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Age-age Correlations in, and Relationships between Basic Density and Growth in *Eucalyptus nitens*

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Abstract

Pith to bark density was measured on cores cut from 588 7-year-old *Eucalyptus nitens* trees. Heritability of ring density averaged 0.37 and was consistently higher than the heritability of earlywood or latewood density. Earlywood, latewood, and ring densities were highly genetically correlated. Age-age correlations for ring density declined with increasing age difference, and were moderately described by Lambeth's (1980) relationship with log of age ratio. Disk and core densities were calculated as weighted averages of ring densities. Age-age correlations for disks and cores were higher and better described by Lambeth's relationship than ring density correlations. Age-age correlations for growth assessed at 20 months, 4 years and 7 years were not well described by Lambeth's relationship. Height, diameter, and volume were well correlated at age 7 years ($r_g > 0.9$), as were disk density, core density, outer-ring density and Pilodyn penetration ($r_g > 0.9$). Density showed a weak negative genetic relationship with diameter at age 7 years ($r_g = -0.2$).

Key words: Eucalyptus nitens, basic density, growth, age-age correlations, heritability, genetic correlation.

FDC: 811.4; 812.31; 561.24; 232.1; 181.65; 165.3; 176.1 *Eucalyptus nitens*; (945).

Introduction

Knowledge of the changes in heritability of traits, and correlations between these traits assessed at different ages, are necessary for determination of efficiencies of early selection (Kang, 1985). Determining trends in heritability and age-age correlations is relatively simple for growth traits, requiring only patience and repeated assessment. While there are many reported age-age correlations for growth in conifers (e.g. Lambeth, 1980; McKeand, 1988; Riemenschneider, 1988; King and Burdon, 1991; Matheson *et al.*, 1994) there are few for *Eucalyptus* L'Hér species (Van Wyk, 1990; Borralho *et al.*, 1992b).

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Methods for assessing density (the dry mass of wood per unit of green or dry volume), on the other hand, range from invasive procedures using a Pilodyn (GREAVES *et al.*, 1996) or cores, to destructive sampling via disks or chips. However, reliable repeated measurements are not feasible using these procedures. As an approximation, cores or disks can be sampled at a later-age and inferences can be made regarding density at earlier ages by determining the density of individual growth-rings (e.g. LOO *et al.*, 1984; ROBISON, 1984; ROBISON and MIZE, 1987; GONZALEZ and RICHARDS, 1988; VARGAS-HERNANDEZ and ADAMS, 1992) – age-age correlations can then be determined using inferred densities. There are, however, no reported genetic age-age correlations for density in plantation-grown eucalypts.

LAMBETH (1980) demonstrated that age-age correlations for growth in a number of coniferous species showed a strong linear relationship with the log of the ratio of ages (*LAR*). He found that the relationship was present across species and growing environments, except when the early age measurement was made at one year after planting. KANG (1985) further refined LAMBETH's (1980) relationship, concluding that selection ages of less than one third of rotation age should be used with caution. MCKEAND (1988) and RIEMENSCHNEIDER (1988) applied LAMBETH's (1980) relationship to early selection for growth in loblolly pine (*Pinus taeda* L.) and Jack pine (*P. banksiana* LAMB.) respectively, while MATHESON *et al.* (1994) found the relationship did not fit observed age-age correlations for growth in 14 year-old radiata pine (*P. radiata* D. DON).

Negative genetic relationships between density and diameter are commonly reported for conifers (e.g. DEAN *et al.*, 1983; LOO *et al.*, 1984; VARGAS-HERNANDEZ and ADAMS, 1991). The few reported genetic correlations in eucalypts also indicate a negative relationship (MALAN, 1988; DEAN *et al.*, 1990; BORRALHO *et al.*, 1992a). This paper will investigate trends in heritability and age-to-age correlations of density through examination of pith-to-bark density measurements made on cores cut from 588 7-year-old plantation-grown *Eucalyptus nitens* (MAIDEN) trees. Three growth measurements assessed over a larger sample of families but including the sampled trees, will be used to make similar inferences for growth.

Methods

Measurements

Total height at 20 months (*HT20M*) and over-bark diameter at 1.3 m at ages 4 and 7 years (*DBH4* and *DBH7*) were assessed on 1316 trees from 94 open-pollinated families established under operational conditions on 2 contrasting sites (*Table 1*) in southeastern Victoria, Australia. The families were arranged in a randomised complete block design, with all families appearing as single-tree plots in each of the 7 blocks at each site. Five hundred and eighty-eight trees from the 50 families with the greatest mean diameter were assessed for Pilodyn penetration (2 penetrations per tree at 1.3 m on the west aspect, after GREAVES *et al.*, 1996) before being felled for density sampling (2 sites by 50 families by 6 trees per family per site, excluding missing trees). Each felled tree was measured (diameter at 1.3 m, diameter at 15% and 35% of total height, height to 5.5 cm over-bark diameter, and total height), and the measurements used for estimation of total stem volume.

Ten centimetre thick disks were cut from each tree from a fixed height of 1.3 m and from 15% of total tree height (approximately 2.5 m). Each disk was sealed in plastic to minimise desiccation, and stored frozen (−18 °C) until analysis. Wood densities for the disks from 1.3 m were determined using the water displacement method T258 om-89 (TAPPI, 1989).

Radial strips of approximately 15 mm tangential width were cut from the frozen 15% height disks, exchanged with ethanol over a period of weeks, and dried from absolute ethanol at room temperature and under reduced pressure to avoid collapse. The strips were reduced on an automated twin-blade saw to 2 mm (tangentially) by 6 mm (longitudinally) and conditioned at 45% relative humidity and 20 °C.

Density profiles were determined at a radial resolution of 50 µm using the x-ray densitometric facility in SilviScan-1 (see EVANS *et al.*, 1995, for a detailed description of the SilviScan density assessment technique). Cu K_a radiation from a fine focus tube was collimated to 50 µm horizontally by 200 µm vertically at the sample and reflected from a flat graphite monochrometer into a scintillation detector. The photon count rate in air was approximately 25000 sec^{-1}. Twenty-five hundred photons were counted at each position, with a standard deviation of approximately 2%, in accordance with Poisson statistics. Mass attenuation coefficient was assumed to be constant within each sample. Each density profile was normalised by the average density determined independently from the sample mass and volume, as measured by micrometry. The standard deviation of sample thickness, which contributes in direct proportion to errors in the estimated density profiles, was less than 1%.

Custom written software (EVANS, 1993) was used to determine the average density of individual annual growth rings and earlywood and latewood components.

Density measured using the water displacement method (1.3 m disks) is basic density, defined as the oven-dry weight of wood per unit of green volume, whereas density measured using SilviScan is dry density, defined as the weight of wood per unit of dry volume at approximately 10% moisture content.

Table 1. – Description of trial sites (after BENNETT *et al.*, 1989).

	Site 1	Site 2
Soil	gradational clay-loam	duplex: sandy loam over clay
Latitude (°S)	38	38
Longitude (°E)	146	147
Altitude (m a.s.l.)	200	80
Rainfall (mm yr^{-1})	1006	728
Previous landuse	Radiata pine plantation	agricultural pasture
Site preparation	winged rip, disc plough	ridge plough
Fertiliser at planting (kg ha^{-1})	N 4.2, P 0.9, K 0.9	N 4.2, P 50.9, K 50.9

While the absolute density values determined using these 2 methods cannot be directly compared, the methods were assumed here to give correlated results.

Whole-disk and whole-core density aggregates

Using individual ring earlywood (*EW*) and latewood (*LW*) densities and the thickness of each band, weighted average whole-core (pith to bark) and whole-disk densities for each age were determined using the following formulae:

$$[1] \quad core.dens_i = \frac{\sum_{i}^{n=3}(densEW_n.widthEW_n + densLW_n.widthLW_n)}{\sum_{i}^{n=3}(widthEW_n + widthLW_n)}$$

$$[2] \quad disk.dens_i = \frac{\sum_{i}^{n=3}(densEW_n.areaEW_n + densLW_n.areaLW_n)}{\sum_{i}^{n=3}(areaEW_n + areaLW_n)}$$

where $core.dens_i$ and $disk.dens_i$ are the core density and disk density in the i^{th} year respectively; $densEW_n$ and $densLW_n$ are the earlywood and latewood density of the n^{th} ring respectively; $widthEW_n$ and $widthLW_n$ are the widths of the earlywood and latewood bands of the n^{th} ring respectively; and $areaEW_n$ and $areaLW_n$ are the areas of the earlywood and latewood bands of the n^{th} ring respectively calculated assuming the disks are circular and the rings concentric.

Statistical analysis

The model used for the multivariate analysis of variance components was, in matrix notation:

$$[3] \quad y = Xb + Z_1f + Z_2i + e$$

where y is the vector of observations for one or multiple traits, b is the vector of fixed effects (replicates within site and seed collection area), f and i are vectors of open-pollinated family effects and family-by-site interaction effects respectively, e is the vector of residuals and X, Z_1 and Z_2 are incidence matrices relating observations to the effects in the model.

The (co)variance structure (V) for the analysis can be described as (after MEYER, 1994):

$V(f) = G_f \times I$

$V(i) = G_i \times I$

$V(e) = R \times I$

where: f and i are vectors of family and family by site effects respectively; e is a vector of residual errors; G_f is the matrix of family variances and covariances amongst traits; G_i is the matrix of family-by-site covariances; R is the matrix of residual covariances; and I is the identity matrix. All covariances between effects were assumed to be zero.

Estimates of variance components were calculated using REML VCE software using a quasi-NEWTON algorithm of variance and covariance (GROENEVELD, 1995). Individual, across-site narrow-sense heritability (h^2) was calculated after:

$$[4] \quad h^2 = \frac{\sigma_f^2}{r.(\sigma_f^2 + \sigma_i^2 + \sigma_e^2)}$$

where σ^2_f is the between-family variance; σ^2_i is the variance of family by site interaction; σ^2_e is the within-family variance; and r is the coefficient of relationship (assumed to be 0.4 after VOLKER *et al.*, 1990). Standard errors for heritability, where presented, were determined after the method described by BECKER (1984).

Age trends in genetic correlation

An empirical relationship between age-age genetic correlations ($r_{j\text{-}m}$) and the natural log of the age ratio (*LAR*), as proposed by LAMBETH (1980), was fitted for each trait:

$$[5] \quad r_{j\text{-}m} = b(LAR) + c$$

where $LAR = \log_e\left(\frac{\text{Early Age}}{\text{Later Age}}\right)$

and c is the intercept (the genetic correlation when $LAR = 0$, theoretically equal to 1).

The goodness of fit of the *LAR* relationships was expressed by the coefficient of determination (r^2).

Results and Discussion

Observed trait means

The observed site means of the assessed growth traits and disk density at 1.3 m are presented in *table 2*.

Table 2. – Site means for assessed total height at 20 month (*HT20M*), over-bark diameter at 1.3 m at ages 4 and 7 years (*DBH4* and *DBH7*) and 1.3 m disk density.

Trait	SITE 1	SITE 2
HT20M	3.03 m	4.38 m
DBH4	10.3 cm	11.6 cm
DBH7	16.9 cm	16.3 cm
1.3 m disk density	0.471 t m^{-3}	0.541 t m^{-3}

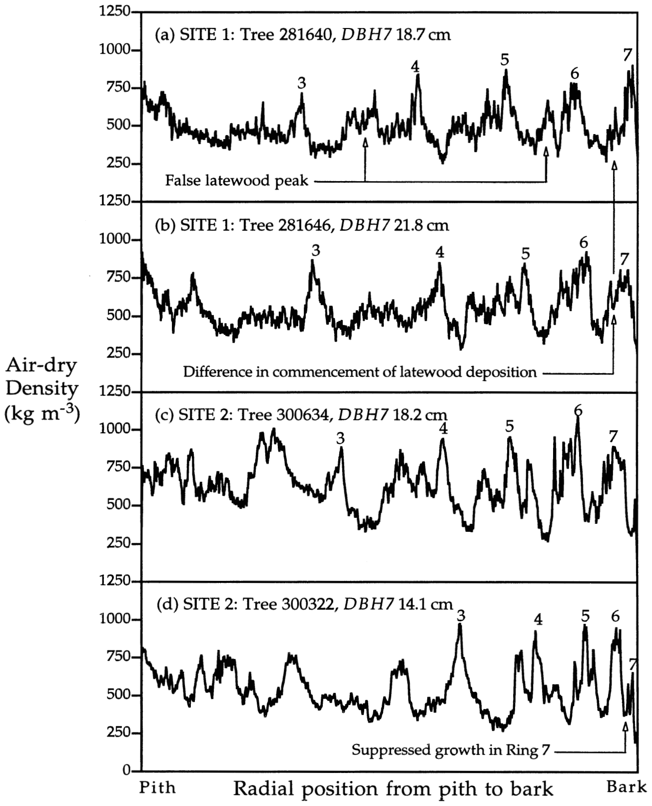

Figure 1. – Pith to bark density traces produced by the SilviScan instrument (*DBH7* refers to tree diameter over-bark at 1.3 m at age 7); plain numbers indicate tree age when latewood peaks were deposited.

It is apparent that Site 2 provided faster initial growth (*HT20M*), but growth declined in relation to Site 1 with time. By age 7 years (*DBH7*) both sites showed similar average annual growth rate. Whole disk density at 1.3 m was considerably higher on Site 2 than Site 1.

Four examples of the SilviScan density traces are presented in *figure 1*. Ring boundaries, between the older latewood and the more recent earlywood, were relatively simple to locate with consistency on the SilviScan traces. The earlywood-latewood transition boundaries within each ring, however, were more difficult to locate with consistency due to the varying presence of *false* latewood peaks (e.g. *Figure 1a*), and time differences in the commencement of deposition of higher-density latewood between individual trees (e.g. *Figures 1a* and *1b).*

Figures 1a and *1b* depict density profiles from 2 trees from Site 1, and *figures 1c* and *1d* are from Site 2. The 2 sites were located relatively close together (35 km apart) and both received adequate nutrition, yet the differences in absolute density and density profile between sites is considerable (*Table 2, Figure 1*). While it is not possible to determine the cause of the density differences, differences in soil type, previous land-use and micro-climate may have been contributing factors.

Whole-ring density (after SilviScan) increased with age of deposition on each site, while maintaining a difference of around 0.08 t m^{-3} between sites (*Figure 2*).

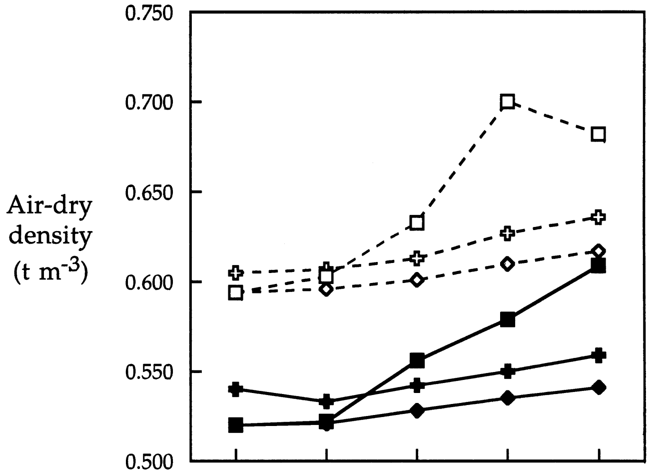

Figure 2. – Outer-most whole-ring density (Site 1 = ■, Site 2 = □), aggregate whole-disk density (Site 1 = ✚, Site 2 = ✙), and aggregate whole-core density (Site 1 = ◆, Site 2 = ◇) with tree age.

The weighted aggregated density traits, core density and disk density (*Eqn. 1* and *2*), similarly increased with age, while maintaining the observed site difference (*Figure 2*). The aggregate densities rose more slowly than the individual-ring densities because the lower density inner-rings are always represented in later-age whole-disk or whole-core aggregates. Aggregate disk density weights the outer-wood density more highly than does aggregate core density and thus disk density was consistently greater than core density.

Genetic Parameters

The narrow-sense heritabilities of earlywood, latewood, and whole-ring density, by growth-ring, are presented in *table 3*. The consistently lower heritability of both earlywood and latewood in comparison with whole-ring is attributed to the difficulty in partitioning each ring into earlywood and latewood in comparison with the relative ease of separating whole-rings. Incorrect placement of the earlywood/latewood boundary within a ring increases the residual variance of each, thus reducing the apparent heritabilities relative to the whole-ring heritability. Vargas-Hernandez and Adams (1991), working with 15-year-old Douglas fir, similarly observed both earlywood and latewood density to have a lower heritability than whole-ring density.

The heritability of individual ring density (*Table 3*) was low in rings 3 ($h^2 = 0.3$) and 7 ($h^2 = 0.2$) and moderate ($h^2 = 0.4$) in rings 4, 5 and 6. While each tree was sampled at a fixed proportion of total height, differences in the degree to which the inner-most earlywood is represented in Ring 3 would be dependent upon the relative height of the tree at the earlier age. The varying proportion of earlywood in Ring 3 may be the cause of the higher relative residual variance for this ring and hence the low heritability. The low heritability for Ring 7 resulted from a reduced family variance for this ring associated with an increased error variance. A number of the smaller trees on Site 2 showed signs of being suppressed: Ring 7 was either completely missing or small and of lower density – *figure 1d* depicts the density trace of a smaller tree showing a much reduced Ring 7.

Table 3. – Narrow-sense heritability of earlywood, latewood, and whole-ring density, by year of deposition of growth-ring (Ring). Standard errors of heritability are in parenthesis.

Ring	h^2 density		
	Earlywood	Latewood	Whole-ring
3	0.29 (0.09)	0.25 (0.08)	0.31 (0.07)
4	0.27 (0.09)	0.31 (0.10)	0.43 (0.10)
5	0.25 (0.08)	0.27 (0.09)	0.43 (0.11)
6	0.31 (0.09)	0.21 (0.09)	0.44 (0.11)
7	0.09 (0.06)	0.05 (0.05)	0.22 (0.06)

The genetic correlations among earlywood, latewood and whole-ring density were generally very high (*Table 4*) suggesting that these traits are manifestations of the same genes. However, since the heritability of whole-ring density was considered to be a more accurate estimate of density heritability than the heritability of earlywood or latewood density, further analysis reported in this paper will concentrate on whole-ring density rather than earlywood or latewood density.

Table 4. – Genetic correlations among earlywood (*EW*), latewood (*LW*), and whole-ring density, by growth-ring.

correlation	Ring 3	Ring 4	Ring 5	Ring 6	Ring 7
EW - *LW*	0.65	1.00	0.99	0.98	0.93
EW - whole-ring	1.00	1.00	1.00	1.00	0.93
LW - whole-ring	0.70	0.99	0.99	0.99	1.00

The variance of family-by-site interaction for ring density was consistently low across rings, varying from 0% to 3% of total variance. Similar low genotype-by-environment variation for ring density has been reported in Douglas fir (Yassin Abdel-Gadir *et al.*, 1993).

The relationships between growth and density traits measured at age 7 years are presented in *table 5*.

There were strong genetic relationships (*Table 5*) between *DBH7* and *VOL7* (0.99) and between *HT7* and *VOL7* (0.92). Similar strong relationships between growth traits in plantation eucalypts have been reported by Van Wyk (1990) and Dean *et al.* (1990). Since volume was calculated from measurements of diameter taken along the stem of each tree, there must be

Table 5. – Relationship between traits at age 7 years. Individual across-site heritabilities (diagonal, *bold),* genetic correlations (above diagonal) and phenotypic correlations (below diagonal).

	DBH7	*HT7*	*VOL7*	*PIL*	*RING7*	*CORE7*	*DISK7*	*DENS1.3*
DBH7	**0.42**	0.90	0.99	0.24	-0.48	-0.35	-0.28	-0.20
HT7	0.79	**0.44**	0.92	-0.02	-0.23	-0.09	-0.03	0.09
VOL7	0.96	0.82	**0.46**	0.30	-0.53	-0.40	-0.33	-0.24
PIL	-0.02	-0.14	0.02	**0.59**	-0.97	-0.98	-1.00	-0.98
RING7	-0.15	0.03	-0.15	-0.55	**0.26**	0.98	0.97	0.93
CORE7	-0.09	0.03	-0.11	-0.56	0.63	**0.51**	0.99	0.98
DISK7	-0.07	0.06	-0.09	-0.61	0.72	0.98	**0.53**	0.98
DENS1.3	0.03	0.13	0.00	-0.74	0.52	0.67	0.70	**0.73**

DBH7 and *HT7* are diameter at 1.3 m and total height respectively; *VOL7* is the whole-tree volume calculated from multiple measurements up each tree; *PIL* is the average Pilodyn penetration of 2 penetrations made under-bark on the west aspect at 1.3 m; *RING7* is the density of the outer-most growth ring at 15% of total tree height (approx. 2.4 m), *CORE7* and *DISK7* are calculated core and whole-disk densities at 15% of tree height; and *DENS1.3* is the measured whole-disk density at 1.3 m.

some degree of auto-correlation between *DBH7* and volume, particularly since the lower portion of a tree makes a greater contribution towards volume than higher stem sections. However, diameter at a fixed height of 1.3 m or 1.4 m is commonly used as a selection trait for total tree volume (COTTERILL and DEAN, 1990) and is useful to confirm such a high genetic relationship between diameter and total volume in a temperate eucalypt species.

Genetic relationships among the density traits were similarly high (*Table 5*). Pilodyn penetration (at 1.3 m) was highly genetically correlated with ring density (–0.97), and with disk density at both 1.3 m and 15% of tree height (–0.98 and –1.00 respectively). Core and disk density at 15% height were both highly genetically correlated with disk density at 1.3 m (both 0.98), supporting the assumption that estimating density via basic density and dry density methods gives correlated results. Diameter and density at 1.3 m were weakly correlated at age seven years ($r_g = -0.2$) confirming genetic relationships reported previously in plantation eucalypts (MALAN, 1988 $r_g = -0.7$ (height) and –1.0 (*dbh*), DEAN *et al.*, 1990 $r_g = -0.4$, BORRALHO *et al.*, 1992c $r_g = -0.1$). The relationship between both *DBH7* and *VOL7*, and density of the outer-most ring (*RING7*), was a moderate –0.5 suggesting that those trees which have shown the highest growth are now producing lower density wood and that the relationship between growth and density may increase (become more negative) with increasing stand age beyond 7 years. The variance of family-by-site interaction was below 3% of the total variance for all traits presented in *table 5*.

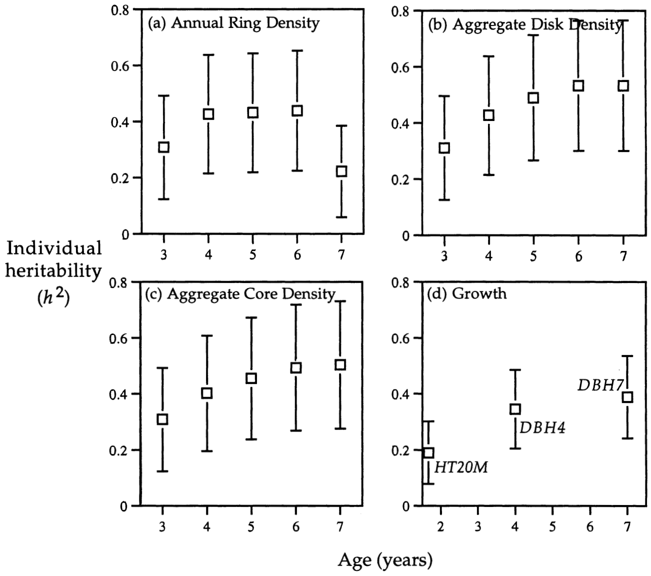

Figure 3. – Individual heritability (h^2) versus age. Heritability observations for growth (d) are from diameter at 1.3 m (*DBH4*, *DBH7*) and total height (*HT20M*) as indicated. Bars represent 95% confidence limits of prediction.

Growth and density traits showed increasing individual heritability with increasing tree age (*Figure 3*), a trend commonly found in short rotation eucalypts (WEI and BORRALHO, 1996).

The observed rise, plateau, and fall in the heritability of individual ring density (*Figure 3a*) may not represent a real trend – all estimates are not significantly different from an average estimate of 0.36.

Age-age correlations

The heritabilities and age-age genetic correlations for: whole-ring densities; disk densities; core densities; and growth traits are presented in tables *6, 7, 8* and *9* respectively.

VARGAS-HERNANDEZ and ADAMS (1992) observed genetic correlation between core density at early age (similarly determined as an aggregate of observed individual ring densities) and core density at 15 years rose gradually from around 0.9 at age 7 years to around 1.0 at age 14 years in Douglas fir.

As the core and disk densities are weighted aggregated traits (*Eqn.s 1* and *2*) there is a component of auto-correlation when these traits are compared across ages. For example, all of

Table 6. – Heritabilities (diagonal, *bold*) and genetic correlations (above diagonal) for ring density between ages.

	Ring 7	Ring 6	Ring 5	Ring 4	Ring 3
Ring 7	**0.22**	0.99	1.00	0.98	0.89
Ring 6		**0.44**	1.00	0.95	0.83
Ring 5			**0.43**	0.96	0.86
Ring 4				**0.43**	0.95
Ring 3					**0.31**

Table 7. – Heritabilities (diagonal, *bold*) and genetic correlations (above diagonal) for disk density between ages.

	Disk 7	Disk 6	Disk 5	Disk 4	Disk 3
Disk 7	**0.53**	1.00	1.00	0.98	0.93
Disk 6		**0.53**	1.00	0.98	0.93
Disk 5			**0.49**	0.99	0.95
Disk 4				**0.43**	0.98
Disk 3					**0.31**

Table 8. – Heritabilities (diagonal, *bold*) and genetic correlations (above diagonal) for core density between ages.

	Core 7	Core 6	Core 5	Core 4	Core 3
Core 7	**0.50**	1.00	1.00	0.99	0.95
Core 6		**0.49**	1.00	0.99	0.96
Core 5			**0.46**	1.00	0.97
Core 4				**0.40**	0.99
Core 3					**0.31**

Table 9. – Heritabilities (diagonal, *bold*) and genetic correlations (above diagonal) for growth traits between ages.

	DBH7	*DBH4*	*HT20M*
DBH7	**0.42**	0.99	0.52
DBH4		**0.37**	0.49
HT20M			**0.23**

Disk 5 is included in the calculated value for Disk 6 leading to high correlations between these traits. Since later-age core densities are more a function of earlier-age density than are later-age disk densities, the age-age correlations were greater for core density than for disk density. While age-age correlations may be inflated by auto-correlation, it is noteworthy that BORRALHO *et al.* (1992a) observed little difference between genetic parameters for absolute and incremental *growth* traits, suggesting little inflation due to auto-correlation.

The observed correlations (*Tables 6* to *9*) are depicted in *figure 4* with fitted relationships with the log of the age ratio (*LAR*) as proposed by LAMBETH (1980).

The age-age correlations for the aggregated density traits, disk density and core density, were clearly well described by LAMBETH's (1980) relationship with *LAR* (r^2 0.88 and 0.90 respectively – *figure 4*). While the observed age-age correlations for individual ring density were not well described by the *LAR* relationship (r^2 0.53) the trend that correlation declines as the age difference increases was still apparent.

The *LAR* coefficients for the density traits were relatively low ranging from 0.066 (cores) to 0.185 (rings) suggesting that very early selection for density may be possible – a low coefficient means correlation declines little with increasing age difference.

The 3 age-age correlations for growth were not well described by the *LAR* relationship (r^2 0.55). Further, the coefficient of *LAR* for growth was a high 0.478 when previous reported *LAR* coefficients for growth, albeit in conifers, range from 0.177 to 0.345. Two of the 3 age-age correlations for growth relate to an early age of 1.7 years (20 months), and these 2 points provided considerable leverage in defining the high *LAR* coefficient (*Figure 4d*). LAMBETH (1980) observed that correlations between height measured at 1 year and later-age growth did not fit the *LAR* relationship observed for later-age correlations. Working with temperate plantation eucalypts both BORRALHO *et al.* (1992b) and GRIFFIN and COTTERILL (1988) concluded height at one year to be an unreliable indicator of subsequent growth performance. It is possible that height at 1.7 years (20 months) is similarly unsuitable for prediction of later-age growth in *E. nitens*. Thus the presented *LAR* relationship for growth (*Figure 4d*) must be considered with caution until further work clarifies the relationship.

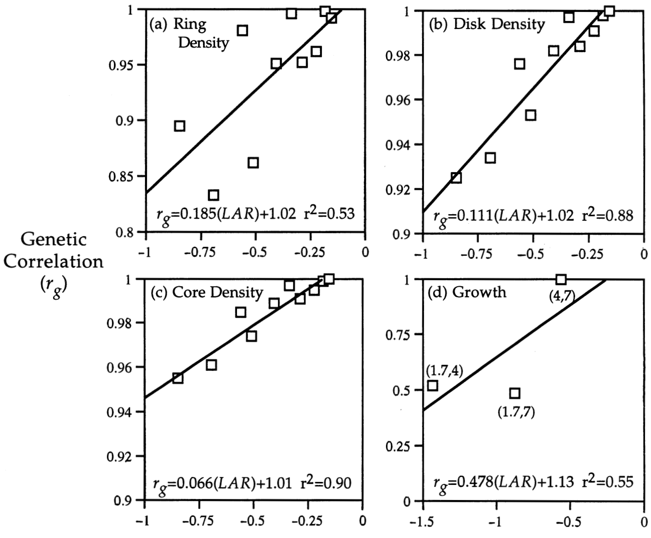

Figure 4. – Relationship between age-age genetic correlation (r_g) and the natural log of the age ratio (*LAR*) for density and growth traits. Datapoint labels in (d) refer to (*early-age, later-age*) – see text.

Finally, selection of sampled families on the basis of growth rate would have resulted in reduced additive variance for growth in the selected population, with the magnitude of the reduction defined by the accuracy of selection (heritability). The variance of traits showing correlation with growth would have also been reduced in the selected population, with the magnitude of reduction defined by the degree of correlation between growth and the correlated traits (VILLANUEVA and KENNEDY, 1990). It is probable that the observed relationships between growth and density traits are lower than would have been observed had all families been sampled. However, as more than 50% of families were sampled, the effect on results presented here is assumed to be small, and influence on conclusions probably negligible.

Conclusions

Age-age correlations for annual-ring density were consistently high (r_g age 6:age 7 years 0.99) and declined with age difference (r_g age 2:age 7 years 0.89). While the densities of earlywood and latewood were found to be very strongly related to whole-ring density (r_g predominantly 0.99 or greater), they showed lower heritability (0.24 and 0.22 respectively) than whole-ring density (0.37). Thus early selection for density using whole-ring density in *E. nitens* should be possible.

Age-age correlations for ring density were moderately described by LAMBETH's (1980) relationship with log of age ratio. Age-age correlations for disk and core densities were consistently higher and better described by LAMBETH's relationship than ring density correlations. Age-age correlations for growth were less conclusive and more work is required to clarify the observed trends. However, growth measurements at 20 months appear to be a quite unreliable indicator of later-age growth performance.

Density appears to be weakly and negatively related to growth in *E. nitens* at age 7 years ($r_g = -0.2$), and diameter at 1.3 m is highly correlated with total tree volume at age 7 years ($r_g = 0.99$) – it is useful to confirm these relationships for *E. nitens*.

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Spruce and Wood Quality: Genetic Aspects (A Review)

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Summary

This paper is a review based on articles about the genetics of wood quality of Norway and Sitka spruce. Among the wood quality traits, wood density is the most widely used. The main topics of the paper are : genetic control (genetic control of wood density, change of genetic control with age, genotype-environment interaction), young-adult relationships, relationships between wood density and other wood properties, and relationships between wood density and growth and adaptation traits (especially about the widely studied unfavourable rela-

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