GENETIC VARIATION IN WOOD BASIC DENSITY AND KNOT INDEX, AND THEIR RELATIONSHIP WITH GROWTH TRAITS FOR *ACACIA AURICULIFORMIS* IN NORTHERN VIETNAM*

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ABSTRACT

One hundred and forty families from 13 provenances of *Acacia auriculiformis*
A. Cunn. ex Benth. were tested in a progeny trial on a typical hill site in

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northern Vietnam. Two selective thinnings were done to retain the single best tree, in terms of vigour and straightness, in each four-tree family plot. All remaining trees were measured to obtain estimates of individual-tree narrow-sense heritabilities ($\hat{h}^2$) and additive genetic correlations ($\hat{r}_A$) for growth traits (height, diameter, tree volume), stem quality traits (bark thickness, straightness, forking, and knot index), pilodyn penetration, and wood basic density. The $\hat{h}^2$ for growth traits and straightness increased over time from age 3 to ages 5 and 9. Similarly, $\hat{h}^2$ for density also increased from corewood to outerwood. For growth traits at age 9, $\hat{h}^2$ ranged from 0.36 to 0.39. The observed heritabilities of density and pilodyn penetration ($\hat{h}^2 = 0.61$ and 0.47, respectively) were consistently higher than for growth traits. However, the values for stem quality traits ($\hat{h}^2$ 0.12 to 0.31) were lower than for growth traits, with the exception of BRK (0.39). Estimated coefficients of additive genetic variation (CV_A) were high for growth traits at all ages (4.5% to 26.2%) and were very high for stem quality traits (14.7 to 26.2%) at age 9. The value of CV_A for density was around 8% at different ages. Age-age correlations for all growth traits, straightness, and density were high. The $\hat{r}_A$ between growth traits and density were not significantly different from zero. The $\hat{r}_A$ between growth traits and stem quality traits, except straightness, were low to moderate ($\hat{r}_A$ –0.45 to 0.65), while strong positive genetic correlations ($\hat{r}_A$ 0.79 to 0.96) were found between growth traits and straightness. Strong negative genetic correlation between pilodyn penetration and density ($\hat{r}_A = -0.88$) indicated that pilodyn would reliably rank trees for basic density.

INTRODUCTION

The Vietnamese Government is currently striving to establish plantations of fast-growing trees to ensure an adequate log supply to sustain the operations of the existing wood-based industries in the country. Trials of *Acacia* species and provenances in Thailand (Chittachumnonk & Sirilak 1991), Hainan Island, China (Yang & Zeng 1991), and Vietnam (Kha 2003; Nghia 2003) indicated that *A. auriculiformis* is a useful multipurpose tree species, being fast-growing and suitable for timber and pulp production (Nghia 2003; Turnbull *et al*. 1997). However, silvicultural research on *A. auriculiformis* has been limited in Vietnam and genetic improvement is at an early stage. Information on genetic variation in economic traits including growth, stem straightness, branch characteristics, and wood basic density is required to guide tree improvement to meet industry requirements.

The goal of most tree improvement programmes now is to combine rapid stem volume growth with high-quality stem form and desired wood properties so as to produce well-adapted trees capable of supplying good-quality logs for lumber, plywood, or pulpwood (Doede & Adams 1998; Zobel & Talbert 1984). Stem form, branch characteristics, and wood density are often considered the most important

wood traits because of their effect on product recovery and nearly all final products of wood (Bendtsen 1978; Zobel & Van Buijtenen 1989; Zobel & Talbert 1984). Fast-growing trees grown on short rotations have a high proportion of low-density juvenile wood (Maeglin 1987), which is undesirable for both wood strength and pulp yield. This raises concerns about the wood density in timber from intensively managed forests as compared to slower growing and more mature natural stands (Zobel & Van Buijtenen 1989).

Incorporation of quality traits such as wood density, bark thickness, stem straightness, and knot index into an existing tree breeding programme requires information about the genetic variation of each quality trait and their genetic relationships with growth traits. Such information is generally lacking for *A. auriculiformis*. In this species reported estimates of narrow-sense heritabilities for most growth and stem form parameters at early ages were low (Luangviriyasaeng & Pinyopusarerk 2002). High age-age correlations for growth traits were found, but height and diameter were not strongly correlated with survival, number of stems, branch angle, and wood density in provenance trials in Zaire (Khasa *et al.* 1995).

Our study aimed to determine genetic variation in growth traits, wood basic density, bark thickness, straightness, and branch characteristics for *A. auriculiformis*, to test the effectiveness of pilodyn penetration as an indirect measure of wood basic density, and to examine the genetic relationships between pilodyn, wood basic density, and growth traits. The implications of these results for the development of a breeding programme of *A. auriculiformis* in northern Vietnam are considered.

MATERIALS AND METHODS
Genetic Material Tested and Trial Description

In August 1997, a progeny test including 140 open-pollinated families from 13 seed sources of *A. auriculiformis* was established in northern Vietnam. The seed sources originated mainly from natural provenances in Queensland, Australia. These provenances were selected on the basis of their known superior growth and tree form in earlier provenance trials in Vietnam (Kha 2003). Natural provenances from Northern Territory, Australia, or Papua New Guinea were not included. Selected families were also sourced from the best trees in two first-generation seedling seed orchards, one located in Melville Island, Australia, based on Papua New Guinea provenances, and the other in Sakaerat, Thailand, based on provenances from Papua New Guinea, Queensland, and Northern Territory, and Thai land race selections (Table 1).

The trial site at Ba Vi in Ha Tay province, 21°07′N, 105°26′E, altitude 60 m a.s.l., was typical of hill sites in the north of Vietnam. The mean annual rainfall was 1680 mm and the mean annual temperature 23°C. The soil was a yellow ferralitic

TABLE 1–Details of seed origins in the *Acacia auriculiformis* progeny test

CSIRO No.	Seed source	Origin*	Latitude (°S/N)	Longitude (°E)	Altitude (m)	No. of families
17961	Olive River	QLD	12°15	142°52	20	4
17966	Boggy Creek	QLD	15°52	144°53	240	6
18854	Archer R & Tribs	QLD	13°26	142°57	90	18
18998	Pascoe R Cape York	QLD	12°34	143°06	15	6
19244	Rocky Creek	QLD	12°47	142°49	100	6
19245	Wenlock River Morton	QLD	12°29	142°40	70	4
19246	Wenlock River	QLD	12°29	142°29	50	4
19249	Wenlock River	QLD	13°05	142°56	120	1
19250	Coen River	QLD	13°57	143°10	200	2
19251	Morehead River	QLD	15°01	143°40	120	4
19254	West Normanby River	QLD	15°49	144°58	110	4
19255	Seed Orch Melville Is†	NT	11°34	130°34	20	6
19326	Seed Orchard Sakaerat‡	THAI	14°13	101°55	500	75

* QLD: Queensland, Australia; NT: Northern Territory, Australia; THAI: Thailand
† Established using Papua New Guinea (PNG) seed sources
‡ Established using PNG, QLD, NT, and Thai seed sources

clay loam with strong laterisation evident in the profile, acidic (pH 3.5–4.5), and infertile, with low levels of phosphorus and potassium.

The test used a row-column design generated by the computer program CycDesign (Williams *et al.* 2002), with 8 replicates, each with 10-row and 14-column incomplete blocks. Each family was represented by a four-tree row plot in each replicate. The original spacing was 1.5 m between trees within rows and 4 m between rows. Three kilograms of well-composted cow manure and 0.2 kg of NPK fertiliser were placed at the bottom of each 30 × 30 × 30-cm planting hole at planting time. The trials were weeded twice per year up to age 4 years. Successive phenotypic thinnings were made in the test at 3 and 5 years. Trees that were inferior in vigour, or which had poor stem straightness, were removed. The thinning at 3 years retained the two best trees per plot, and that at 5 years retained the single best tree. All families were retained in the test.

Assessment

Total tree height (HT), diameter at breast height (DBH), forking (FOK), straightness (STR), wood density (DEN), pilodyn penetration (PIN), bark thickness (BRK), and branch characteristics of each tree were recorded at age 9 years for the 1120 remaining trees in the trial. The growth traits and straightness were also assessed for 4400 trees at 3 years before the first thinning and 2091 remaining trees at 5 years before the second thinning. Diameter of the largest branch, length of the longest branch, and number of the branches were also measured and counted for the 1120 remaining trees at age 9 years.

Stem straightness was scored using a 5-point scale:

    1 = very crooked stem with >2 serious bends;

    2 = crooked stem with 2 serious bends;

    3 = slightly crooked stem with 1 serious and/or > 2 small bends;

    4 = almost straight stem with 1-2 small bends and

    5 = perfectly straight stem.

Forking reflects the ability of the tree to retain its primary axis. It was scored on a 6-point scale:

    1 = double or multiple stems from ground level

    2 = axis loses persistence in the first (lowest) quarter of the tree

    3 = axis loses persistence in the second quarter of the tree

    4 = axis loses persistence in the third quarter of the tree

    5 = axis loses persistence in the fourth quarter of the tree, and

    6 = complete persistence of forking.

Pilodyn penetration was measured using a 6J Forest Pilodyn, by removing a small section of the bark at 1.3 m above the ground and taking two readings for each tree, one from the east side and one from the north. Bark thickness was measured using a bark gauge at both sampling points.

A 5-mm bark-to-pith increment core was taken from every remaining tree at 1.3 m using a hand-held corer; it was immediately stored in an aluminium tube with the two ends sealed, and later taken to a freezer. Since it is difficult to recognise annual rings in the cores of this species, the cores were cut into three equal segments to estimate correlation between segments: (1) corewood where heartwood formation had already been initiated, (2) transition wood, and (3) outerwood. Density was based on the water displacement method (Olesen 1971). Two weights (g) were recorded for every sample: weight of water displaced by immersion of core (W_1), and oven-dry weight (W_2). Density of each segment (DEN_1, DEN_2, DEN_3) was calculated as: $DEN = W_2 / W_1$ (g/cm^3), and total core density (DEN) was then calculated as:

$$\text{DEN} = \frac{W_{2(1)} + W_{2(2)} + W_{2(3)}}{W_{1(1)} + W_{1(2)} + W_{1(3)}} \ (\text{g/cm}^3) \tag{1}$$

where $W_{1(1)}$, $W_{1(2)}$. and $W_{1(3)}$ are weights of water displaced by immersion of Segments 1, 2, and 3, respectively. Similarly, $W_{2(1)}$, $W_{2(2)}$, and $W_{2(3)}$ are oven-dry weights of Segments 1, 2, and 3.

The conical stem volume over bark of each tree was calculated using the following formula:

$$VOL = \frac{\pi}{12} \times HT \times DBH^2 \tag{2}$$

where *VOL* is conical stem volume (dm³), *HT* (m), and *DBH* (cm).

Knot index was calculated as follows (Doede & Adams 1998):

(1) Branch diameter ratio (BDIA; mm/mm): Diameter of the largest branch (mm) on the tree divided by DBH

(2) Branch length ratio (BLEN; cm/mm): Length (cm) of the longest branch on the tree divided by DBH

(3) Branch number (BNUM): number of branches in the tree. Branch number was counted on the upper part of the tree, for the main branches which had to be more than 3 cm in diameter.

(4) Knot index (KI): Ratio of the branch cross-sectional area (mm²) to the stem cross-sectional area (mm²) estimated as

$$KI = BNUM \times BDIA^2 / DBH^2 \tag{3}$$

Statistical Analysis

Stem straightness and forking data deviated from normal distributions. It was assumed that these traits were controlled genetically by an underlying polyfactorially determined liability scale (Falconer & Mackay 1996), and that the given scores were caused by imposed thresholds. Prior to analysis, class scores were therefore transformed into asymptotic "normal scores" (Gianola & Norton 1981) in order to adjust for non-adequate or variable spacing of classes and to improve the efficiency of subsequent analyses (Ericsson & Danell 1995).

The statistical analysis was based on individual tree observations according to the linear mixed model:

$$\mathbf{y} = \mathbf{X}_B\mathbf{m} + \mathbf{X}_P\mathbf{p} + \mathbf{Z}_W\mathbf{w} + \mathbf{Z}_N\mathbf{n} + \mathbf{Z}_T\mathbf{t} + \mathbf{Z}_F\mathbf{f} + \mathbf{e} \tag{4}$$

with $\mathbf{y} = (\mathbf{y}_1, \mathbf{y}_2, ... \mathbf{y}_n)$,
$\mathbf{m} = (\mathbf{m}_1, \mathbf{m}_2, ... \mathbf{m}_n)$,
$\mathbf{p} = (\mathbf{p}_1, \mathbf{p}_2, ... \mathbf{p}_n)$,
$\mathbf{w} = (\mathbf{w}_1, \mathbf{w}_2, ... \mathbf{w}_n)$,
$\mathbf{n} = (\mathbf{n}_1, \mathbf{n}_2, ... \mathbf{n}_n)$,
$\mathbf{f} = (\mathbf{f}_1, \mathbf{f}_2, ... \mathbf{f}_n)$,
$\mathbf{e} = (\mathbf{e}_1, \mathbf{e}_2, ... \mathbf{e}_n)$,
$\mathbf{X} = \sum_\oplus \mathbf{X}_{Bi}$, $\mathbf{X} = \sum_\oplus \mathbf{X}_{Pi}$, $\mathbf{Z}_W = \sum_\oplus \mathbf{Z}_{Wi}$, $\mathbf{Z}_N = \sum_\oplus \mathbf{Z}_{Ni}$, $\mathbf{Z}_T = \sum_\oplus \mathbf{Z}_{Ti}$, and $\mathbf{Z}_F = \sum_\oplus \mathbf{Z}_{Fi}$, $\sum_\oplus$ denotes the direct sum, and *i* the number of traits from 1 to *n*, $\mathbf{y}$ is the vector of individual observations for the different traits, $\mathbf{m}$ is the vector of fixed effect of replicate, $\mathbf{p}$ is the vector of fixed effect of seed source, $\mathbf{w}$ is the vector of random row within replicate effect, $\mathbf{n}$ is the vector of random column within replicate

effect, **t** is the vector of random effect of plot for assessments at age 3 and age 5, **f** is the vector of random family within seed source effects, and **e** is the vector of random residuals. $\mathbf{X}_B, \mathbf{X}_P, \mathbf{Z}_W, \mathbf{Z}_N, \mathbf{Z}_T$ and $\mathbf{Z}_F$ are incidence matrix relating **m, p, w, n, t,** and **f** to **y**. The data analyses were implemented using ASReml software (Gilmour *et al*. 2002).

Assuming a multivariate normal distribution (MND), the expected mean and covariance were:

$$
V \begin{bmatrix} \mathbf{w} \\ \mathbf{n} \\ \mathbf{t} \\ \mathbf{f} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{W} \oplus \mathbf{I} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{N} \oplus \mathbf{I} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{T} \oplus \mathbf{I} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{F} \oplus \mathbf{A} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{R} \oplus \mathbf{I} \end{bmatrix}
\tag{5}
$$

where **0** is a null matrix, **I** is an identity matrix of order equal to the total number of rows, columns, plots, genetic, and residuals, respectively, and $\oplus$ is the direct (Kronecker) product operation. $\mathbf{W} = \{\sigma_{wi,wj}\}$, $\mathbf{N} = \{\sigma_{ni,nj}\}$, $\mathbf{T} = \{\sigma_{ti,tj}\}$, $\mathbf{F} = \{\sigma_{fi,fj}\}$, and $\mathbf{R} = \{\sigma_{ei,ej}\}$ are the row, column, plot, family, and residual variance-covariance matrices between traits i and j, denoting variance when $i = j$. **A** is the additive genetic relationship matrix. To ensure that the variance-covariance matrix was positive definite, restrictions were in some cases applied to the parameters. In cases with single-tree plots, the plot effects are omitted. The significance of seed source effects was assessed using F-tests.

Genetic parameters

Age-age and trait-trait genetic correlations and heritabilities were estimated simultaneously based on multivariate REML analysis using Model (4). Family variance (σ_f^2), phenotypic variance (σ_P^2), plot variance (σ_t^2), and environmental variance (σ_e^2) for different traits and ages were estimated using ASReml. The estimated variance components were used to calculate the narrow-sense heritabilities for the characters under consideration. Since open-pollinated families in the progeny test came from open-pollinated parent trees in wild stands or seed orchards, the additive genetic variance (σ_A^2) was estimated as three times the family variance component. Because some degree of inbreeding (about 10%) was expected, the coefficient of relationship was assumed to be 0.33, making heritability values more conservative than if a value of 0.25 was assumed (Squillace 1974). The additive genetic variance (σ_A^2), total phenotypic variance (σ_P^2), and individual-tree heritability ($\hat{h}^2$) estimates were calculated as follows:

$$\sigma_A^2 = 3\sigma_f^2 \tag{6}$$

$$\sigma_P^2 = \sigma_f^2 + \sigma_t^2 + \sigma_e^2 \text{ , and} \tag{7}$$

$$\hat{h}^2 = \frac{\sigma_A^2}{\sigma_f^2 + \sigma_t^2 + \sigma_e^2} \tag{8}$$

Coefficient of additive variation (CV_A), additive genetic correlation ($\hat{r}_A$) and phenotypic correlation ($\hat{r}_P$) between traits or between ages were estimated as:

$$CV_A = \frac{100\sigma_A}{\overline{x}} \tag{9}$$

$$\hat{r}_A = \frac{\sigma_{A1A2}}{\sigma_{A1}\sigma_{A2}} \tag{10}$$

$$\hat{r}_P = \frac{\sigma_{P1P2}}{\sigma_{P1}\sigma_{P2}} \tag{11}$$

where $\overline{x}$ is the phenotypic mean, σ_{A1A2} and σ_{P1P2} are the genotypic and phenotypic covariance between two traits, respectively. σ_{A1}, σ_{A2} and σ_{P1}, σ_{P2} are the genotypic and phenotypic standard deviations of trait 1 and trait 2, respectively. Standard errors of the estimates of heritabilities, genotypic, and phenotypic correlations were calculated using a standard Taylor series approximation implemented in the ASReml program (Gilmour *et al*. 2002).

The relative selection efficiency (RSE) for forward selection expressing the relative genetic gain per time unit was calculated according to Falconer & Mackay (1996):

$$RSE = r_A i_j h_j t_m / i_m h_m t_j \tag{12}$$

where r_A is the additive genetic correlation, i is the selection intensity, h is the square root of the heritability, t is the tree age at selection, and j and m are the indices for the juvenile and mature traits, respectively. The same selection intensity for the juvenile and mature traits was used in the calculations.

RESULTS
Seed Source Differences

There were significant differences between seed sources for diameter at breast height, volume, and the quality traits (bark thickness, pilodyn penetration, knot index, and wood density), but not for total height, forking, and straightness (Table 2). Trees descended from the Coen River provenance generally grew fastest, followed by those from Sakaerat (Thailand) and Morehead River. However, density and knot index of Sakaerat and Morehead River were higher than those of Coen River. At age 9 years, the mean values for Coen River were 13.1 m for height, 14.9 cm for diameter at breast height, 84.0 dm³/tree for volume, and 0.58 g/cm³ for density. The lowest density was found in Wenlock River (0.55 g/cm³), but its knot index was the best in the test (0.71).

Heritability and Coefficient of Variation Estimates

The family variance component was significantly different from zero for all studied traits at age 9 years (p<0.05). The individual heritabilities ($\hat{h}^2$) for growth traits

TABLE 2–Seed source means for studied traits at age 9 years in the progeny test.

CSIRO No.	HT (m)	DBH (cm)	STR	VOL (dm³/tree)	FOK	BRK (mm)	PIN (mm)	KI	DEN (g/cm³)
17961	12.4	14.4	1.8	68.8	3.0	6.0	6.9	1.26	0.57
17966	12.0	14.4	2.1	67.5	3.0	6.3	6.7	1.22	0.56
18854	11.7	14.3	2.3	65.1	3.0	5.8	7.0	0.90	0.58
18998	12.0	14.1	2.0	66.5	3.0	4.8	8.9	1.14	0.56
19244	12.2	14.4	1.9	71.8	2.8	5.1	8.5	0.94	0.56
19245	11.7	13.9	1.9	63.5	2.5	4.7	8.5	0.90	0.58
19246	11.2	13.6	1.8	62.0	2.6	4.9	8.2	1.14	0.57
19249	11.7	13.6	1.7	64.8	3.0	4.9	8.3	0.71	0.55
19250	13.1	14.9	1.9	84.0	3.2	5.6	7.9	1.16	0.58
19251	12.3	14.9	2.1	78.1	3.6	4.9	8.3	1.02	0.59
19254	12.3	14.6	1.7	72.8	2.9	5.4	7.7	1.03	0.56
19255	11.5	14.4	1.7	55.3	2.7	5.6	7.8	0.76	0.58
19326	12.4	15.3	1.8	80.3	2.8	5.8	7.8	0.87	0.59
F- test	n.s	**	n.s.	**	n.s.	**	***	**	*

HT = tree height; DBH = diameter at breast height; STR = straightness; VOL = tree volume; FOK = forking; BRK = bark thickness; PIN = pilodyn penetration; KI = knot index; DEN = wood density

n.s: not significant; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$

and straightness increased over time from age 3 to ages 5 and 9 years (Table 3). Before the first thinning, at age 3 years, height and diameter at breast height had $\hat{h}^2$ of 0.13 and 0.17, respectively, while at age 9 years, $\hat{h}^2$ for height, diameter at breast height, and volume were in the range 0.36 to 0.39. The heritabilities for wood quality traits were also high, 0.61 for density and 0.47 for pilodyn penetration. The heritabilities for stem quality traits were lower than for basic density, ranging from 0.12 to 0.39. Knot index had the lowest heritability (0.12). Coefficients of additive variation (CV_A) were high for growth traits at all ages, ranging from 4.5% to 26.2% and were very high for most quality traits (14.7 to 26.2%) at age 9. The value of CV_A for wood basic density was stable, at around 8 to 9% for the different ages. As with heritability, CV_A for growth traits increased over time.

The heritabilities for wood basic density also increased from corewood to outerwood (Table 3). The heritability for Segment 1 (DEN_1) was lowest (0.40), with mean basic density of 0.53 g/cm³. The heritabilities for Segment 2 (DEN_2) and Segment 3 (DEN_3) were higher than DEN_1 and stabilised at 0.55 compared to 0.61 for total core density.

Genetic Correlations

Trait-trait genetic correlations between growth and quality traits at age 9 years are shown in Table 4. The correlation between height and diameter at breast height

TABLE 3–Trial means, individual heritabilities and coefficients of additive genetic variation for the studied traits at ages 3, 5, and 9 years.

Trait	Unit	Trial mean	Age	$\hat{h}^2$	SE of $\hat{h}^2$	CV_A
HT3	m	7.38	3	0.13	0.07	4.5
HT5	m	9.84	5	0.14	0.06	5.4
HT9	m	12.19	9	0.36	0.10	11.2
DBH3	cm	7.93	3	0.17	0.06	6.7
DBH5	cm	11.06	5	0.24	0.07	6.8
DBH9	cm	14.83	9	0.36	0.09	7.0
VOL3	dm^3/tree	12.88	3	0.18	0.06	17.6
VOL5	dm^3/tree	33.11	5	0.24	0.07	19.7
VOL9	dm^3/tree	74.61	9	0.39	0.09	25.7
STR5	score	2.55	5	0.20	0.07	16.2
STR9	score	1.86	9	0.27	0.10	26.2
DEN	g/cm^3	0.58	9	0.61	0.12	8.3
DEN$_1$	g/cm^3	0.53	≈0–3	0.40	0.10	8.6
DEN$_2$	g cm^3	0.58	≈4–6	0.55	0.11	8.3
DEN$_3$	g/cm^3	0.63	≈7–9	0.55	0.12	9.0
BRK	mm	5.63	9	0.39	0.10	15.9
PIN	mm	7.73	9	0.47	0.11	14.7
FOK	score	2.9	9	0.31	0.10	20.7
KI		0.93	9	0.12	0.01	21.4

HT = tree height at 3, 5, and 9 years
DBH = diameter at breast height at 3, 5, and 9 years
VOL = tree volume at 3, 5, and 9 years
STR = straightness at 5 and 9 years
DEN = wood density basic and density of the three segments
BRK = bark thickness
PIN = pilodyn penetration
FOK = forking
KI = knot index

was strong (0.79). Similarly, straightness correlated strongly with the growth traits, 0.79 with height and 0.96 with diameter. There were low to moderate negative genetic correlations between wood density, pilodyn penetration, and knot index and the growth traits, but none of these relationships was significantly different from zero. A strong negative association was found between density and pilodyn penetration, with genetic correlation of –0.88. Straightness correlated strongly with the growth traits, but moderately with bark thickness. The correlations between knot index and the growth traits were negative and low. Forking had weak positive correlations with the growth traits. The correlations among the quality traits were weak, ranging from –0.24 to 0.50. The age-age genetic correlations for the growth traits and straightness were strong (0.64–0.99). Corresponding correlations for wood density were strong and close to unity (Table 5).

TABLE 4–Additive genetic (upper triangle), phenotypic correlations (lower triangle), and standard errors of correlations between and within growth, wood density, pilodyn penetration, and other quality traits at age 9 years

Trait	HT	DBH	DEN	PIN	STR	FOK	BRK	KI
HT		0.79±0.09	−0.07±0.18	−0.07±0.18	0.79±0.15	0.33±0.19	0.59±0.15	−0.45±0.28
DBH	0.70±0.02		−0.08±0.19	−0.06±0.18	0.96±0.13	0.37±0.20	0.65±0.13	−0.11±0.30
DEN	−0.06±0.02	−0.07±0.04		−0.88±0.05				
PIN	0.02±0.04	0.005±0.04	−0.08±0.04					
STR	0.40±0.03	0.43±0.03				0.30±0.22	0.50±0.20	0.47±0.35
FORK	0.24±0.03	0.19±0.04			0.32±0.03		0.16±0.21	−0.05±0.34
BRK	0.33±0.03	0.50±0.03			0.15±0.04	0.09±0.04		−0.24±0.31
KI	−0.21±0.04	−0.14±0.04			−0.02±0.04	−0.16±0.04	−0.02±0.04	

HT = tree height; DBH = diameter at breast height; DEN = wood density; PIN = pilodyn penetration; STR = straightness; FOK = forking; BRK = bark thickness; KI = knot index;

TABLE 5–Age-age additive genetic correlation (r_A), phenotypic correlation (r_P), standard error, age of selection for juvenile (t_j) and mature (t_m), and relative selection efficiency (RSE, expressed as genetic gain per time unit) of indirect selection at the juvenile age for mature traits.

Trait	r_A	r_P	t_j	t_m	RSE
HT3-HT5	0.91±0.13	0.66±0.02	3	5	1.46
HT3 HT9	0.64±0.17	0.53±0.03	3	9	1.16
HT5-HT9	0.91±0.08	0.83±0.01	5	9	1.01
DBH3-DBH5	0.99±0.12	0.72±0.02	3	5	1.39
DBH3-DBH9	0.86±0.10	0.53±0.03	3	9	1.79
DBH5-DBH9	0.93±0.05	0.76±0.01	5	9	1.31
STR5-STR9	0.87±0.18	0.27±0.03	5	9	1.37
VOL5-VOL9	0.91±0.05	0.80±0.01	5	9	1.27
DEN1-DEN2	0.97±0.05	0.66±0.02	3	6	1.65
DEN1-DEN3	1.02±0.03	0.80±0.01	3	9	2.61
DEN2-DEN3	0.99±0.02	0.91±0.01	6	9	1.49

Ages for the trait density are assumption

Relative Selection Efficiency

Forward selection for the growth traits and wood density was shown to give a higher genetic gain per time unit at ages 3 and 5 years than at age 9 (Table 5). Similarly, genetic gain per year was higher at age 5 than at age 9 for growth traits and straightness. Assuming that the tree core segments corresponded approximately to ages 0–3, 4–6, and 7–9 years, relative selection efficiency for wood density also decreased with the age of selection.

DISCUSSION

The natural provenances tested in the present study were selected on the basis of their known superior growth in earlier provenance trials in Vietnam, and were therefore not a random selection of provenances. Specifically, Papua New Guinea provenances were only represented via the seed orchard families and Northern Territory provenances were excluded. This reduced the expected differences compared to a random selection of provenances. However, significant differences among seed sources were found for all the traits studied in the test except height, straightness, and forking (Table 2). This indicated considerable potential for improvement in the growth and quality of *A. auriculiformis* through selecting among superior provenances. Coen River and Morehead River provenances grew faster than other seed sources. The result is consistent with findings from previous studies in Zaire, Thailand, and Vietnam (Kha 2003; Khasa *et al*. 1995; Luangviriyasaeng & Pinyopusarerk 2002; Mahat 1999; Nghia 2003). The slowest-growing provenances in the present study were those from Wenlock River.

The first-generation seedling seed orchard at Sakaerat was established from many natural provenances of Papua New Guinea, Queensland, and Northern Territory origin, and from Thai landrace families (Luangviriyasaeng & Pinyopusarerk 2002). Thai landraces were the poorest performing in all tests and their exclusion from the improvement programme of *A. auriculiformis* in Thailand was recommended (Luangviriyasaeng & Pinyopusarerk 2002). The families from this orchard were collected primarily from mother trees of Queensland provenance origin, and displayed the best growth in the trial, which may reflect the intensity of selection and/or hybrid vigour from combinations among many different provenances. In contrast, the families selected from the Melville Island seed orchard, derived solely from Papua New Guinea provenances, did not display outstanding vigour.

Trees from Morehead River provenance had the highest wood density (0.59 g/cm^3) in this study, followed by those from the Sakaerat and Melville Island seed orchards and Coen River. Khasa *et al*. (1995) also found significant differences between provenances for wood density in Zaire, with provenance means ranging from 0.49 to 0.53 g/cm^3 at age 21 months.

Heritability and Coefficient of Variation Estimates

At age 3 years, estimates of heritabilities for growth traits were low, but still higher than those in a previous study in Thailand (Luangviriyasaeng & Pinyopusarerk 2002). In *A. crassicarpa* and *A. mangium* Willd., Arnold & Cuevas (2003) estimated that heritabilities for growth traits and stem straightness were low to very low (0.07 to 0.15) with the exception of straightness in *A. crassicarpa* which was moderate (0.25). In the present study, heritabilities for growth traits, straightness, and density increased with age. The heritabilities for the wood and stem quality traits density, pilodyn penetration, bark thickness, and forking were moderate to high, at 0.61, 0.47, 0.39, and 0.31, but that for knot index was low (0.12). Our results suggest that considerable response to selection could be expected for growth, straightness, density, pilodyn penetration, bark thickness, and even knot index. There are no other reports on the individual heritability estimates for density, pilodyn penetration, bark thickness, and knot index available for comparison.

High heritabilities and CV_A in the present study would have been influenced by the two within-family selective thinnings carried out at ages 3 and 5 years. Up to three trees from each original four-tree family plot were removed, but all families were retained in the trial. This may have reduced the error variance. Heritabilities for height and diameter at breast height at age 9 years were substantially higher than those at age 3 years prior to the first thinning and age 5 years prior to the second thinning. This result was in accordance with a previous study of *Pinus radiata* D.Don (Matheson & Raymond 1984). Here, the authors reported that heritability estimates for unthinned plots were much lower than for thinned plots

in two progeny trials. By contrast, in analysis based only on trees remaining after thinning in *Eucalyptus urophylla* S.T.Blake, Wei & Borralho (1998) reported lower estimates of heritabilities and age-age genetic correlations for thinned plots than for unthinned plots, but genetic parameters for pilodyn penetration and bark thickness were not affected by the thinning.

The CV_A for all studied traits were in accordance with the general range of values presented in a review on forest tree species (Cornelius 1994). The CV_A for quality traits were high and ranged from 15.9 to 26.2%. Reports on heritability and CV_A for *A. auriculiformis* are scarce. However, in another *Acacia* species (*A. nilotica* Willd. ex Dil.), Ginwal & Mandal (2004) reported that the CV_A were 7.3% for height and 6.6% for diameter at breast height in a 6-year-old trial in India. In *E. urophylla*, Wei & Borralho (1997) reported high CV_A for pilodyn penetration and bark thicknesss in four progeny tests in China.

Genetic Age-age Correlations

High genetic age-age correlations for growth traits and straightness between ages 5 and 9 were observed in this study (Table 5). The magnitude and trend in genetic age-age correlations estimated in this study are in accordance with earlier provenance-level studies on the same species (Khasa *et al*. 1995). The high genetic correlations, close to unity, for wood density between Segments 1, 2, and 3 indicate high age-age genetic correlations for wood density. Nevertheless, a potential source of error is the thinning at ages 3 and 5, as sampling for wood density was done only on the retained stems. One hypothesis for high genetic age-age correlations for wood density is that these traits are influenced by a lower number of genes than growth traits, which generally show lower genetic age-age correlations than wood density (Dieters *et al*. 1995; Hannrup & Ekberg 1998; Hodge & White 1992; Xie & Ying 1996).

Genetic Correlations Between Quality Traits and Growth Traits

Genetic correlations between the quality traits (pilodyn penetration, density, and knot index) and the growth traits (height and diameter at breast height) at age 9 years were low and unfavourable with large standard errors. The relationships between growth traits and forking, and bark thickness were favourable, but still low to moderate. The moderate heritabilities for height and diameter at breast height, and the relatively small sample size (total of 1120 trees from 134 families) contributed to the uncertainty of estimation of these correlations. However, the growth traits were strongly correlated with straightness. In a study of *A. auriculiformis* in a clonal test in Vietnam, high trait-trait correlations were also found between the growth traits and straightness were also found (Hai *et al*. 2008). In provenance trials in Zaire growth traits were not correlated to survival, number of stems, straightness, branch angle, and wood density (Khasa *et al*. 1995). Also, genetic

correlations between quality traits and growth traits in *Eucalyptus* species have been reported weak and often unfavourable (Greaves *et al*. 1996; Wei & Borralho 1997). Examination of a plot of breeding values of diameter at breast height and total core density (DEN) for the families and seed sources in our trial confirms the possibility of selecting simultaneously for improved growth and wood density at both the provenance and family levels for *A. auriculiformis* in northern Vietnam. The feasibility of clonal forestry using selected individuals of *A. auriculiformis* mass-propagated from stem cuttings (Hai *et al*. 2008) will enable effective capture of favourable non-additive genetic variation as well as additive genetic variation that is obtained through sexual breeding

The genetic correlation between pilodyn penetration and wood basic density was strong and negative, with lower density resulting in higher penetration. The strong correlation indicated that pilodyn penetration is generally reliable as an indirect measure of wood basic density in *A. auriculiformis*. There is no other report on genetic correlation between pilodyn penetration and wood basic density in *Acacia* species. However, strong correlations were found in *Eucalyptus* species (Greaves *et al*. 1996, 1997; Wei & Borralho 1997)

Implications for Tree Improvement in *A. auriculiformis*

The selective thinning of the trials and the limited number of repeat measurements meant that the optimum selection age for the studied traits could not be reliably determined in this study. However, the results indicated that the optimum age of selection could be as little as 3 years for growth traits and wood density. Similarly, Raymond (2002) reported that the early selection of wood basic density could be made at age 3 years with high heritability in *Eucalyptus* species. It should be relatively easy to select at this age for growth, stem straightness, and wood density or pilodyn penetration. Forking, bark thickness, and knot index cannot be selected for effectively at 3 years in northern Vietnam because trees, with a mean height of about 7 m and mean 8 cm dbh, have not attained sufficient size; 5 years is probably the minimum age for the expression of these traits. Our data demonstrate strong potential for gains in growth both within and between seed sources. However, improvement based on growth traits alone could prejudice some quality traits, such as wood basic density, knot index, and bark thickness. For selection of superior individuals, a selection index assigning appropriate weights to wood density, knot index, and volume should be defined, with the exact coefficients dependent on the specific breeding objectives (Borralho *et al*. 1993).

CONCLUSION

In a provenance-progeny trial of *A. auriculiformis* in northern Vietnam, significant differences between seed source and families were found for most studied traits,

with the exception of height, forking, and stem straightness at the seed source level. Heritabilities of growth traits were low to moderate, with high age-age correlations. Also, wood density was under strong genetic control, as indicated by direct measurements on increment cores or indirect measurement of pilodyn penetration. These two traits were highly correlated, confirming that pilodyn penetration is a useful predictor of wood basic density in this species. Straightness, bark thickness, and forking had moderate heritabilities, while knot index had low heritability. High age-age correlations for wood density and stem straightness indicate that selection of the best families for these traits could be carried out at a young age (3–5 years). Genetic correlations between quality traits (pilodyn penetration, wood density, forking, bark thickness, and knot index) and growth traits were weak and unfavourable with large standard errors. The substantial coefficients of additive genetic variation and significant heritabilities for most traits indicate that it should be possible to use a selection strategy that combines improvements in growth, stem, and wood quality for *A. auriculiformis* in northern Vietnam.

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