GENETIC CONTROL OF GROWTH AND FORM IN *EUCALYPTUS UROPHYLLA* IN NORTHERN VIETNAM

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KIEN ND, JANSSON G, HARWOOD C & THINH HH. 2009. Genetic control of growth and form in *Eucalyptus urophylla* in northern Vietnam. Genetic parameters for growth, stem straightness and branch size were estimated in two open-pollinated progeny trials of *Eucalyptus urophylla* at two sites in northern Vietnam. Each trial tested 144 open-pollinated families from nine natural provenances, with 134 of these families being common to both trials. Height (HT) and diameter at breast height (DBH) were measured at ages 1, 2, 3 and 5 years in both trials, also at age 8 years in one trial, and at ages 7 and 9 years in the other trial. Stem straightness (STR) and branch size (BRA) were assessed at age 5 years and at the final measurement. At age 5 years, the Lewotobi provenance displayed the fastest growth, with only minor differences among other provenances. Growth traits had within-provenance, narrow-sense heritabilities ranging from 0.10 to 0.31. Heritability for DBH increased with age, but for HT it became stable after age two years. Coefficients of additive genetic variation for growth traits ranged from 7.3 to 12.4%. Heritabilities for STR and BRA were from 0.09 to 0.22. Age–age genetic correlations for growth traits between earlier and later measurements increased with age from 0.27 to 0.97. The genetic correlations between growth (DBH, HT) and form (STR, BRA) were weak to moderate. Genetic correlations between sites for DBH and HT increased with age and became stable after age 3 years. Optimum selection efficiency for growth traits was reached at age 2 or 3 years, depending on the anticipated plantation rotation age.

Keywords: Provenance, heritability, age–age correlation, genotype by environment interaction, longitudinal data analysis, optimum selection age

KIEN ND, JANSSON G, HARWOOD C & THINH HH. 2009. Kawalan genetik pertumbuhan dan bentuk *Eucalyptus urophylla* di utara Vietnam. Parameter genetik bagi pertumbuhan, kelurusan batang dan saiz dahan dianggarkan dalam dua ujian progeni pendebungaan bebas bagi *Eucalyptus urophylla* yang dijalankan di dua tapak di utara Vietnam. Dalam setiap ujian, 144 famili pendebungaan bebas yang terdiri daripada sembilan provenans asli diuji. Sebanyak 134 daripada famili tersebut didapati dalam kedua-dua ujian. Ketinggian (HT) dan diameter aras dada (DBH) diukur pada usia satu, dua, tiga dan lima tahun dalam kedua-dua ujian. Selain itu, kedua-dua parameter ini diukur pada usia lapan tahun dalam satu ujian dan tujuh serta sembilan tahun dalam ujian yang satu lagi. Kelurusan batang (STR) dan saiz dahan (BRA) dinilai pada usia lima tahun dan juga pada ukuran terakhir. Pada usia lima tahun, provenans Lewotobi menunjukkan pertumbuhan paling cepat sedangkan provenans lain sekadar menunjukkan perubahan kecil. Antara provenans, ciri pertumbuhan mempunyai keterwarisan erti sempit dan berjulat antara 0.10 hingga 0.31. Keterwarisan DBH meningkat dengan usia tetapi HT menjadi stabil selepas dua tahun. Pekali variasi genetik tambahan bagi ciri pertumbuhan adalah antara 7.3% hingga 12.4%. Keterwarisan STR dan BRA adalah antara 0.09 hingga 0.22. Korelasi genetik usia–usia bagi ciri pertumbuhan antara ukuran awal dan ukuran yang kemudian meningkat dengan usia dan mempunyai nilai antara 0.27 hingga 0.97. Korelasi genetik antara pertumbuhan (DBH, HT) dan bentuk (STR, BRA) adalah lemah hingga sederhana. Korelasi genetik antara tapak bagi DBH dan HT meningkat dengan usia dan menjadi stabil selepas usia tiga tahun. Kecekapan pemilihan optimum bagi ciri pertumbuhan dicapai pada usia dua atau tiga tahun bergantung pada usia yang dijangka bagi giliran ladang.

INTRODUCTION

As the global population grows and areas of native forest decreases, tree plantations and agroforestry have become an increasingly important source of timber, fuelwood and raw materials for pulp and

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paper, particularly in developing countries. From these new forests, species of the genus *Eucalyptus* are now being widely used throughout the world to provide wood products in regions of scarcity of wood and other tree products. The total area of eucalypt plantation in the world in the year 2000 was nearly 18 mil ha, mainly in South America, China, India, South Africa and South-East Asia (FAO 2000).

For nearly 20 years, eucalypts have been important species for plantations in Vietnam at elevations below 800 m, where they are grown to produce pulpwood and poles for construction purposes. The total area of eucalypt plantations in Vietnam in 2001 was 348 000 ha, which represent about 30% of the total plantation area (MARD 2002).

Eucalyptus urophylla occurs naturally in Indonesia, with the most extensive natural populations occurring on the islands of Alor, Flores, Pantar, Timor and Wetar. The popularity of this species for plantations has increased markedly in humid and subhumid tropical climates of Africa, Latin America, southern China and South-East Asia (Eldridge *et al.* 1993). It is planted as a pure species but has also become very important as a parental species in hybrid combinations such as *E. grandis* × *E. urophylla*. Intensive breeding and silviculture have been reported to raise mean annual increment of clonal plantations of *E. urophylla* hybrids to between 33 and 70 m^3 ha^{-1} $year^{-1}$ in southern China (Yang 2003) and Brazil (Turnbull 1999).

Eucalyptus urophylla was introduced into Vietnam in the 1980s (Tai 1994). It has performed well on sites with reasonably deep soils in central and northern Vietnam and also in areas in the central highlands where elevation is below 900 m (Kha *et al.* 2003), and it has been widely planted since the early 1990s. The total plantation area of *E. urophylla* and its interspecific hybrids established up to the end of 2001 was about 200 000 ha, mainly in the provinces Phu Tho, Vinh Phuc, Yen Bai, Thai Nguyen and Quang Ninh in northern Vietnam (MARD 2002). The species is mainly used for pulpwood, fibreboard and mining timber. The rotation age in Vietnam is six to eight years for pulpwood.

Despite its importance in plantation forestry, the productivity of *E. urophylla* plantations in Vietnam is still poor (8–10 m^3 ha^{-1} $year^{-1}$). One reason is the lack of genetically-improved planting material. To initiate a genetic improvement programme, provenance trials were established in the early 1990s in northern and central Vietnam. Some promising provenances such as Lembata, Lewotobi and Egon from Flores Island were identified (Kha *et al.* 2003). It is valuable when developing breeding strategies to have estimates of genetic parameters of economically important traits; in this case growth, stem form, wood properties and disease resistance. Estimating genetic correlations between traits of interest and genotype by environment interaction (G × E) is also necessary in proposing the basis for setting up breeding populations and selecting environmentally stable genotypes. Some information on genetic parameters for *E. urophylla* is available from Brazil (Mori *et al.* 1988, Santos *et al.* 1990), Indonesia (Kurinobu *et al.* 1996, Nirsatmanto *et al.* 1996), Philippines (Arnold & Cuevas 2003) and China (Wei & Borralho 1998b). However, unlike Indonesia, Philippines and Brazil, northern Vietnam experiences a cool and dry winter and soils available for planting are generally degraded and of low fertility.

The aims of this study were (1) to estimate genetic parameters including genotype by environment interaction and the optimal age for selection for growth traits in two progeny trials of *E. urophylla* in northern Vietnam and (2) to consider the implications for its genetic improvement.

MATERIALS AND METHODS

Genetic material

Open-pollinated seeds were collected from randomly selected trees located in nine provenances in Flores, Wetar, Pantar and Alor islands in Indonesia (Table 1). The parent trees of all provenances tested were situated at elevations of less than 600 m. Higher-elevation provenances, from earlier trials in other tropical countries known to display slower growth (CABI 2000), were not included. Pryor *et al.* (1995) has suggested that populations on Wetar, the easternmost island with natural stands of *E. urophylla*, are a separate species, *E. wetarensis*, due to differences in their capsule morphology and other traits. However, this newer classification has not been widely accepted internationally (CABI 2000) and is not followed here.

Table 1 *Eucalyptus urophylla* provenance origins and numbers of families sampled per provenance

CSIRO seedlot	Provenance	Latitude	Longitude	Altitude (m)	No. of families	
					Ba Vi	Van Xuan
17564	Mandiri, Flores	8° 15' S	122° 58' E	410	9	11
17565	Lewotobi, Flores	8° 32' S	122° 48' E	375	31	35
17567	Egon, Flores	8° 38' S	122° 27' E	450	36	36
17831	N Ilwaki, Wetar	7° 52' S	126° 27' E	515	19	13
17836	SW Uhak, Wetar	7° 39' S	126° 29' E	350	22	25
17840	Wai Kui, Alor	8° 14' S	124° 44' E	540	5	5
17841	Piritumas, Alor	8° 19' S	124° 31' E	355	9	8
17842	Dalaki, Pantar	8° 31' S	124° 05' E	440	5	5
17843	Baubilatung, Pantar	8° 20' S	124° 02' E	285	8	6

Description of sites and trial design

A total of 144 families were planted in two progeny tests located at Ba Vi (1997) and Van Xuan (1996) in the north central region of Vietnam (Table 2) with 134 families being common to both sites. Individual provenances were represented by between 5 and 36 families at each site. Both trial sites have climatic and soil conditions typical of the areas where *E. urophylla* is planted in northern Vietnam. The soil is a degraded ferralitic clay-loam (Chieu & Thuan 1996) with general loss of topsoil through erosion and a depth of 40–70 cm to parent material. The soil has low fertility, with low levels of nitrogen, phosphorus and potassium (Chieu & Thuan 1996). The mean annual rainfall at both sites is between 1700 and 1800 mm, with a peak from May to October.

In both trials, 144 open-pollinated families were planted as four-tree row plot in a row-column design (Williams & Matheson 1994) with eight replicates. Rows and columns were treated as incomplete blocks within replicates of 12 rows × 12 columns. The tree spacing was 4.0 × 1.5 m. Further details on trial layout and establishment are given in Table 2. Both trials were thinned after the second-year measurement to convert progeny trials to seedling seed orchards, reducing stocking from four trees to one tree per plot. The thinning generally retained the largest, straightest tree in each plot but with the restriction that within planting rows, retained trees were not immediately adjacent, i.e. were at least 3 m apart. In Ba Vi, after 5 years, an additional thinning was conducted by removing the worst families and some poor trees from other families, leaving 127 families with four to eight trees per family. Comparisons of provenance effects were therefore based on five-year data in Ba Vi, i.e. before removing the worst families.

Diameter at breast height (DBH) and height (HT) were measured on all surviving trees, at ages 1, 2, 3, 5 and 8 years at Ba Vi, and 1, 2, 3, 5, 7 and 9 years at Van Xuan. Stem straightness (STR) and branch size (BRA) were assessed subjectively at ages 5 and 8 years in Ba Vi and 5 and 9 years in Van Xuan, using a five-class absolute scale by Kha and Hung (1998), where class 3 denotes acceptable stem straightness and branch size, class 1 denotes a very crooked stem or very thick branches, and class 5 denotes a very straight stem or very thin branches.

Statistical analysis

The data analyses were implemented using the ASReml software (Gilmour *et al.* 2006). Statistical analyses were conducted in two stages. Firstly, each trial was analysed separately to estimate narrow-sense heritabilities within provenances (h^2), coefficients of additive genetic variation (CV_A) and age–age genetic correlations for DBH, HT, STR and BRA and correlations between these traits. Secondly, genetic correlations between sites and across-site heritabilities for each trait were also estimated.

Since class frequencies for STR and BRA scores were not normally distributed, they were linearized by a normal score transformation

Table 2 Description of the progeny trial sites

Trial	Ba Vi	Van Xuan
Latitude	21° 08' N	21° 15' N
Longitude	105° 28' E	105° 15' E
Altitude	60 m	36 m
Soil type	Degraded ferralitic clay loam	Degraded ferralitic clay loam
Soil depth	40–50 cm	50–70 cm
Annual rainfall	1700 mm	1800 mm
Rainy season	May–September	April–October
Dry season	October–April	November–March
Mean annual temperature (°C)	23.2	23.1
Mean daily maximum temperature of hottest month (°C)	31.8	31.2
Mean daily minimum temperature of coldest month (°C)	14.3	14.7
Planting date	May 1997	May 1996
Site preparation	Ploughed (both sites)	
Fertiliser (kg ha^{-1})	3300 kg cattle manure + 330 kg NPK (both sites)	
Design	Row-column design, 8 replicates, 12 rows and 12 column, 4 tree-row plot (both sites)	
Spacing	4 m between rows × 1.5 m within rows (both sites)	
Number of families	144	144

(Norton & Gianola 1981). 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' (Norton & Gianola 1981) in order to adjust for non-adequate or variable spacing of classes and to improve the efficiency of subsequent analyses (Ericsson & Danell 1995).

Since thinning at an early stage and mortality occurred at all sites, a longitudinal multivariate analysis approach was applied to minimize the effects of reducing the number of trees in the progeny tests. This approach of using data on all trees prior to thinning and then measurements of only those that remained should result in almost unbiased estimates of genetic parameters (Wei & Borralho 1998a, Apiolaza *et al.* 2000).

It was not possible to analyse all the traits in one run. Therefore, subsets of data were analysed together, DBH or HT at different ages to estimate genetic parameters, age–age correlations; DBH and HT at similar ages to estimate correlations between them; all traits at age 5 and 8 or 9 years to estimate correlation between growth (DBH, HT) and form traits (STR, BRA) respectively.

Single-site analysis

The following general linear mixed model equation was used in the analyses based on individual tree observations:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_W\mathbf{w} + \mathbf{Z}_C\mathbf{c} + \mathbf{Z}_T\mathbf{t} + \mathbf{Z}_U\mathbf{u} + \mathbf{e} \quad (1)$$

with
$\mathbf{y} = (\mathbf{y}'_1, \mathbf{y}'_2, \ldots, \mathbf{y}'_n)'$, $\mathbf{b} = (\mathbf{b}'_1, \mathbf{b}'_2, \ldots, \mathbf{b}'_n)'$,
$\mathbf{w} = (\mathbf{w}'_1, \mathbf{w}'_2, \ldots, \mathbf{w}'_n)'$, $\mathbf{c} = (\mathbf{c}'_1, \mathbf{c}'_2, \ldots, \mathbf{c}'_n)'$,
$\mathbf{t} = (\mathbf{t}'_1, \mathbf{t}'_2, \ldots, \mathbf{t}_n)'$, $\mathbf{u} = (\mathbf{u}'_1, \mathbf{u}'_2, \ldots, \mathbf{u}'_n)'$,
$\mathbf{e} = (\mathbf{e}'_1, \mathbf{e}'_2, \ldots, \mathbf{e}'_n)'$, $\mathbf{X} = \Sigma_{\oplus}\mathbf{X}_n$, $\mathbf{Z}_W = \Sigma_{\oplus}\mathbf{Z}_{W_n}$, $\mathbf{Z}_C = \Sigma_{\oplus}\mathbf{Z}_{C_n}$, $\mathbf{Z}_T = \Sigma_{\oplus}\mathbf{Z}_{T_n}$, and $\mathbf{Z}_U = \Sigma_{\oplus}\mathbf{Z}_{U_n}$

and
- $\Sigma_{\oplus}$ = the direct sum
- n = number of traits from 1 to n
- **y** = the vector of individual tree observations
- **b** = the vector of fixed effects, including replicate and provenance effects
- **w** = the vector of random row within replicate effect
- **c** = the vector of random column within replicate effect
- **t** = the vector of random plot within replicate effects

u = the vector of random individual effects
e = the vector of random residuals.

X, $\mathbf{Z_W}$, $\mathbf{Z_C}$, $\mathbf{Z_T}$, and $\mathbf{Z_U}$ are incidence matrix relating **b**, **w**, **c**, **t**, and **u** to **y**. The random effects were assumed to follow an independent multivariate normal distribution with zero means and (co)variances

$$V\begin{bmatrix}\mathbf{w}\\ \mathbf{c}\\ \mathbf{t}\\ \mathbf{u}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{W}\otimes\mathbf{I} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{C}\otimes\mathbf{I} & \mathbf{0} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{T}\otimes\mathbf{I} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{G}\otimes\mathbf{A} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{R}\otimes\mathbf{I}\end{bmatrix}$$

where

0 = a null matrix
I = an identity matrix of order equal to the total number of rows, columns, plots, genetic, and residuals respectively
⊗ = direct (Kronecker) product operation.

$\mathbf{W} = \{\sigma_{w_i w_j}\}$, $\mathbf{C} = \{\sigma_{c_i c_j}\}$, $\mathbf{T} = \{\sigma_{t_i t_j}\}$, $\mathbf{G} = \{\sigma_{u_i u_j}\}$ and $\mathbf{R} = \{\sigma_{e_i e_j}\}$ are the row, column, plot, additive genetic and residual variance–covariance matrices between traits *i* and *j*, denoting variance when *i* = *j* and **A** = the numerator 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 were omitted.

Studies of out-crossing rate in the natural populations of *E. urophylla* using isozyme (House & Bell 1994) or RAPD (Gaioto *et al.* 1997) indicated out-crossing around 0.9, which is higher than that reported in other *Eucalyptus* species. The selfing rate was therefore assumed to be 0.1 (corresponding to a relationship of $^1/_3$) and this coefficient was included in the individual model in ASReml to estimate the additive genetic variance ($\hat{\sigma}^2_A$).

The significance of provenance effects was assessed using F-tests and provenance performance was grouped by least significant difference (LSD) calculated as:

LSD = $t_{0.05}$(degree of freedom of residual error) × standard error of difference between means

Genetic correlations between sites were estimated based on multivariate REML analysis, by treating measurements from different sites as different traits based on model (1). In **R**, all off-diagonal elements were assumed to be zero for a combination of traits measured in different trials.

Across-site analysis

The aim of this analysis was to estimate heritabilities of traits pooled across sites. The following univariate mixed linear model was applied in the pooled analysis:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z_W w} + \mathbf{Z_C c} + \mathbf{Z_T t} + \mathbf{Z_U u} + \mathbf{Z_Q q} + \mathbf{e} \quad (2)$$

i.e. model (1) extended with $\mathbf{Z_Q q}$ where

q = the vector of the effect of family by site (G × E) interaction
$\mathbf{Z_Q}$ = the corresponding incidence matrix.

In model (2) **Xb** also include the fixed site effect. Before conducting the pooled analysis, data was standardized to the same additive variance by dividing it by the square root of family variance from each site. This eliminates the effect of heterogeneous genetic variances across different sites.

Genetic parameters

Within-provenance heritabilities at single sites ($\hat{h}^2$) and across-site heritabilities ($\hat{h}^2_p$), coefficient of additive genetic variation (CV_A), additive genetic correlation ($\hat{r}_g$) and phenotypic correlation ($\hat{r}_p$) between traits or between ages were estimated as:

$$\hat{h}^2 = \frac{\hat{\sigma}^2_A}{\hat{\sigma}^2_A + \hat{\sigma}^2_T + \hat{\sigma}^2_E}$$

$$\hat{h}^2_p = \frac{\hat{\sigma}^2_A}{\hat{\sigma}^2_A + \hat{\sigma}^2_{fs} + \hat{\sigma}^2_T + \hat{\sigma}^2_E}$$

$$CV_A = \frac{100\hat{\sigma}_A}{\overline{X}}$$

$$\hat{r}_g = \frac{\hat{\sigma}_{A_1 A_2}}{\hat{\sigma}_{A_1}\hat{\sigma}_{A_2}}$$

$$\hat{r}_P = \frac{\hat{\sigma}_{P_1 P_2}}{\hat{\sigma}_{P_1}\hat{\sigma}_{P_2}}$$

where
$\bar{X}$ = mean value of the trait
$\hat{\sigma}^2_{fs}$ = family by site interaction variance
$\hat{\sigma}^2_T$ = plot variance (row by column), which is equal to zero in cases of single tree plots
$\hat{\sigma}^2_E$ = the environmental variance.

Standard errors of the estimates of heritabilities, genetic and phenotypic correlations were calculated using a standard Taylor series approximation in the ASReml software (Gilmour *et al.* 2006). Provenance normal score values ($\hat{u}$) were converted into percentage value (P) centred around a reference value (P_{ref}) using (Ericsson & Danell 1995)

$$P = 100\ \Phi\ (\Phi^{-1}(P_{ref}) - \hat{u})\ \%$$

where Φ is the standard normal distribution function. In our calculations of STR and BRA we used a reference value of 80%, which approximately corresponded to the average percentage of trees having acceptable STR and BRA in the trials.

Trends in genetic parameters

A simple model using the logarithm of age was used to test the trend in heritability of each trait:

$$h^2 = a + b\ln(\text{age})$$

The following model (Lambeth 1980) was used to predict additive genetic age–age correlations:

$$r_{g_{age1,age2}} = a + b(LAR)$$

where
a and b = intercept and slope respectively in a linear regression of the models above
$LAR = \ln\left(\frac{age1}{age2}\right)$, i.e. the logarithm of the ratio between measurement at a younger age (*age 1*) and an older age (*age 2*).

Efficiency of early selection for forward selection relative to gain from selection at mature age was estimated as (Falconer & Mackay 1996):

$$E = \frac{r_{g_{jm}} h_j (m + t)}{h_m (j + t)}$$

where
E = the efficiency of early selection relative to gain from selection at rotation age, i.e. E = 1 for selection at rotation age
$r_{g_{jm}}$ = age–age genetic correlation between age j and rotation age (m)
h_j and h_m = square root values of heritability of trait at age j and rotation age m respectively
t = the time lag for breeding activities, e.g. selection, grafting, early flowering in clone bank and crossing.

RESULTS

Provenance performance

Provenance performance at age 5 years (Ba Vi) and 9 years (Van Xuan) is shown in Table 3. The provenance means for all traits at Ba Vi are given at age 5 years as the worst families were thinned after measurement. The F-statistic showed significant differences between provenances in all traits measured. The Lewotobi provenance grew significantly faster than all other provenances, and had the best straightness and acceptable branch size at both sites. The differences in growth rate among all other provenances in the trials were generally not significant. It should be noted that within-plot selection had been done at age 2 years, possibly biasing results at later ages.

Heritabilities and in single sites

Within-provenance individual-tree heritabilities ($\hat{h}^2$) and coefficients of additive genetic variation (CV_A) from the single-site analyses are shown in Table 4. It appears that all traits measured are under weak to moderate genetic control in both trials, with heritability for DBH increasing with age to 0.31 by age 8–9 years, and similarly for HT to 0.24, with standard error of estimation between 0.03 and 0.08 for both traits. The coefficient of additive genetic variation (CV_A) estimated for DBH ranged from 8.7 to 12.4% and for HT from 7.3 to 11.2%. The heritabilities for STR were from 0.17 to 0.22 and from 0.09 to 0.14 for BRA. Generally, heritabilities estimated for DBH and HT increased with age, but CV_A tended to be stable at both sites. Heritabilities for HT became stable from age 2 years and averaged heritabilities across ages for DBH and HT were about 0.20 at both sites.

Table 3 Provenance means for diameter at breast height (DBH), height (HT), stem straightness (STR) and branch size (BRA) at Ba Vi and Van Xuan

Provenance	Ba Vi (5 years)				Van Xuan (9 years)			
	DBH (cm)	HT (m)	STR (%)	BRA (%)	DBH (cm)	HT (m)	STR (%)	BRA (%)
Mandiri Flores	11.4	12.6	79.8	73.5	15.8	16.5	83.1	81.5
Lewotobi Flores	13.6	15.2	87.9	85.7	17.8	18.1	86.0	84.2
Egon Flores	12.1	13.1	81.8	81.6	16.4	17.5	83.0	83.0
N Ilwaki Wetar	11.8	13.6	86.3	88.0	15.9	16.2	84.0	81.0
SW Uhak Wetar	10.9	13.5	84.2	85.0	15.4	16.2	88.1	87.4
Wai Kui Alor	11.8	13.0	67.1	76.2	16.3	17.1	73.0	79.6
Piritumas Alor	12.2	12.7	78.7	68.9	16.0	15.6	73.4	77.1
Dalaki Mt Pantar	12.3	13.4	63.2	68.5	16.2	15.6	70.2	72.2
Baubillatung Pantar	11.5	13.5	83.9	86.0	16.3	16.9	81.2	78.6
Trial mean	12.1	13.1	79.2	79.3	16.2	16.7	80.2	80.5
p-value for differences between provenances	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.004
Least Significant Difference (LSD) at 5%	0.8	0.8	7.1	7.1	1.1	1.0	7.0	6.9

Note: STR and BRA were expressed as percentage of trees having acceptable stem straightness and branch size.

Table 4 Within provenance heritability with standard error (SE) and coefficient of additive genetic variation (CVA) estimated for diameter at breast height (DBH), height (HT), stem straightness (STR) and branch size (BRA) at Ba Vi and Van Xuan

Trials	Age	No. of trees	DBH			HT			STR	BRA
			Mean (cm)	h^2 ± SE	CV_A (%)	Mean (cm)	h^2 ± SE	CV_A (%)	h^2 ± SE	h^2 ± SE
Ba Vi	1	4458	1.9	0.10 ± 0.03	10.1	2.4	0.13 ± 0.03	9.5		
	2	4274	5.0	0.12 ± 0.03	10.3	5.5	0.22 ± 0.04	11.2		
	3	1106	8.5	0.18 ± 0.04	9.2	9.0	0.18 ± 0.04	9.2		
	5	1053	12.1	0.25 ± 0.06	12.4	13.1	0.19 ± 0.04	9.8	0.22 ± 0.07	0.14 ± 0.07
	8	611	18.1	0.31 ± 0.08	10.6	18.9	0.24 ± 0.08	10.2	0.21 ± 0.07	0.09 ± 0.07
	Average for all ages			0.18	10.5		0.19	10.0	0.21	0.11
Van Xuan	1	4408	2.3	0.13 ± 0.03	8.7	2.9	0.13 ± 0.04	7.3		
	2	4254	4.9	0.16 ± 0.03	9.3	6.2	0.19 ± 0.04	9.8		
	3	1137	8.4	0.23 ± 0.06	9.4	8.7	0.22 ± 0.06	8.9		
	5	1086	12.3	0.26 ± 0.06	10.8	14.3	0.23 ± 0.06	9.3	0.18 ± 0.07	0.14 ± 0.07
	7	1032	14.8	0.28 ± 0.07	11.3	15.6	0.21 ± 0.06	10.5		
	9	985	16.5	0.27 ± 0.08	10.5	16.8	0.23 ± 0.07	9.8	0.17 ± 0.07	0.14 ± 0.06
	Average for all ages			0.22	10.0		0.20	9.26	0.17	0.14

Table 5 Age–age phenotypic (below diagonal) and genetic correlations (above diagonal) and standard errors for diameter at breast height (DBH) and height (HT) at Ba Vi and Van Xuan

(a) Ba Vi

	DBH1	DBH2	DBH3	DBH5	DBH8
DBH1		0.72 ± 0.10	0.63 ± 0.15	0.48 ± 0.16	0.30 ± 0.15
DBH2	0.71 ± 0.01		0.84 ± 0.08	0.66 ± 0.11	0.52 ± 0.12
DBH3	0.56 ± 0.02	0.71 ± 0.01		0.86 ± 0.06	0.70 ± 0.11
DBH5	0.45 ± 0.02	0.64 ± 0.01	0.84 ± 0.01		0.97 ± 0.05
DBH8	0.28 ± 0.03	0.48 ± 0.02	0.59 ± 0.02	0.85 ± 0.01	
	HT1	HT2	HT3	HT5	HT8
HT1		0.87 ± 0.06	0.70 ± 0.13	0.51 ± 0.16	0.27 ± 0.15
HT2	0.70 ± 0.01		0.85 ± 0.07	0.78 ± 0.11	0.59 ± 0.13
HT3	0.54 ± 0.02	0.81 ± 0.01		0.91 ± 0.13	0.71 ± 0.11
HT5	0.45 ± 0.02	0.70 ± 0.02	0.81 ± 0.01		0.90 ± 0.06
HT8	0.32 ± 0.03	0.55 ± 0.03	0.68 ± 0.03	0.83 ± 0.01	

(b) Van Xuan

	DBH1	DBH2	DBH3	DBH5	DBH7	DBH9
DBH1		0.83 ± 0.08	0.78 ± 0.14	0.51 ± 0.16	0.41 ± 0.16	0.36 ± 0.15
DBH2	0.62 ± 0.01		0.84 ± 0.13	0.78 ± 0.14	0.72 ± 0.14	0.64 ± 0.13
DBH3	0.36 ± 0.02	0.63 ± 0.02		0.93 ± 0.06	0.86 ± 0.10	0.76 ± 0.12
DBH5	0.27 ± 0.02	0.57 ± 0.02	0.83 ± 0.01		0.96 ± 0.01	0.86 ± 0.06
DBH7	0.25 ± 0.03	0.52 ± 0.02	0.74 ± 0.01	0.87 ± 0.01		0.91 ± 0.03
DBH9	0.22 ± 0.03	0.47 ± 0.02	0.67 ± 0.02	0.83 ± 0.01	0.93 ± 0.01	
	HT1	HT2	HT3	HT5	HT7	HT9
HT1		0.86 ± 0.06	0.72 ± 0.12	0.51 ± 0.11	0.41 ± 0.14	0.37 ± 0.14
HT2	0.58 ± 0.01		0.86 ± 0.09	0.73 ± 0.09	0.65 ± 0.12	0.56 ± 0.14
HT3	0.39 ± 0.02	0.56 ± 0.02		0.88 ± 0.08	0.80 ± 0.08	0.74 ± 0.07
HT5	0.24 ± 0.03	0.51± 0.02	0.78 ± 0.01		0.95 ± 0.01	0.87 ± 0.05
HT7	0.25 ± 0.03	0.44 ± 0.03	0.71 ± 0.02	0.87 ± 0.01		0.97 ± 0.01
HT9	0.22 ± 0.03	0.36 ± 0.03	0.67 ± 0.02	0.82 ± 0.01	0.91 ± 0.01	

Genetic correlation at single sites

Age–age phenotypic and genetic correlations estimated for DBH and HT from year 1 to year 8 at Ba Vi and year 9 at Van Xuan are shown in Table 5. Genetic correlations became weaker with increasing difference between age of measurement for both DBH and HT in both trials, ranging from 0.30 to 0.97 for DBH, and from 0.27 to 0.97 for HT. There were very high genetic correlations for STR and BRA between assessments at ages 5 and 8 years at Ba Vi and between ages 5 and 9 years at Van Xuan (Table 6). STR and BRA were moderately correlated ($\hat{r}_g$ = 0.47 to 0.61) with high standard errors (Table 6). Genetic correlations between growth (DBH and HT) and form (STR and BRA) at similar ages were low to moderate (0.21 to 0.61, Table 7). Genetic correlations at similar ages between DBH and HT were strong at all ages at both sites ($\hat{r}_g$ = 0.75 to 0.98, with small standard errors) (Table 8).

Across-sites heritabilities and genetic correlation between sites

Heritabilities of DBH from analysis across-sites (Table 9) ranged from 0.06 at age 1 to 0.24 at age 9; and for HT from 0.08 at age 1 to 0.18 at age 9, with low to moderate standard errors. Pooled heritabilities estimates for STR and BRA were also low (0.10 to 0.17), with

Table 6 Phenotypic (below diagonal) and genetic (above diagonal) with standard errors for stem straightness (STR) and branch size (BRA) at Ba Vi and Van Xuan for the same traits at different ages and for different traits at the same age

	Ba Vi					Van Xuan			
	STR5	STR8	BRA5	BRA8		STR5	STR9	BRA5	BRA9
STR5		0.99 ± 0.03	0.61 ± 0.32		STR5		0.97 ± 0.01	0.52 ± 0.28	
STR8	0.93 ± 0.01			0.51 ± 0.51	STR9	0.93 ± 0.01			0.47 ± 0.33
BRA5	0.46 ± 0.03			0.97 ± 0.03	BRA5	0.37 ± 0.03			0.98 ± 0.01
BRA8		0.39 ± 0.03	0.91 ± 0.01		BRA9		0.33 ± 0.03	0.91 ± 0.01	

Table 7 Estimates of phenotypic and genetic correlations (with standard errors) at similar age, between diameter at breast height (DBH) and height (HT), and stem straightness (STR) and branch size (BRA) at Ba Vi and Van Xuan

(a) Ba Vi

	Phenotypic correlations				Genetic correlations			
	DBH5	DBH8	HT5	HT8	DBH5	DBH8	HT5	HT8
STR5	0.23 ± 0.03		0.33 ± 0.03		0.21 ± 0.26		0.35 ± 0.22	
STR8		0.13 ± 0.04		0.21 ± 0.04		0.24 ± 0.33		0.23 ± 0.29
BRA5	0.12 ± 0.03		0.30 ± 0.03		0.51 ± 0.32		0.61 ± 0.26	
BRA8		-0.09 ± 0.04		0.09 ± 0.04		0.31 ± 0.68		0.57 ± 0.67

(b) Van Xuan

	Phenotypic correlations				Genetic correlations			
	DBH5	DBH9	HT5	HT9	DBH5	DBH9	HT5	HT9
STR5	0.12 ± 0.03		0.21 ± 0.03		0.23 ± 0.26		0.28 ± 0.24	
STR9		0.14 ± 0.03		0.22 ± 0.03		0.29 ± 0.21		0.28 ± 0.22
BRA5	0.22 ± 0.03		0.32 ± 0.03		0.41 ± 0.31		0.47 ± 0.19	
BRA9		0.23 ± 0.03		0.18 ± 0.03		0.35 ± 0.26		0.48 ± 0.42

Table 8 Genetic and phenotypic correlations (with standard errors) between diameter at breast height (DBH) and height (HT) at similar ages at Ba Vi and Van Xuan

Site	Age	1	2	3	5	7	8	9
Ba Vi	Phenotypic	0.91 ± 0.01	0.73 ± 0.02	0.71 ± 0.07	0.73 ± 0.01		0.58 ± 0.02	
	Genetic	0.98 ± 0.01	0.87 ± 0.03	0.76 ± 0.11	0.75 ± 0.13		0.76 ± 0.16	
Van Xuan	Phenotypic	0.60 ± 0.01	0.68 ± 0.01	0.63 ± 0.02	0.76 ± 0.02	0.68 ± 0.03		0.80 ± 0.03
	Genetic	0.81 ± 0.04	0.78 ± 0.07	0.75 ± 0.09	0.96 ± 0.11	0.98 ± 0.15		0.87 ± 0.05

moderate standard errors. Additive genetic correlations between sites for DBH and HT increased with age, ranging from 0.38 to 0.92 for DBH and 0.41 to 0.86 for HT, paralleling the increase in respective heritabilities. Genetic correlations between sites for both DBH and HT became stable after 3 years. Estimated genetic correlations between sites for STR and BRA were also strong at both ages 5 and 9 years (0.78 to 0.92, Table 9).

Time trend in genetic parameters

The regression of individual tree heritability (dependent variable) (using observed heritabilities from both trial sites, Table 4) on logarithm of age (independent variable) gave a good fit to the data for DBH and HT (R^2 = 0.88 and 0.63 respectively), indicating a high significant age effect, i.e. $p < 0.001$ for DBH and $p = 0.002$ for HT respectively (Figure 1).

Table 9 Genetic correlations (with standard errors) between Ba Vi and Van Xuan for diameter at breast height (DBH), height (HT), stem straightness (STR) and branch size (BRA), and across-sites heritability at different ages

Trait	Age	$r_g \pm$ SE	$h^2_p \pm$ SE
DBH	1	0.38 ± 0.13	0.06 ± 0.02
	2	0.63 ± 0.12	0.13 ± 0.03
	3	0.81 ± 0.22	0.22 ± 0.05
	5	0.90 ± 0.23	0.24 ± 0.06
	9[1]	0.92 ± 0.32	0.24 ± 0.07
HT	1	0.41 ± 0.12	0.08 ± 0.03
	2	0.67 ± 0.10	0.16 ± 0.03
	3	0.85 ± 0.23	0.19 ± 0.06
	5	0.86 ± 0.30	0.20 ± 0.06
	9[1]	0.86 ± 0.33	0.18 ± 0.07
STR	5	0.90 ± 0.33	0.17 ± 0.07
	9[1]	0.92 ± 0.33	0.15 ± 0.06
BRA	5	0.78 ± 0.28	0.10 ± 0.07
	9[1]	0.89 ± 0.31	0.10 ± 0.07

[1] Additive genetic correlation and pooled heritability estimated across-sites between measurement at 8 years (Ba Vi) and 9 years (Van Xuan)

A regression model using observed age–age genetic correlations for DBH and HT at both sites (Table 5) and the logarithm of age ratio between measurement at a younger age and an older age (LAR) as an independent variable showed a good fit to the data and a significant effect of LAR ($p < 0.001$) in both traits (Figure 2). Predicted values of age–age genetic correlation were used to estimate selection efficiency.

Efficiency of early selection age

Efficiency of early selection (Figure 3) at identical selection intensity generally increased to a maximum between ages 2 and 4 years, depending on rotation age of the production system. For a 5-year rotation production system (mainly for pulp wood) with a 2-year time lag for breeding activities (grafting, flowering and crossing of selected trees) (Figure 3a) maximum selection efficiency for HT was reached after 2 years, and after 3 years for DBH but the decrease in selection efficiency to age 4 years was slight. Selection efficiency in a production system with 10-year rotation (for larger saw logs and pulpwood) and 2 years time lag for breeding activities reaches a maximum after 3 years for both DBH and HT (Figure 3b).

DISCUSSION

Effect of thinning on heritabilities and correlations

Heavy selective thinning in the current study, with about 75% of trees removed at age 2 years, had a significant effect on the within- and among-family variance distributions, affecting heritabilities and genetic correlations based on a single trait analysis. Estimates of genetic parameters from a culled population may not be applicable to the base population before thinning, and the changes in parameters may simply reflect selection rather than changes in the expression of genetic effects. This is particularly relevant

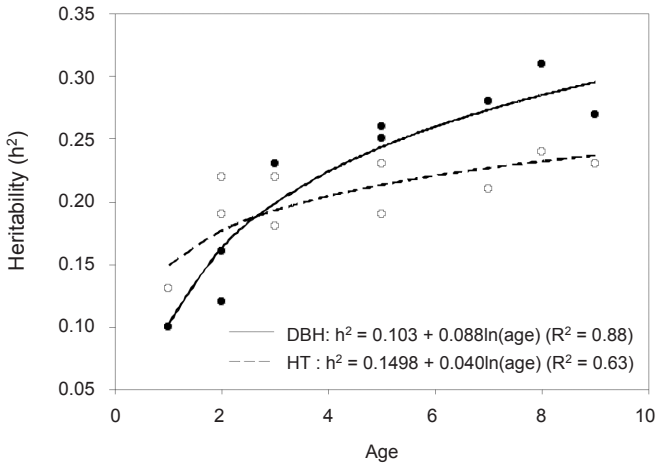

Figure 1 Time trend in heritability for diameter at breast height (DBH ●) and height (HT ○)

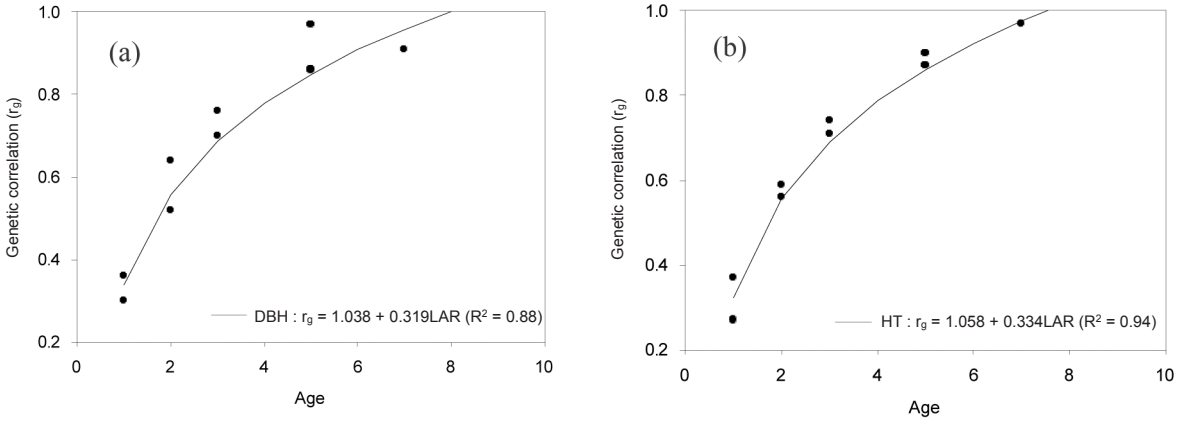

Figure 2 Time trend in age-age genetic correlations (a) for diameter at breast height (DBH), and (b) for height (HT) (LAR is logarithm of age ratio between measurement at a younger age and an older age)

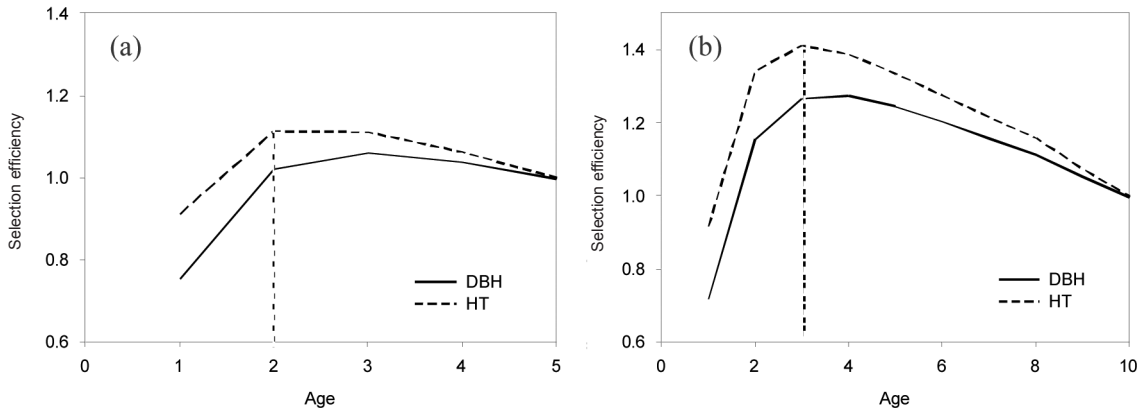

Figure 3 Selection efficiency at different ages for diameter at breast height (DBH) and height (HT) with (a) 5- and (b) 10-year rotation. The vertical lines show the optimum selection age.

to the study of heritability. The use of genetic parameters from selectively-thinned trials may result in biased estimates of breeding values, both in current and future generations. In general, selective thinning tends to inflate heritabilities (Matheson & Raymond 1984).

However, the use of longitudinal multivariate REML analysis approach has been reported to reduce the effect of thinning and selection on the estimation of genetic parameters (Wei & Borralho 1998a, Apiolaza *et al.* 2000). The basis of the method is the central role of the genetic relationship matrix **A** in accounting for changes in variance of trait 2 brought about by selection on trait 1 (Wei & Borralho 1998a). Therefore, the genetic effect for trees that were removed can be estimated using early measurements on those trees and early and late measurements of their relatives. In our study, genetic effects of removed trees were predicted by using measurement on them at ages 1 and 2 years and measurement on their relatives in later ages. A simulated thinning, assuming that the trees which were thinned after 2 years had been thinned just before measurement at age 2 years was done, and family breeding values from the best linear unbiased prediction at age 2 years was predicted at Ba Vi in three cases: (1) longitudinal multivariate analysis of unthinned data which is believed to give the most accurate prediction (Apiolaza *et al.* 2000), (2) longitudinal multivariate analysis of thinned data, and (3) univariate analysis of thinned data. The results, as in Figure 4, showed a stronger relationship between breeding values from unthinned data and those from longitudinal analysis of thinned data (R^2 = 0.68, Figure 4a) than that those from univariate analysis of thinned data (R^2 = 0.54, Figure 4b), suggesting that the longitudinal multivariate analysis could reduce bias in prediction of breeding values.

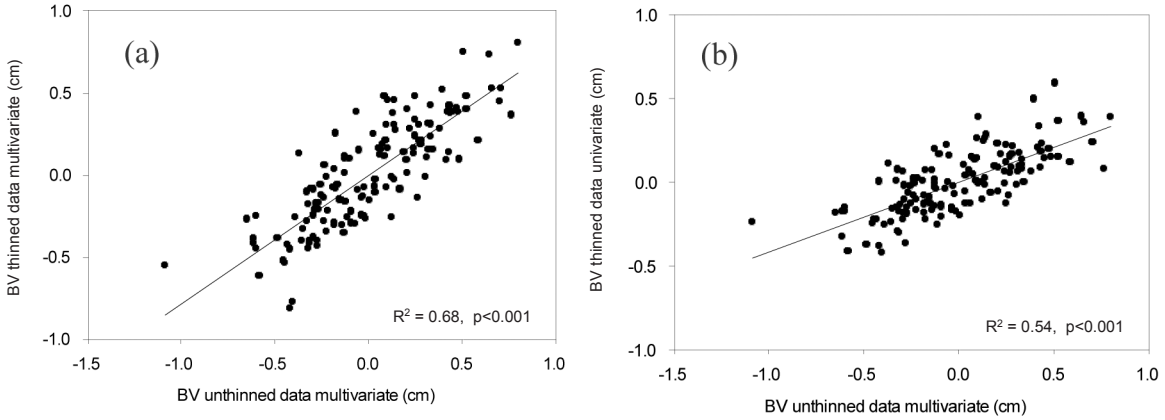

Figure 4 Relationship between family breeding values (BV) for diameter at breast height (DBH) at age 2 years at Ba Vi from longitudinal multivariate analysis of unthinned data (*x*-axis) and breeding values following simulated thinning at age 2 years (*y*-axis) predicted by (a) longitudinal multivariate analysis, and (b) univariate analysis

The breeding values from univariate analysis are based on less data and, therefore, regressed more towards the mean value. Heritabilities of growth traits estimated by longitudinal multivariate analysis had slightly higher heritability and lower standard errors than the observed from univariate analysis.

Provenance performance

It was clear that the Lewotobi provenance from Flores Island was superior in growth traits than all other provenances at both sites and the differences among other provenances were small. The results agreed well with previously published studies from provenance trials of *E. urophylla* in northern Vietnam, where it was reported that the most promising provenances were Lewotobi and Egon from Flores Island (Tai 1994, Kha *et al.* 2003). These two provenances also grow well in the central and central highland areas of Vietnam (Kha *et al.* 2003). The superiority of the Lewotobi provenance for growth has earlier been reported from provenance trials in south-eastern China (Wei & Borralho 1998b, Bai *et al.* 2003), where the poorest provenances came from high elevations. Some provenance trials in northern Vietnam also reported good growth of provenances Ulubaha from Wetar island (Tai 1994) and Lembata from Flores island (Kha 2001). However, these provenances were not included in the current study. The Lembata provenance also showed good growth in a provenance trial in central Vietnam (Kha *et al.* 2003). In a series of international provenance trials, lower elevation provenances, mainly from Flores and Timor, showed good performance at lower elevation planting sites (Vercoe & Clarke 1994).

In our study, most provenances from Flores and Wetar islands and Baubillatung from Pantar island had the highest proportions of trees having good STR, ranging from 81.2 to 88.1%, clearly higher than provenances from Alor island and the Dalaki provenance from Pantar island. This is comparable with the results reported by Kha (2001) in which the Lewotobi provenance was best for STR, while Egon provenance was middle-ranking among the nine provenances tested in another provenance trial in Ba Vi.

Growth of trees in this study was relatively slow compared with studies in other countries. Annual mean height growth in both trials up to age 5 years were in the range 1.9–2.7 m, compared with 3–5 m achieved in China or Brazil where growing conditions are more favorable (Santos *et al.* 1990, Wei & Borralho 1998b). Clearly, genetic improvement of *E. urophylla* in northern Vietnam should emphasize increased growth performance, but with cool, dry winter and degraded soils in this area, growth rates will most likely remain below those of many other countries.

Family breeding values were predicted for both DBH and HT at Ba Vi at age 5 years and Van Xuan at age 9 years. Among the top 50 families for DBH at each site, Lewotobi contributed the largest number with 15–18 families, followed by Egon with 10–13 families, SW Uhak Wetar 8–10 families, and the other provenances, 1–5 families.

Breeding populations for genetic improvement of *E. urophylla* in Vietnam should certainly incorporate unrelated individuals from good families in Lewotobi provenance, but also good individuals from other provenances.

Genetic parameters

The heritabilities estimated for DBH and HT agree well with previous estimates that have been reported for *E. urophylla* (Mori *et al.* 1988, Santos *et al.* 1990, Kurinobu *et al.* 1996, Nirsatmanto *et al.* 1996, Wei & Borralho 1998b, Arnold & Cuevas 2003, Xu *et al.* 2003). Both heritability and CV_A estimated for DBH and HT are in the range for growth traits in forest trees reported by Cornelius (1994). The trend of increasing heritability with age was also reported in the study of *E. urophylla* in China (Wei & Borralho 1998b), and in other eucalypt species (Bouvet & Vigneron 1995, Osorio *et al.* 2001, Gapare *et al.* 2003). The increased heritability with age for growth traits could also result from competitive effects occurred in later ages in the stand, which may cause overestimation of heritability.

Heritabilities for STR and BRA were lower than those for growth traits at the same ages. There are to our knowledge no published estimates of heritability for STR and BRA for *E. urophylla* and few in other eucalypt species. However, low heritability for STR was observed in *E. grandis* (Gapare *et al.* 2003) and in *E. camaldulensis* (Mahmood *et al.* 2003), but it was moderate in *E. dunnii* (Arnold *et al.* 2004). Very low to moderate heritability was reported for STR in *E. grandis* and *E. dunnii* across six sites in Argentina (Marcó & White 2002). It has been suggested that the STR assessment in breeding programmes using absolute rather than relative scores results in lower heritability (Gwaze *et al.* 1997). The results reported in this study could be biased as assessment was conducted in thinned progeny tests from which trees with poor straightness and heavy branches had been removed.

The estimated values of heritability in these progeny trials testing seedlots collected from natural forests of *E. urophylla* in Indonesia depend on assumptions about outcrossing rates, which are affected by the insect pollination system (Gaito *et al.* 1997, House & Bell 1993). The outcrossing rates under Vietnamese conditions might be different from those in natural stands. This possibility should be taken into account by estimating outcrossing rate when calculating heritability in advanced generation breeding populations.

The heritabilities estimated should also be interpreted carefully because of unequal number of families per provenance presented in the trials (Table 1). In a multiprovenance progeny trial, the family variance is averaged across the different provenances, with more information provided by the better-represented provenances, and in this study, more by Lewotobi, Egon and SW Uhak provenances and less by the rest. The heritabilities estimated in this study are average within-provenance heritabilities, which should be used to estimate gain from selection within provenances. The effects of crossing between different provenances of *E. urophylla* are not yet well understood.

The magnitude and trend in genetic age–age correlations estimated in this study are consistent with findings in the same species in south-eastern China reported by Wei and Borralho (1998b), and in other eucalypt species (Borralho *et al.* 1992, Osorio *et al.* 2003). The strong correlation between growth traits at age 3 years and at age 8 or 9 years, together with relatively stable heritabilities after age 3 years for both DBH and HT indicate efficient selection at age 3 years in *E. urophylla*.

The genetic correlations between STR and growth traits in this study were lower than those reported in *E. grandis* in Zimbabwe (Gapare *et al.* 2003), but similar to those in *E. dunnii* (Arnold *et al.* 2004). Genetic correlations between DBH and HT were strong at all ages and in both sites. Therefore, DBH alone would be sufficient as a selection trait for growth, greatly reducing costs of measurement, especially in later ages.

Genotype by environment interaction

The high additive genetic correlations for DBH and HT between sites in this study from age 3 years on may be due to their similarity in both soil and climatic conditions between the two sites, which are less than 60 km apart. Genotype by environment interaction effects (G × E) would be practically negligible for growth in sites similar to these. Low G × E effects in *E. urophylla* were also reported by Wei and Borralho (1998b) who found non-significant G × E effects across four testing sites in south-eastern China. In our study, genetic correlation between sites increased

with age and increasing heritability and became stable after 3 years, indicating that selection at a single site could be efficient elsewhere. The results also indicate that it would be possible to develop a single breeding population targeted at hillside planting environments with similar soil and climate in Phu Tho, Vinh Phuc, Ha Tay, and some parts of Yen Bai and Thai Nguyen provinces in northern Vietnam.

Efficiency of early selection

In northern Vietnam, plantations of *E. urophylla* are managed on short rotations of 6 to 8 years for pulpwood supplying raw material for pulp mills in the region and small quantities of larger logs for small sawmills. Given that 2 years are needed from selection, grafting and control pollination in clone bank to produce seed, predicted selection efficiency indicated that age 2 years was the optimum selection age for growth of *E. urophylla* in the north of Vietnam. In another study in China, 1 year was the optimum selection age for HT and DBH in *E. urophylla* (Wei & Borralho 1998b). Several published reports for tropical eucalypt species, managed for a short rotation, indicated that 2 to 3 years is the optimum selection age for growth (Bouvet 1991, Osorio *et al.* 2003). Our results showed no large difference in selection efficiency for DBH between 2 and 3 years of age for a 5-year rotation. Calculations for a rotation of 10 years showed that selection at age 3 years gave the highest selection efficiency. As discussed above, genetic correlation between sites is high and stable after 3 years. Therefore, it is recommended that the optimum selection age should be 3 years.

CONCLUSIONS

Eucalyptus urophylla displayed relatively slow growth rates at the trial sites in northern Vietnam, compared with those recorded in other countries where this species is grown. Lewotobi was the best-performing provenance, with only minor differences among the other low-elevation provenances that were tested. The results indicate that good families can be found within all provenances. Therefore, the breeding population should incorporate families from several provenances to maintain genetic diversity and delay build-up of coancestry in the breeding programme. Growth traits in *E. urophylla* are under low to moderate genetic control. Heritability for DBH increased with age while it generally remained stable for HT after age 2 years. Genetic correlation between earlier and final measurements were weak for both DBH and HT, in the case of year-1 measurements, but increased as the earlier measurement age increased, indicating a significant age effect. Maximum selection efficiency was reached with selection implemented at age 2 or 3 years depending on whether the rotation length for wood production is 5 or 10 years. Correlation between sites was high from age 2 years indicating similar ranking of families across site. Therefore, a single breeding population will be appropriate for an improvement programme of this species for hilly areas in northern Vietnam with similar soils and climate.

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