritability and phenotypic and genetic correlations were obtained for five characteristics, viz., ring width, maximum, minimum and average density and late wood ratio for each site and by combining data from both locations.

Expected gains of 6.4 per cent in core wood density per generation are possible in a practical breeding strategy involving selection of the highest density tree out of 5.

Key words: Heritability, Wood density, *Pinus radiata.*

Zusammenfassung

An Holzproben aus *Pinus radiata*-Nachkommenschaftsversuchen, die an zwei Standorten in Victoria angelegt worden waren, wurden Dichte-Bestimmungen durchgeführt. An beiden Orten wurden je 17 Familien so ausgewählt, daß jeweils 5 Gruppen mit denselben Vätern entstanden. Jede der Gruppen hatte gemeinsame Väter, aber unterschiedliche Mutterbäume. Auf diese Weise konnte sowohl die additive als auch die nicht additive genetische Varianz ermittelt werden.

Die Schätzung der Heritabilität sowie phänotypischer und genetischer Korrelationen erfolgte für 5 Merkmale, wie Jahrringbreite, maximale, minimale und mittlere Dichte sowie Spätholzanteil, getrennt und kombiniert für die beiden Standorte.

Bezüglich der Kernholzdichte ist ein zu erwartender Gewinn von 6,4% je Generation durch praktische Züchtungsstrategie möglich, bei der von jeweils 5 Bäumen derjenige mit der höchsten Dichte selektiert wird.

Introduction

Juvenile (core) wood of *Pinus radiata* is typically associated with wider growth rings, shorter tracheids, lower density and larger angles of micellar orientation and spiral grain compared to mature wood. In addition, wind and other external agencies may produce large disturbances in the orientation of the young stem so that the incidence of compression wood is likely to be maximal in the wood formed near the pith. These are all undesirable characteristics for most wood usages.

A reduction of the rotation age or an increase in growth rate incurs the risk of increasing the proportion of core wood in the raw material. It may be possible to offset this tendency by suitable silvicultural practices, and to ameliorate the undesirable characteristics by appropriate selection and breeding. However, very little basic information is available with which to estimate possible rates of progress.

Wood density is considered to be the most important of the features listed above. An estimate of narrow sense heritability of 0,7 was recently obtained for this characteristic based on young wood (Morris, 1974). This indicates excellent possibilities for improvement by selection of the density of the core wood.

The X-radiographic method of Polge (1965) is a widely used technique for the determination of wood density which enables continuous records of density from pith to bark to be obtained. The resulting cyclic density profiles are described in terms of maximum, minimum and average density, and late wood ratio (Nicholls and Brown, 1971), which are interrelated such that:
average density = late wood ratio × (max. density - min. density) + min. density. Thus, a particular value of average density may be the resultant of a variety of combinations of the component parameters and the manipulation of average density may proceed by the appropriate modification of one or more of these. As maximum and minimum density are controlled by different physiological processes (Nicholls and Wright, 1976) it should also be possible to reduce density variations within a growth ring. The question of environmental influence on these parameters is unresolved (Nicholls and Wright, 1976) and more information is needed. The present investigation was undertaken to satisfy this need, and is concerned with determining the relative contribution of genetic and environmental factors to the variation of these parameters in juvenile *Pinus radiata* wood. Phenotypic and genetic correlations between these characteristics are also reported.

Material

The trees for examination originated in two controlled-pollination progeny trials in Victoria, one established in 1967 in the Warrenbayne plantation (36°40'S, 145°50'E), and the other in 1968 at Rennick (37°50'S, 141°00'E). The trees at both locations were grown from the same seedlots sown in a nursery at the same time (October 1966). The parent trees in each case were all plus trees from a number of plantations selected on the basis of vigour, crown and stem form, tracheid length and absence of excessive spiral grain.

The Warrenbayne trial was established on a more or less flat site on a plateau at an elevation of 600 m. The soil is a light textured podsolic formed on granitic parent material. A small outcrop of parent rock exists in one area of the trial, but for the most part the site appears to be uniform. The site had been cleared for many years and originally carried a forest of *Eucalyptus radiata* and *E. globulus* subsp. *bicostata.*

The trial at Rennick is on the south slope of an east-west ridge at an elevation of approximately 70 m. The slope varies from 0—5 degrees and the soil is a deep sandy podsolic. The site carried a low forest of *E. baxteri* which was cleared prior to planting.

The progeny trials included seven replications of 37 families common to the two locations planted in a randomized block design. From these, 17 families in five replications at each site were sampled, the families being chosen to provide five "male groups", each containing families derived from a common pollen parent but differing mother

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*) Division of Soils, CSIRO, South Melbourne.
**) Forests Commission, Victoria.

trees (*see table 1*). Each replication contained a plot of ten trees of each family. From each plot four trees were selected at random but excluding any trees which were obviously suppressed or showed severe lean, sweep or crook. Thus both full-sib (between trees within a family) and half-sib (between families within a male group) relationships were incorporated in the material measured, enabling evaluation of both additive and non-additive genetic variance. The sampling design is based on the North Carolina Design 1 described by COMSTOCK and ROBINSON (1952).

Table 1. — Designation of full-sib families from which wood specimes were collected.

MALE GROUP	MALE PARENT	FAMILY	FEMALE PARENT
1	30055	1	12112
		2	10956
		3	30016
		4	30041
		5	30056
		6	80037
2	30054	7	12038
		8	30026
		9	30040
		10	30053
3	30007	11	10957
		12	80055
		13	30028
4	30004	14	30037
		15	80007
5	70057	16	30048
		17	30002

Note: The male and female parent numbers are those allotted to trees in the Australian Plus Tree Register maintained on behalf of the Forest Genetics Research Working Group by the Division of Forest Research, CSIRO.

Experimental Procedure

Two 5 mm borings extending from bark to bark and including the pith were removed from each tree, near the centre of an internode at a nominal height of 0.75 m, the height being adjusted so that all cores would show the same number of complete growth rings. For each tree, one core was taken in a north-south direction and the other at right angles to it some 20 mm vertically along the stem. There were thus 680 cores from each locality. The cores were labelled and kept immersed in water pending examination at the laboratory.

Each diametrical core was divided at the pith and the shortest of the two radial pieces retained for examination as being most likely to exhibit the least amount of compression wood. The cores were first air-dried and then conditioned over a saturated solution of sodium dichromate to an equilibrium moisture content of approximately 10 per cent (POLGE and NICHOLLS, 1972).

Using the technique of POLGE (1965), contact radiograms of the cores were obtained and scanned by means of a double beam microdensitometer. Individual growth rings were identified and marked on the resulting densitometric traces for each tree.

From each tree, the third and fourth growth rings from the pith were chosen for examination, that is, the rings formed in 1970/71 and 1971/72 at Warrenbayne, and in 1971/72 and 1972/73 at Rennick. For these, the ring width and the maximum and minimum density were read directly from the curves. The late wood ratio, which is the proportion of late wood in a growth ring, assuming a linear change from early wood to late wood and an early wood/late wood boundary at the mid-density point, was also determined in each case and used to calculate values of average density (NICHOLLS and BROWN, 1971).

The results of the various determinations were tabulated separately for each growth ring and each locality and subjected to statistical analyses to separate components of variance and covariance. Means were calculated for each family and group at each location for the five characteristics and are listed in *tables 2* and *3*.

Table 2. — Means with standard deviations for ring width, late wood ratio, maximum density, minimum density and average density for 17 families of *P. radiata* growing at Rennick.

MALE GROUP NO.	FAMILY NO.	RING WIDTH (mm)		LATE WOOD RATIO (%)		MAX. DENSITY (kg m^{-3})		MIN. DENSITY (kg m^{-3})		AVER. DENSITY (kg m^{-3})	
		RING 3	RING 4	RING 3	RING 4	RING 3	RING 4	RING 3	RING 4	RING 3	RING 4
1	1	12.3 (3.3)	13.2 (3.1)	27 (3)	35 (5)	610 (45)	625 (44)	288 (27)	284 (21)	374 (21)	402 (25)
	2	13.3 (2.4)	13.4 (2.1)	31 (5)	37 (5)	621 (42)	635 (41)	296 (23)	297 (22)	395 (24)	419 (22)
	3	12.0 (2.5)	12.7 (2.3)	33 (6)	40 (6)	622 (57)	602 (51)	295 (28)	280 (25)	401 (35)	409 (33)
	4	11.9 (3.4)	11.7 (2.9)	31 (5)	41 (7)	619 (63)	637 (58)	303 (31)	289 (21)	399 (31)	431 (35)
	5	11.6 (2.5)	12.2 (2.8)	30 (4)	39 (6)	651 (49)	641 (50)	301 (20)	292 (18)	406 (25)	429 (32)
	6	10.4 (2.6)	11.8 (2.5)	31 (6)	35 (5)	636 (48)	689 (39)	321 (25)	307 (22)	418 (32)	442 (32)
	Mean	11.9 (2.9)	12.5 (2.7)	30 (5)	38 (6)	627 (52)	638 (54)	301 (28)	291 (23)	399 (31)	422 (33)
2	7	13.5 (2.9)	13.2 (2.3)	31 (5)	40 (6)	539 (53)	578 (50)	275 (16)	269 (23)	357 (22)	393 (33)
	8	14.2 (3.0)	14.7 (1.3)	32 (5)	39 (6)	539 (48)	545 (40)	293 (22)	280 (21)	370 (27)	383 (25)
	9	13.5 (2.4)	13.6 (2.4)	32 (5)	40 (7)	550 (74)	576 (49)	270 (19)	266 (26)	359 (25)	390 (29)
	10	13.3 (2.3)	12.9 (2.4)	33 (5)	43 (6)	544 (46)	551 (48)	263 (20)	254 (19)	356 (26)	382 (29)
	Mean	13.6 (2.7)	13.6 (2.2)	32 (5)	41 (6)	543 (56)	562 (49)	275 (22)	267 (24)	360 (25)	387 (29)
3	11	12.7 (2.8)	13.7 (2.0)	34 (9)	35 (6)	605 (49)	622 (55)	288 (27)	291 (35)	395 (39)	405 (40)
	12	13.2 (3.0)	14.7 (2.8)	33 (9)	33 (4)	593 (56)	634 (48)	277 (29)	277 (37)	379 (45)	393 (37)
	13	12.1 (2.7)	12.9 (2.5)	32 (5)	36 (5)	591 (45)	637 (43)	289 (21)	284 (19)	385 (25)	412 (21)
	Mean	12.7 (2.9)	13.8 (2.5)	33 (8)	35 (5)	597 (50)	631 (49)	284 (27)	284 (31)	386 (38)	403 (34)
4	14	12.1 (1.9)	12.4 (2.2)	32 (6)	37 (6)	578 (29)	598 (31)	277 (28)	276 (19)	373 (30)	393 (22)
	15	13.4 (2.5)	13.1 (2.6)	32 (5)	37 (6)	596 (49)	616 (50)	277 (33)	280 (34)	378 (33)	405 (36)
	Mean	12.8 (2.3)	12.7 (2.4)	32 (5)	37 (5)	587 (41)	607 (42)	277 (31)	278 (28)	375 (32)	399 (30)
5	16	13.2 (2.1)	13.3 (2.5)	29 (4)	34 (5)	635 (39)	652 (42)	298 (25)	306 (17)	396 (25)	424 (27)
	17	13.4 (1.7)	14.0 (1.6)	29 (4)	34 (5)	612 (43)	655 (39)	298 (18)	300 (21)	389 (23)	421 (31)
	Mean	13.3 (1.9)	13.6 (2.1)	29 (4)	34 (5)	623 (43)	653 (41)	298 (21)	303 (19)	392 (24)	422 (29)
Grand Mean		12.7 (2.8)	13.1 (2.5)	31 (6)	37 (6)	597 (60)	617 (59)	289 (28)	284 (28)	384 (34)	408 (35)

Table 3. — Means with standard deviations for ring width, late wood ratio, maximum density, minimum density and average density for 17 families of *P. radiata* growing at Warrenbayne.

MALE GROUP NO.	FAMILY NO.	RING WIDTH (mm)		LATE WOOD RATIO (%)		MAX. DENSITY (kg m^{-3})		MIN. DENSITY (kg m^{-3})		AVER. DENSITY (kg m^{-3})	
		RING 3	RING 4	RING 3	RING 4	RING 3	RING 4	RING 3	RING 4	RING 3	RING 4
1	1	14.1 (4.0)	15.0 (3.4)	36 (7)	30 (4)	579 (46)	603 (55)	268 (28)	287 (26)	381 (34)	380 (25)
	2	14.2 (2.4)	14.7 (3.0)	32 (5)	34 (6)	610 (58)	545 (61)	283 (22)	291 (17)	387 (22)	377 (28)
	3	13.5 (1.8)	13.7 (2.0)	32 (6)	33 (9)	633 (45)	569 (46)	288 (33)	302 (30)	397 (32)	386 (36)
	4	11.5 (3.5)	13.2 (3.1)	41 (7)	29 (6)	571 (44)	636 (50)	293 (28)	298 (20)	406 (30)	397 (22)
	5	12.9 (3.7)	14.4 (2.6)	40 (6)	31 (4)	584 (53)	622 (62)	283 (30)	296 (30)	401 (32)	397 (33)
	6	15.1 (1.9)	14.4 (2.4)	31 (3)	28 (4)	610 (44)	575 (59)	277 (23)	294 (21)	380 (25)	371 (25)
	Mean	13.6 (3.2)	14.2 (2.8)	35 (7)	31 (6)	598 (53)	592 (64)	282 (29)	295 (25)	392 (31)	385 (30)
2	7	11.6 (4.6)	14.0 (3.4)	44 (6)	37 (12)	487 (47)	513 (98)	273 (28)	257 (49)	365 (29)	346 (62)
	8	12.3 (3.0)	13.8 (3.0)	43 (6)	34 (4)	496 (55)	522 (59)	271 (21)	278 (20)	367 (25)	360 (27)
	9	13.4 (3.6)	14.3 (3.2)	41 (6)	34 (7)	516 (53)	552 (59)	263 (26)	274 (25)	366 (29)	366 (25)
	10	11.5 (2.7)	14.2 (2.2)	42 (7)	34 (6)	498 (43)	518 (47)	256 (25)	260 (19)	356 (26)	348 (17)
	Mean	12.2 (3.6)	14.1 (3.0)	42 (6)	35 (8)	499 (50)	526 (70)	266 (26)	267 (32)	363 (27)	355 (37)
3	11	13.5 (3.8)	14.3 (2.4)	39 (5)	32 (5)	548 (42)	598 (36)	274 (23)	283 (23)	382 (27)	384 (26)
	12	12.5 (3.6)	15.0 (2.9)	38 (5)	29 (4)	552 (44)	601 (41)	259 (20)	259 (19)	370 (27)	358 (20)
	13	14.2 (2.9)	15.1 (2.2)	33 (3)	32 (7)	617 (45)	569 (50)	268 (26)	295 (22)	381 (31)	382 (30)
	Mean	13.4 (3.5)	14.8 (2.5)	37 (5)	31 (5)	572 (54)	589 (45)	267 (24)	279 (26)	378 (29)	375 (28)
4	14	11.5 (3.6)	14.8 (2.7)	44 (6)	34 (5)	507 (45)	537 (38)	264 (30)	265 (21)	370 (41)	357 (22)
	15	11.7 (4.2)	13.3 (2.6)	42 (8)	34 (5)	511 (56)	559 (39)	280 (34)	275 (28)	376 (41)	370 (24)
	Mean	11.6 (3.9)	14.1 (2.7)	43 (7)	34 (5)	509 (51)	548 (40)	272 (33)	270 (25)	373 (41)	364 (24)
5	16	10.9 (3.7)	12.9 (2.4)	40 (7)	32 (3)	593 (53)	639 (31)	284 (31)	294 (20)	405 (32)	403 (22)
	17	12.2 (3.0)	13.4 (2.6)	38 (5)	31 (4)	579 (45)	624 (45)	277 (20)	283 (22)	389 (24)	388 (22)
	Mean	11.6 (3.4)	13.2 (2.5)	39 (6)	31 (4)	586 (49)	632 (39)	280 (26)	288 (21)	397 (30)	396 (23)
Grand Mean		12.7 (3.6)	14.1 (2.8)	39 (7)	32 (6)	558 (67)	576 (67)	274 (28)	282 (29)	381 (33)	375 (33)

Analytical procedures

The data for each characteristic were subjected to analyses of variance of the form set out in *table 4*. Analyses of covariance of similar form were also undertaken in which the expected mean cross products resembled the expected mean squares but provided estimates of covariance. The analyses are based on the assumptions of a random effects model, additivity, homogeneous variance, zero correlations and normally distributed variables.

In order to estimate genetic parameters from the components of variance and co-variance a set of assumptions is made that:

1. the parent trees are random members of a non-inbred population
2. there is regular diploid Mendelian inheritance
3. the parent population is in linkage equilibrium
4. there is no epistasis
5. there are no maternal effects

The first of these is not entirely true as the parent trees were selected on the basis of vigour and form and therefore the variance estimates could be biased, especially for ring width, or for those characteristics which are strongly correlated with ring width. However, previous work has shown that ring width is poorly correlated with density in *P. radiata* and the heritability for ring width is small (Nicholls *et al.*, 1964), so that bias is not expected to be large. The validity of the remaining assumptions is uncertain but they have been accepted as reasonable in similar studies (Stonecypher *et al.*, 1973).

The late wood data were subjected to a reciprocal transform to improve the homogeneity of the variances for this characteristic.

The estimates of variance components were obtained by matching mean squares to their expectations as set out in *table 5* and solving the resulting series of equations. Where in a few cases the calculations yielded small negative components, these were set to zero to provide better estimates.

For quantitative characteristics as in the present case

$$V_P = V_G + V_E$$
$$V_G = V_A + V_{NA}$$
$$V_{NA} = V_D + V_I$$

where V_P = total phenotypic variance
V_G = variance due to genetic factors
V_E = variance due to environmental factors
V_A = additive genetic variance
V_{NA} = non-additive genetic variance
V_D = genetic variance due to dominance
V_I = genetic variance due to epistasis, assumed negligible

Returning to *table 4* for the meaning of symbols

$$\hat{\sigma}^2_m = (1/4)\, V_A$$

and $\hat{\sigma}^2_f = (1/4)\, V_A + (1/4)\, V_D$, neglecting V_I

If $\hat{\sigma}^2_f$ was found to be less than $\hat{\sigma}^2_m$, V_D was concluded to be negligible, and V_A was estimated as four times the mean of $\hat{\sigma}^2_m$ and $\hat{\sigma}^2_f$. *(Table 5).*

V_P within locations is estimated as:

$$V_P = \hat{\sigma}^2_{rl} + \hat{\sigma}^2_m + \hat{\sigma}^2_f + \hat{\sigma}^2_{mr} + \hat{\sigma}^2_{fr} + \hat{\sigma}^2_t + \hat{\sigma}^2_w.$$

V_P also included $\hat{\sigma}^2_{ml}$ and $\hat{\sigma}^2_{fl}$ in the combined location analysis. Narrow sense heritability, appropriate to selection using one sample per tree, and sexual propagation, is given as:

$$h^2_{NS} = \frac{V_A}{V_P}$$

Estimates of heritability are set out in *table 6*.

Standard errors for the estimates of heritability were calculated using the formula below which is based on the first term of that given by Robertson (1959) for the sample variance of the intraclass correlation.

$$\hat{\sigma}^2_s = \frac{2\,(1-s)^2}{r\,(m-1)\,f^2 n^2}\,[1-2s + n\,(f+1)\,s]^2$$

where $\hat{\sigma}^2_s$ is the variance of the intraclass correlation coefficient, s
m is the number of male groups (= 5, in this study)
n is the number of offspring per family (= 4)

r is the number of replications (= 5)
f is the harmonic mean of females per male group (= 3.24)
$h^2 = 2s$ for full sib families

The standard errors ($2\hat{\sigma}_s$) are listed in *table 6*.

The expected gains for each characteristic were calculated for each location on the basis that selection is applied at the rate of one standard deviation above the population means using the formula in Falconer (1961) (p. 193) and these are also listed in *table 6*.

The phenotypic and genetic correlation coefficients set out in *table 7* were calculated as the appropriate covariances to the product of the two standard deviations (Falconer, 1961). The genetic correlations were based on the means of male groups and females in male groups components of variance and covariance respectively. The standard error of the genetic correlations was calculated using the formula provided by Tallis (1961) and used to indicate the significance of the correlations. Estimates of variances and covariances required by this formula were the means of those for male groups and females in male groups weighted by their degrees of freedom. The significance of the phenotypic correlation coefficients — based on 678 degrees of freedom is also shown in *table 7*.

Results and Discussion

Growth rate is the most likely characteristic to reveal non-uniformity within a site, but in only one case, viz., the width of ring 3 at Warrenbayne, was there a significant difference between replications. For this ring, replication 3 at Warrenbayne shows better growth than the

Table 4. — Format of analysis used for the estimation of variance components.

SOURCE OF VARIATION	DEGREES OF FREEDOM	EXPECTED MEAN SQUARES
Locations	$\ell-1$	$\sigma^2_w+n\sigma^2_t+nt\sigma^2_{fr}+ntf^1\sigma^2_{mr}+nt\Sigma f_i\sigma^2_{r\ell}$ $+ntr\sigma^2_{f\ell}+ntrf^1\sigma^2_{m\ell}+ntr\Sigma f_i\sigma^2_{\ell}$
Replications in locations	$\ell(r-1)$	$\sigma^2_w+n\sigma^2_t+nt\sigma^2_{fr}+ntf^1\sigma^2_{mr}+nt\Sigma f_i\sigma^2_{r\ell}$
Male groups	$m-1$	$\sigma^2_w+n\sigma^2_t+nt\sigma^2_{fr}+ntf^1\sigma^2_{mr}+ntr\sigma^2_{f\ell}+$ $ntrf^1\sigma^2_{m\ell}+ntr\ell\sigma^2_f+ntr\ell f^1\sigma^2_m$
Females in male groups	$\sum_{i=1}^{m}(f_i-1)$	$\sigma^2_w+n\sigma^2_t+nt\sigma^2_{fr}+ntr\sigma^2_{f\ell}+ntr\ell\sigma^2_f$
Male groups x locations	$(\ell-1)(m-1)$	$\sigma^2_w+n\sigma^2_t+nt\sigma^2_{fr}+ntf^1\sigma^2_{mr}+ntr\sigma^2_{f\ell}+$ $ntrf^1\sigma^2_{m\ell}$
Females in male groups x locations	$(\ell-1)\sum_{i=1}^{m}(f_i-1)$	$\sigma^2_w+n\sigma^2_t+nt\sigma^2_{fr}+ntr\sigma^2_{f\ell}$
Male groups x replications within locations	$\ell(r-1)(m-1)$	$\sigma^2_w+n\sigma^2_t+nt\sigma^2_{fr}+ntf^1\sigma^2_{mr}$
Females in male groups x replications within locations	$\ell(r-1)\sum_{i=1}^{m}(f_i-1)$	$\sigma^2_w+n\sigma^2_t+nt\sigma^2_{fr}$
Trees in plots	$\ell r\sum_{i=1}^{m}f_i(t-1)$	$\sigma^2_w+n\sigma^2_t$
Within trees	$\ell rt\sum_{i=1}^{m}f_i(n-1)$	σ^2_w
Total	$\ell rtn\sum_{i=1}^{m}f_i-1$	

l = number of locations = 2
r = number of replications = 5
m = number of male groups = 5
f_i = number of females crossed with i^{th} male $f_1 = 6$, $f_2 = 4$, $f_3 = 3$, $f_4 = 2$, $f_5 = 2$. $\Sigma f_i = 17$
t = number of trees per plot = 4

$$f^1 = \text{mean number of families per male group} = \frac{1}{m-1}\left(\sum_{i=1}^{m} f_i - \frac{\sum_{i=1}^{m} f_i^2}{\sum_{i=1}^{m} f_i}\right) = 3.24$$

σ^2_w = variance due to differences within trees
σ^2_t = variance due to differences between trees within plots
σ^2_f = variance due to differences between families of females crossed to the same male (between families within male groups)
σ^2_m = variance due to differences between progenies of different males (male group effects)
σ^2_l = variance due to differences between locations
σ^2_{fl} = variance due to interactions among families and locations
σ^2_{ml} = variance due to interactions among male groups and location effects
σ^2_{rl} = variance due to differences between replications within locations
σ^2_{fr} = variance due to interactions among families and replications
σ^2_{mr} = variance due to interactions among progenies of different males (male groups) and replications
1 means l

Table 5. — Expected mean squares used in the analysis of variance.

SOURCE OF VARIATION	D.F.	EXPECTED MEAN SQUARES
Locations	1	$\sigma_w^2+2\sigma_t^2+8\sigma_{fr}^2+25.88\sigma_{mr}^2+136\sigma_{r\ell}^2+40\sigma_{f\ell}^2+129.4\sigma_{m\ell}^2+680\sigma_\ell^2$
Reps. in locations	8	$\sigma_w^2+2\sigma_t^2+8\sigma_{fr}^2+25.88\sigma_{mr}^2+136\sigma_{r\ell}^2$
Male groups	4	$\sigma_w^2+2\sigma_t^2+8\sigma_{fr}^2+25.88\sigma_{mr}^2+40\sigma_{f\ell}^2+129.4\sigma_{m\ell}^2+80\sigma_f^2+258.8\sigma_m^2$
Females in male groups	12	$\sigma_w^2+2\sigma_t^2+8\sigma_{fr}^2+40\sigma_{f\ell}^2+80\sigma_f^2$
Locations x male groups	4	$\sigma_w^2+2\sigma_t^2+8\sigma_{fr}^2+25.88\sigma_{mr}^2+40\sigma_{f\ell}^2+129.4\sigma_{m\ell}^2$
Locations x females in male groups	12	$\sigma_w^2+2\sigma_t^2+8\sigma_{fr}^2+40\sigma_{f\ell}^2$
Replications x male groups	32	$\sigma_w^2+2\sigma_t^2+8\sigma_{fr}^2+25.88\sigma_{mr}^2$
Replications x females in male groups	96	$\sigma_w^2+2\sigma_t^2+8\sigma_{fr}^2$
Trees in plots	510	$\sigma_w^2+2\sigma_t^2$
Within trees	680	σ_w^2
Total	1359	

For explanation of terms, see *Table 4*.

Table 6. — Variance components, heritabilities with standard errors, and expected gains for selection at one standard deviation from the mean for 5 wood characteristics from 2 growth rings in *P. radiata* trees growing at 2 locations in Victoria.

LOCATION		RING WIDTH		LATE WOOD RATIO		MAX. DENSITY		MIN. DENSITY		AVER. DENSITY	
		RING 3	RING 4	RING 3	RING 4	RING 3	RING 4	RING 3	RING 4	RING 3	RING 4
RENNICK	$\hat\sigma_r^2$	0.0000	0.0000	0.0042	0.0000	157.1	0.0	48.31	15.64	11.83	0.0
	$\hat\sigma_m^2$	0.4200	0.2383	0.0105	0.0288	1382.4	1266.8	127.99	150.24	264.46	240.11
	$\hat\sigma_f^2$	0.0000	0.1840	0.0088	0.0125	0.8	323.6	71.59	60.86	69.52	77.44
	$\hat\sigma_{mr}^2$	0.1895	0.3164	0.0000	0.0006	0.0	0.0	18.36	25.86	7.18	20.94
	$\hat\sigma_{fr}^2$	1.6514	0.6954	0.0095	0.0318	278.6	148.5	49.51	0.00	48.91	33.64
	$\hat\sigma_t^2$	4.6913	4.1233	0.0857	0.0670	1124.3	1260.1	298.26	216.94	445.17	560.25
	$\hat\sigma_w^2$	0.8805	0.9839	0.1620	0.0709	1134.6	806.9	227.33	357.75	374.31	348.82
	V_A	0.8399	0.8445	0.0387	0.0827	2766.5	3180.9	399.16	422.20	667.95	635.09
	V_{NA}	0.0000	0.0000	0.0000	0.0000	0.0	0.0	0.00	0.00	0.00	0.00
	V_P	7.8327	6.5413	0.2806	0.2117	4077.9	3806.0	841.34	827.28	1221.38	1281.19
	h^2	0.11	0.13	0.14	0.39	0.68	0.84	0.47	0.51	0.55	0.50
	S.E.	0.08	0.09	0.09	0.15	0.20	0.21	0.17	0.18	0.18	0.17
	Gain*	0.3	0.3	1	2	41	49	13	14	19	17
WARRENBAYNE	$\hat\sigma_r^2$	1.0981	0.0378	0.0164	0.0066	118.3	121.1	0.00	29.97	0.00	0.14
	$\hat\sigma_m^2$	0.6186	0.1454	0.0451	0.0205	2188.2	1225.0	46.44	128.95	180.43	190.62
	$\hat\sigma_f^2$	0.2516	0.0000	0.0554	0.0192	410.4	501.7	19.61	59.36	11.89	73.17
	$\hat\sigma_{mr}^2$	0.7655	0.4355	0.0008	0.0001	14.2	0.0	27.56	2.41	0.00	0.00
	$\hat\sigma_{fr}^2$	1.8733	0.7596	0.0115	0.0276	180.7	193.2	124.81	94.11	158.54	83.51
	$\hat\sigma_t^2$	7.0932	5.0356	0.0500	0.1126	1262.5	1435.6	330.95	233.66	473.45	396.50
	$\hat\sigma_w^2$	1.5446	1.3521	0.0780	0.1090	861.3	852.8	280.95	200.25	346.07	204.00
	V_A	1.7404	0.2847	0.1804	0.0795	5197.2	3453.4	132.11	376.62	384.63	527.58
	V_{NA}	0.0000	0.0000	0.0413	0.0000	0.0	0.0	0.00	0.00	0.00	0.00
	V_P	13.2448	7.7629	0.2572	0.2956	5035.7	4329.5	830.33	748.71	1170.38	947.94
	h^2	0.13	0.04	0.70	0.27	1.03	0.80	0.16	0.50	0.33	0.56
	S.E.	0.09	0.06	0.20	0.13	0.21	0.20	0.00	0.17	0.14	0.18
	Gain*	0.5	0.1	5	2	69	50	5	13	11	17
COMBINED	V_A	0.0000	0.0000	0.410	0.0438	3429.8	2742.6	239.88	328.86	509.47	526.00
	V_{NA}	0.0000	0.2148	0.0000	0.0000	0.0	0.0	0.00	0.00	0.00	0.00
	V_P	11.0553	7.0492	0.2795	0.2533	4558.3	4142.7	829.84	776.91	1193.96	1126.07
	h^2	0.00	0.00	0.15	0.17	0.75	0.66	0.29	0.42	0.43	0.47
	S.E.	0.05	0.05	0.09	0.10	0.20	0.19	0.13	0.16	0.16	0.17
	Gain*	0.00	0.00	1	1	50	43	8	11	14	17

* Ring width (mm), late wood ratio (%) and densities (kg m−3).

Table 7.— Genetic correlations (below diagonal line) and phenotypic correlations (above diagonal line) for 5 wood characteristics measured on two growth rings in trees from 17 families of *P. radiata* growing at Rennick and Warrenbayne in Victoria

CHARACTERISTIC	RING NO.	RING WIDTH		LATE WOOD RATIO +		MAX. DENSITY		MIN. DENSITY		AVER. DENSITY	
		RENN.	WARR.	RENN.	WARR.	RENN.	WARR.	RENN.	WARR.	RENN.	WARR.
Ring Width	3			0.23**	0.27**	-0.08*	0.01^{ns}	-0.53**	-0.43**	-0.44**	-0.39**
	4			0.41**	0.04^{ns}	-0.25**	-0.24**	-0.21**	-0.16**	-0.50**	-0.28**
Late Wood Ratio	3	-0.61^{ns}	1.12^{ns}			0.28**	0.56**	-0.06^{ns}	0.04^{ns}	-0.36**	-0.15**
	4	0.21^{ns}	-0.03^{ns}			0.31**	0.41**	0.01*	0.12**	-0.32**	-0.15**
Max. Density	3	-1.06^{ns}	0.91^{ns}	0.59^{ns}	0.92**			0.31**	0.31**	0.62**	0.62**
	4	-0.48^{ns}	-0.53^{ns}	0.71*	0.78*			0.49**	0.35**	0.69**	0.67**
Min. Density	3	-0.73^{ns}	0.62^{ns}	0.70^{ns}	0.44^{ns}	0.86**	0.68^{ns}			0.77**	0.75**
	4	-0.24^{ns}	-0.29^{ns}	0.73*	0.66^{ns}	0.89**	0.64^{ns}			0.75**	0.78**
Aver. Density	3	-0.94^{ns}	0.50^{ns}	0.50^{ns}	0.54^{ns}	0.96**	0.82**	0.85**	0.92**		
	4	-0.65^{ns}	-0.56^{ns}	0.44^{ns}	0.67^{ns}	0.92**	0.90**	0.88**	0.87**		

** Significant at 1 % level
* Significant at 5 % level
ns Not significant
+ Late wood ratio data have been subjected to an inverse transform

Table 8. — Means for percentage of variation contributed to total variance of a single core by individual components, and means of the standard errors of the variance components for five wood characteristics determined on two growth rings in *P. radiata* trees growing at two locations in Victoria.

VARIANCE COMPONENT	MEAN PERCENTAGE CONTRIBUTION TO VARIATION WITHIN LOCATIONS						MEAN STANDARD ERROR				
	RING WIDTH	LATE WOOD RATIO	MAXIMUM DENSITY	MINIMUM DENSITY	AVERAGE DENSITY	MEAN	RING WIDTH X 100	LATE WOOD RATIO X 10^3	MAXIMUM DENSITY	MINIMUM DENSITY	AVER. DENSITY
Between replications σ^2_r	2.2	2.2	2.2	2.9	0.2	2.0	31.0	5	75.1	20.5	9.6
Between male groups σ^2_m	3.9	10.5	34.7	14.1	19.0	16.4	32.3	22	954.4	81.4	145.8
Between families σ^2_f	1.2	9.3	7.1	6.5	5.1	5.8	25.7	13	167.5	33.1	41.2
Male groups x replications interaction σ^2_{mr}	4.7	0.2	0.1	2.2	0.6	1.6	45.3	6	66.7	25.2	28.6
Families x replications interaction σ^2_{fr}	13.9	8.1	4.7	8.4	7.2	8.5	55.6	11	132.1	34.1	49.7
Between trees in plots σ^2_t	60.3	29.9	29.7	33.2	40.6	38.7	51.6	12	154.4	37.1	56.7
Within trees σ^2_w	13.8	39.6	32.7	27.2	27.0	27.0	9.1	8	69.9	20.4	24.3

others but in all other respects, the sites are considered to be uniform.

In spite of wide differences in climatic and edaphic factors, both growth rate and densitometric characteristics in this young material are generally similar at the two sites. The mean ring width (12.9 mm) and mean average density (396 kg m^{-3}) at Rennick, *(Table 2)* are 4 per cent less than and 5 per cent greater than the corresponding means at Warrenbayne (13.4 mm, 378 kg m^{-3}), *(Table 3)*, and the standard deviations of the densitometric parameters are comparable at the two locations. Furthermore, at both Rennick and Warrenbayne, the progeny of male group 5 generally have the greatest, and those of male group 2 the least values for all density parameters including uniformity within a growth ring measured by the difference between maximum and minimum density *(Table 2 and 3)*.

The relative importance of genetic and environmental sources of variation for each characteristic may be gauged by the percentage contribution of each variance component to the total phenotypic variance. Means of these percentages are set out in *table 8*. Maximum density shows the strongest genetic control with a large component from the male parent and this is consistent at both sites and for both growth rings. As expected, the variation for ring width is almost entirely from environmental sources, but late wood ratio, minimum density and average density display average genetic control. Late wood ratio exhibits the largest within-tree component of all the characteristics.

The standard errors of components of variance are notoriously quite large. Means of these errors are listed in *table 8*. Those for the between male group components are very large and reflect the limited number of such groups in the study.

The component of variance due to differences among male groups ($\hat{\sigma}^2_m$) exceeds that due to differences among families of females ($\hat{\sigma}^2_f$) in all but one case *(Table 6)*, and it is concluded for such cases that the non-additive genetic variance (V_{NA}) is negligible. Even for the exception, viz. late wood ratio for ring 3 at Warrenbayne, V_{NA} is not large. If the analyses are extended to calculate the variance components for individual male groups and families within groups, it is found, particularly for maximum, minimum and average density, that certain male groups contribute more than the families within them to $\hat{\sigma}^2_m$ and

$\hat{\sigma}^2_f$ respectively. Thus Group 1 usually, Group 3 rarely, and Groups 2,4 and 5 almost always follow this pattern. Therefore, because of the small number of parent trees used in this trial genetic control of wood density appears to be dominated by the influence of the male parent.

For the estimates of heritability listed in *table 6,* there are published values for comparison only in the case of ring width and average density (equivalent to 10 % moisture content or air-dry density). For *P. radiata* NICHOLLS, *et al.* (1964) reported estimates of $h^2_{NS} = 0.05$ for ring width and 0.16 for basic density, and MORRIS (1974) calculated $h^2_{NS} = 0.14$ for tree diameter and 0.72 for basic density, the latter being higher than the estimates for average density presented in *table 6.* As the non-additive genetic variance for average density is negligible, the estimates for this feature may also be compared with broad sense values of 0.5 and 0.7 for basic density reported by DADSWELL *et al.* (1961.

There is a large male group × location interaction for the width of rings 3 and 4, and the late wood ratio of ring 3. For example, a male group such as group 1 which has a large ring width (13.6 mm — *Table 3)* at Warrenbayne has typically a low value (11.9 mm — *Table 2)* at Rennick. Although there are inconsistencies in ranking between locations, the rankings are consistent between replications within locations, this being confirmed by analyses which included a male group × replication-within-locations term. In all cases this term was not significant.

The phenotypic and genetic correlations are set out in *table 7,* and in all six cases the phenotypic correlations are highly significant. It will be appreciated that for correlations involving late wood ratio the inverse transform has introduced a spurious change of sign which must be taken into account when reading *table 7.* In some cases, (especially those involving ring width and late wood ratio), the genetic correlations have large standard errors.

The large difference between locations in estimates of genetic correlations for some pairs of characteristics *table 7)* emphasizes the need to evaluate such relationships over as wide a range of environments as possible.

On the basis of the negative correlations between ring width and late wood ratio and ring width and minimum density, there is apparently a tendency for faster growth to be associated with fewer thick-walled cells and larger diameter early wood tracheids. This is in keeping with the expected pattern of economy of photosynthates in this extremely early phase of growth. These relationship result in a negative correlation between ring width and average density. However, experience with the latter has shown that it may not be realised in later growth rings. The relationships expressed between average density and the densitometric parameters are to be expected from the previously cited relationship between them (see "Introduction").

For this juvenile material, selection for increased wood density should result substantial genetic gains. in the following example it is asumed that trees have already been selected for growth rate and form and therefore a higher selection intensity than 1 in 5 is not practicable on account of the limited number of trees available. For such an intensity ($i = 1.40$, where i is the selection differential in terms of standard deviations from the population mean) and using the estimates listed in *table 6,* averaged for two growth rings, expected gains may be calculated based on sampling growth rings 3 and 4 in two specimens per tree within an environment equivalent to that of the Rennick site. A gain of 25 kg m^{-3} is obtained in the resulting offspring with respect to the unselected population mean of 396 kg m^{-3} that is, a 6.4 % increase in average density in a single generation of breeding. Accompanying this increase there is likely to be a small loss of growth rate and a small increase in the density range within the growth rings. The correlated response in ring width accompanying selection for density would normally be calculated using the formula in FALCONER (1961). However, this cannot be calculated because of the non-significant genetic correlation between ring width and average density.

Estimates of heritability and expected gain are strictly applicable to sites and conditions analogous to those on which the experimental trees are grown. However, estimates are used as guidelines in breeding programs which service a variety of sites and therefore realised gains over a wider range of environments would be less than those expected from a uniform site similar to that of the experimental area.

The enviroments at Rennick and Warrenbayne are different in many respects, so that it is not surprising that the analyses of the combined data from the two localities has yielded significant genotype × location interactions, and reduced estimates of heritability and gain with respect to either site alone (Table 6). Nevertheless, the variation between these two areas is considered to be greater than that nomally covered by one breeding program. In order to maximise the gains from a breeding program preference should be given to those families which are both high yielding in the desired characteristics and at the same time stable over the range of expected site conditions.

It should be emphasized that reliable gain predictions for older trees must be based on estimates of heritability and genetic correlations appropriate to those age groups and such estimates are known to change with age (see for example, NICHOLLS 1967). It may also be noted that no worthwhile correlations between juvenile (core) and mature (outer) wood density in *P. radiata* have been observed (NICHOLLS and DADSWELL, 1965).

Typical variation patterns for *P. radiata* grown in Australia show basic density values of 350 kg m^{-3} at *ca.* growth ring 3, and outer wood readings in the mature zone ranging between 415 and 455 kg m^{-3} (NICHOLLS and DADSWELL, 1965). Increasing the core wood density would improve the acceptability of this inferior zone of wood and at the same time increase the overall mean density of the raw material and the within-tree uniformity. Such improvements at the present time are particularly important as the proportion of core wood in a tree is tending to increase, because of decreasing rotation ages and/or increasing growth rates due to improved silvicultural methods.

Conclusions

Estimates of variance and covariance components have been obtained and used to calculate narrow sense heritabilities and phenotypic and genetic correlations for five wood characteristics. For maximum, minimum and average density, the non-additive genetic components appear to be unimportant.

Using these estimates expected gains resulting from direct selection were calculated, and by selecting 1 in 5 trees (i = 1.40) gains of 6.4 per cent per generation in average density are possible. Some slight loss in growth rate is likely as a result of indirect selection based on the negative genetic correlations between ring width and average density.

Finally, a large genotype × environment (location × year) interaction was found for ring width, and, to a lesser extent, late wood ratio. The calculated gains per generation, such as those for average density, will only be realized from breeding programs which service areas similar to either of the experimental sites. For sites with a larger variation in environmental factors there is likely to be a reduction in expected gain.

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