

# Variation in growth traits and wood density in whitewood (*Endospermum medullosum*): a major timber species in Vanuatu

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## SUMMARY

A breeding program aimed at increasing economic value of whitewood plantations in Vanuatu and conserving declining genetic resources will take direction from the results of this study. Genetic parameters for stem diameter breast height over bark (DBHOB), straightness and branching were estimated in an 11.4-year-old whitewood breeding population on Espiritu Santo Island. Wood density variation in one subpopulation was also studied. Trees with the fastest growth and best form were from Espiritu Santo. Growth and form trait heritability estimates ( $\hat{h}^2 = 0.10\text{--}0.16$ ) were low to moderate, with moderate phenotypic variation ( $CV_p = 17\text{--}36\%$ ). DBHOB at 11.4-years and 4-years were very closely genetically correlated ( $r_A = 1.00 \pm 0.17$ ). Mean unextracted wood basic density at breast height was 330 (SD±21) kg/m<sup>3</sup>, or similar to mature-tree densities. Economic gain in growth traits can be expected from a recurrent selection and breeding program given the heritable genetic variation indicated in this study. Conserving genetic diversity in this species is a high priority.

Keywords: volume, diameter, height, form, heritabilities, genetic correlations

## Variation de traits de croissance et de densité du bois pour le bois blanc (*Endospermum Medullosum*), une essence de bois majeure à Vanuatu

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Un élevage de production visant à accroître la valeur économique des plantations de bois blanc à Vanuatu et à conserver les ressources génétiques déclinantes va prendre sa direction à partir des résultats de cette étude. Les paramètres génétiques pour le diamètre du tronc à hauteur de poitrine écorce incluse (DBHOB), la droiture et le branchage ont été estimés dans une population de production de bois blanc de 11.4 ans sur l'île d'Espiritu Santo. La variation de densité du bois dans une population différente a elle aussi été étudiée. Les arbres à croissance la plus rapide et les plus droits provenaient d'Espiritu Santo. Les estimations de croissance et d'heritabilité des traits ( $\hat{h}^2 = 0.10\text{--}0.16$ ) étaient de basses à modérées, avec une variation phénotypique modérée ( $CV_p = 17\text{--}36\%$ ). Les DBHOB à 11.4 ans et à 4 ans faisaient preuve d'une corrélation génétique très proche ( $r_A = 1.00 \pm 0.17$ ). La densité de base moyenne du bois non extrait à hauteur de poitrine était de 330 (SD±21) kg/m<sup>3</sup>, ou semblable aux densités des arbres mûrs. Le gain économique provenant des traits de croissance peut être attendu d'une sélection récurrente et d'un élevage de production basé sur la variation génétique d'heritabilité indiquée dans cette étude. La conservation de la diversité génétique de cette espèce est une haute priorité.

## Variación en las características de crecimiento y densidad de la madera en madera blanca (*Endospermum medullosum*): una de las principales especies maderables de Vanuatu

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Los resultados de este estudio guiarán un programa de mejora dirigido a incrementar el valor económico de las plantaciones de madera blanca en Vanuatu y a conservar unos recursos genéticos actualmente en declive. Se estimaron parámetros genéticos para el fuste como el diámetro a la altura del pecho con corteza (DAPcc), la rectitud y la ramosidad de una población de mejora de madera blanca de 11,4 años de edad, en la isla de Espiritu Santo. También se estudió la variación en la densidad de la madera en una subpoblación. Los árboles con el crecimiento más rápido y mejor forma procedían de Espiritu Santo. Las heredabilidades estimadas para los rasgos de crecimiento y forma ( $\hat{h}^2 = 0,10\text{--}0,16$ )

fueron bajas a moderadas, con una variación fenotípica moderada ( $CV_p = 17\text{--}36\%$ ). Se encontró una correlación genética muy fuerte ( $r_A = 1.00 \pm 0.17$ ) entre el DAPcc a los 11,4 años y los 4 años. La densidad básica media de la madera (no libre de extractos) a la altura del pecho fue de  $330$  ( $SD \pm 21$ )  $\text{kg/m}^3$ , o similar a las densidades de árboles maduros. En virtud de la variación genética heredable encontrada en este estudio se pueden esperar ganancias económicas en las características de crecimiento mediante una selección continua y un programa de mejoramiento. Se considera que la conservación de la diversidad genética de esta especie tiene una alta prioridad.

## INTRODUCTION

*Endospermum medullosum* L.S. Smith (family Euphorbiaceae), with the common name whitewood in Vanuatu, is described in detail by Thomson (2001, 2006). It is typically a tall forest tree with a long, straight bole, to 45 m in total height, sometimes with steep buttresses, and usually in the 50 cm to 100 cm diameter range after 30 years. The species is dioecious, insect pollinated, with fruits that are fleshy drupes consumed and dispersed by birds and flying foxes. *E. medullosum* occurs naturally in Indonesia (West Papua), Papua New Guinea, Solomon Islands and in Vanuatu (Corrigan *et al.* 2000). It is predominantly a pioneer species of lowland to mid-elevation sites in humid tropical climates of high rainfall (2,500–4,500 mm/year) and short to no dry season. The wood of *E. medullosum* is of commercial value, although rather soft, of low density (365–450  $\text{kg/m}^3$  air-dry density at 12% moisture content) and strength and lacking durability in the ground (Keating and Bolza 1982, Thomson 2006). The wood works and dries easily and is readily treated with preservatives and stains making it suitable for many purposes including mouldings, boards, joinery, furniture and for veneer and plywood manufacture (Gunn *et al.* 2004).

In Vanuatu, *E. medullosum* occurs naturally on more than a dozen islands from Erromango (circa 19°S latitude) in the south of the archipelago to the Banks Group (c.14°S) in the north (Vutilolo *et al.* 2008). Annual harvesting of whitewood averaged c. 20,000  $\text{m}^3$  between 1990 and 2004 but declined dramatically thereafter. Unsustainable commercial exploitation in most parts of its natural range has resulted in its disappearance from or occurrence at very low frequency in all but the most inaccessible stands (Vutilolo *et al.* 2008). By 2008 whitewood accounted for only 20% of the 11,000  $\text{m}^3$  of wood harvested commercially throughout Vanuatu (Page 2009). Dwindling supplies of whitewood logs has reduced important export income and has led to the importation of most timber needed by the domestic market (Mele 2011).

Plantation and woodlot establishment and agroforestry is seen as crucial for ensuring an ongoing supply of forest products to support sustainable livelihoods in Vanuatu. The Vanuatu Forest Policy (Anon 2011, Mele 2011) includes a target of 20,000 ha of plantations and woodlots by the year 2020 - the total area of plantations was estimated at 4,800 ha in 2006. Whitewood has been identified in this policy as a key candidate plantation species with good timber properties at a young age (rotation length of 15 years anticipated) coupled with rapid growth rate, high cyclone resistance, relative freedom from serious pests and diseases and an established export market to Japan (Nichols *et al.* this publication). However, despite its market potential and highly suitable land being

available for plantation development on islands like Espiritu Santo, planting of whitewood woodlots has been slow (less than 500 ha planted to date). Aru *et al.* (2012) suggest that increased training of landholders in all aspects of the value-chain for whitewood and the promotion/adoption of community forestry principles is the preferred way to facilitate increased establishment of whitewood woodlots.

The Vanuatu Department of Forests (VDoF) has implemented a tree improvement programme for Vanuatu whitewood, aimed at increasing the economic value of the industry. A key objective of the strategy is the progressive provision of more productive germplasm to growers while conserving genetic resources both *in-* and *ex-situ*. This program is focussed on enhancing grower uptake, increasing planting rates and conserving genetic resources. This work started during AusAID's South Pacific Regional Initiative on Forest Genetic Resources Project (SPRIG) (Thomson 2003) with the establishment in December 1998- January 1999 of two (one major and one minor) provenance/family trials of whitewood on the Industrial Forestry Plantations (IFP) site near Shark Bay on the east coast of Espiritu Santo. Statistically significant and heritable provenance and family-within-provenance variation in growth (height, diameter and volume) traits was found in the major trial at 4 years-of-age (Viji 2005, Vutilolo *et al.* 2008).

In this study we (i) determine patterns of genetic variation in diameter at breast height over bark and form in the IFP trials (ii) assess relationships of these (11.4-year) measures to the earlier (4-year) measures and (iii) quantify variation in unextracted wood basic density in a single bulked provenance seedlot. This latter task was undertaken to provide information in support of future plans to undertake a detailed study of genetic variation in this trait throughout the trials.

## MATERIALS AND METHODS

### Trial site, genetic materials and experimental designs

Two provenance/family trials of whitewood were established on IFP land near Shark Bay on the east coast of Espiritu Santo – one major and one minor (Figure 1). Summary details of the two whitewood provenance/family trials at IFP including a description of the planting site, trial design, provenances and families compared, thinning schedules and the previous measure at 4 years-of-age are given in Tables 1 and 2. A total of 110 open-pollinated families from 15 different provenances are included in the two trials (Figure 1). These include whitewood provenances on the islands of Ambae (West), Maewo, Malekula (Uri-Wiaru), and Pentecost (Central), two separate provenances (Forari and Teouma) on

TABLE 1 Details of the two whitewood trials establish by VDoF at IFP, Espiritu Santo under the auspices of the SPRIG project

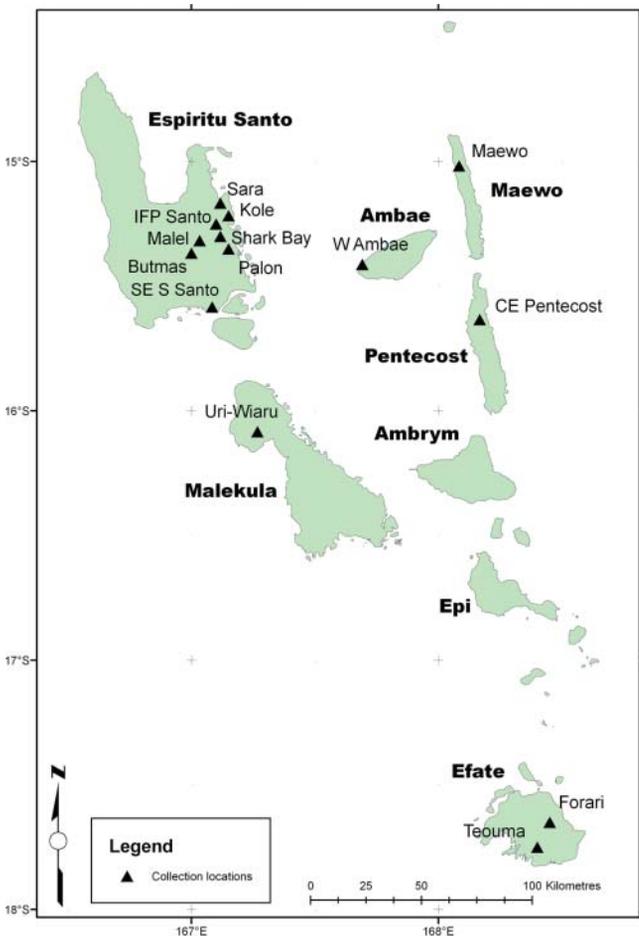
Trial details	Major trial	Minor trial
Date planted	12/1998 and 01/99	01/1999
Location	15°15'S 167°04'E	
Altitude	200 m	
Slope	Flat (<3°)	
Soils	Weakly humic ferralitic cambisols, neutral pH 5.5–6 and of generally good fertility	
Annual rainfall	c. 3500 mm (summer-dominant)	
Statistical design	Latinised row-column design	
Spacing (stocking)	6 m between rows and 2 m within rows (833 stems per ha)	
Trial area	6.25 ha including buffers	1.05 ha including buffers
No. of replicates	8	6
Trees per plot	6	
Previous measure at 4 years-of-age (Jan 2003)	Height, DBHOB, volume and form	
Thinning schedule	2003, removal of 1 tree/plot 10/2004, removal of a further 3 trees/plot 10/2005, removal of 1 tree/plot in reps 6 to 8 to create a Provenance SSO of 2.7 ha	No formal thinning regime but trial underwent substantial self-thinning
Age at measure, June 2010	11.4 years	

TABLE 2 Summary details of the 110 whitewood seedlots in the provenance-progeny trials established at IFP, Espiritu Santo in 1998/99 with comment on the conservation status of the wild stands of origin

Island	Provenance name	Conservation status of wild stand	No of families (major trial)	No of families (minor trial)	No common to both
Ambae	West Ambae	V	6	0	0
Efate	Forari	X	13	1	1
Efate	Teouma	X	7	3	0
Maewo	Maewo	P	10	2	0
Malekula	Uri-Wiaru	X	8	1	0
Pentecost	Central Pentecost	X	20	4	3
Espiritu Santo	Butmas, Central Santo	X	1	1	0
Espiritu Santo	IFP Plantation	planted	1	0	0
Espiritu Santo	Kole, East Santo	E	11	0	0
Espiritu Santo	Malel, Central Santo	X	6	3	2
Espiritu Santo	Palon, East Santo	X	1	1	0
Espiritu Santo	South Santo (mapped as SE S Santo)	P	1	0	0
Espiritu Santo	Sara, East Santo	X	1	1	0
Espiritu Santo	Southeast Santo (mapped as SE S Santo)	P	8	2	1
Espiritu Santo	Shark Bay, East Santo	X	3	2	1
Totals			<b>97</b>	<b>21</b>	<b>8</b>

**Conservation status code:** 'X' - populations which are no longer known to exist in the wild due to harvesting or changes in land use; 'E' - endangered populations at serious risk of disappearing within one or two decades; 'V' - vulnerable populations not presently endangered but at risk over a longer period through continued depletion, or potential changes in land use; 'P' - populations not currently considered endangered or vulnerable.

FIGURE 1 Location of provenances in the whitewood provenance/family trials established at Industrial Forestry Plantations (IFP), Espiritu Santo in 1998/99. The contiguous major and minor trial sites are in close proximity to IFP Santo



Efate, and eight small natural provenances and one planted one (SBC 13) on Espiritu Santo. The Espiritu Santo provenances were grouped by region (region-of-provenance) by Viji (2005) but are treated separately here. Further details of the main trial and earlier measures are given in Viji (2005) and Vutilolo *et al.* (2008).

### Diameter measurements and form scores

Data were collected at age 11.4-years on stem diameter at breast height over bark (DBHOB) [at 1.3m above ground] and subjective assessment of tree form (5 levels from 5 excellent to 1 extremely poor) and branching habit (3 levels from 3 excellent to 1 poor) (Table 3).

The 4-year data from the main trial (Viji 2005) was available for comparison with the 11.4-year data collected in this study.

### Estimation of wood volume

Calculation of wood volume was based on a volume equation. It was determined from 20 selected trees from a single row of

95 trees planted as a buffer to a similarly fast-growing plot of *Terminalia catappa* adjacent to replicates 1–5. Selection proceeded by separating the 95 trees into six DBHOB size-classes and making a stratified random selection from each size-class to represent the spread of sizes in the population. The buffer trees were from an operational seedlot derived from populations on the east coast of Espiritu Santo, one of the better performing regions-of-provenance (Viji 2005).

Once felled, each of the 20 trees were measured for total height and diameter over bark recorded at the base of the log (30 cm above ground), 10%, 30%, 50% and 70% of tree height. For each tree, Huber's formula ( $V = \pi L m d^2 / 4$  where  $L$  is the length of the billet and  $m d$  is its mid-diameter) (West 2004) was used to calculate the volume of individual billets (i.e., 0–10%, 10–30%, 30–50% and 50–70%) and the formula for volume of a cone ( $\pi r^2 L / 3$ ) was applied to the top section above 70% of tree height. The estimate of volume per individual tree was taken as the sum of the volume of each billet from that tree.

### Statistical analysis

Restricted maximum likelihood analysis of variance in each measured trait was carried out using a general linear mixed-model of the form:

$$y = \mathbf{X}b + \mathbf{Z}u + e \quad [1]$$

where  $y$  is the vector of observations on  $n$  traits,  $b$  and  $u$  are vectors of fixed and random effects respectively,  $\mathbf{X}$  and  $\mathbf{Z}$  are incidence matrices for fixed and random model terms and  $e$  is a vector of random residual terms. Variants of this model were implemented in ASREML (VSN International, Hemel Hempstead) as follows:

#### i) Preliminary investigation of pooling major and minor trial data

An exploratory analysis of genotype-by-site interaction (GxE) between the spatially contiguous 'major' and 'minor' trials was carried out on the common families. Differences between the thinning treatments in the two trials are confounded at the replicate level - replicates 1 to 5 in the main trial having been selectively thinned to two trees per plot with replicates 6 to 8 thinned to one tree per plot and the six replicates in the minor trial having self-thinned. The vector  $b$  (Eq. 1) contained sub-vectors for fixed effects including trial, family, trial-by-family interaction and replicate-within-trial, while  $u$  contained sub-vectors for the random residual effects which were estimated separately for each trial to investigate homogeneity. Since there was no indication of genotype-by-site interaction, the decision was made to jointly analyse the data in subsequent analyses. This benefits the precision of estimation for the common families and increases the generally low sample of families per provenance available in each trial if analysed separately.

#### ii) Variation and genetic parameter estimation among and within islands, provenances and families

Vector  $b$  (Eq. 1) contained sub-vectors for fixed effects of replicate and island, and  $u$  contained sub-vectors for the

TABLE 3 Scoring system applied to individual trees in the IFP whitewood trials at 11.4 years-of-age: (a) scoring for stem form/straightness and (b) scoring for branching habit

## (a) Stem form/straightness scores

Rating	Description
5	Excellent tree, very straight
4	Good tree, one minor deviation from straightness
3	Fair tree, two deviations from straightness
2	Poor tree, three to four deviations from straightness
1	Extremely poor tree, five or more deviations from straightness and inclusive of major faults like multiple leaders, ramiforms, large hollows/swellings

## (b) Branching habit

Rating	Description
3	Excellent - small diameter branches (relative to tree size), branch angle close to horizontal, good branch occlusion, long internode length, low incidence of branching, no ramiforms, no green branches at low height on bole.
2	Good - medium diameter branches, branch angle horizontal to moderately inclined, branch occlusion fair, long-intermediate internode length, low incidence of branching, no ramiforms, no green branches at low height on bole
1	Poor - large diameter branches and/or major defects such as poor branch occlusion/hollows/decay/termites; large branch stubs; high incidence of double whorls, short internode length-high incidence of branching; ramiforms; retention of green branches to a low height on the bole

random effects of provenance-within island, family-within provenance, plot and incomplete blocks (rows and columns). Provenance was treated as a random effect because the sample of families for some provenances was very small, and parameter estimates for these poorly sampled provenances will be regressed towards the mean.

Bivariate genetic correlation estimates between traits  $x$  and  $y$  were obtained from the estimated additive covariance and variance components as:

$$r_G = \frac{\sigma_{a_x a_y}}{\sqrt{\sigma_{a_x}^2 \sigma_{a_y}^2}} \quad [2]$$

where  $\sigma_{a_x a_y}$  is the additive (family) genetic covariance component between traits, and  $\sigma_{a_x}$  and  $\sigma_{a_y}$  are the additive variance components for traits  $x$  and  $y$  respectively.

Narrow-sense heritability was estimated as:

$$\hat{h}^2 = \frac{\rho \sigma_a^2}{\sigma_a^2 + \sigma_p^2 + \sigma_e^2}, \quad [3]$$

where  $\sigma_a^2$  is the additive (family) variance,  $\sigma_p^2$  is the plot variance,  $\sigma_e^2$  is the error variance and  $\rho$  represents a coefficient of relationship of 1/3 accommodating some mixed-mating effects such as full-sibs and inbreeding, effectively causing families to be more related than are true half-sibs. The software estimates standard errors of variance components using the Taylor-series expansion method.

### Determination of wood density

Wood discs 50 mm thick were taken from each of the 20 trees felled for volume estimation. Wood discs were taken at the base, breast height, 10%, 30%, 50% and 70% of tree height for half of the samples, while for the remaining 10 trees, a single wood disc was taken at breast height only. The 70 wood disc samples were reduced by band saw to a north to south, bark to bark, wood block approximately 50 mm square including the pith. Bark was removed, cut surfaces planed smooth and each sample was labelled by aluminium tag and then immersed in water to avoid splitting.

After one week, the blocks were re-sawn into defect free, 15–20 mm thick wedges with a width of approximately 50 mm at the outer edge. Smaller wedges were processed and measured whole and wedges longer than 140 mm were sectioned for ease of measurement. Wedge samples were immersed in water and later weighed and volume measured green (swelled) by immersion in water. The wood samples were first air-dried and later oven-dried for determination of wood basic density without removing extractives in accordance with Standards Association of Australia (1981).

Whole tree weighted basic densities of eight of the ten intensively sampled trees (two trees were omitted due to loss of labels during drying) were calculated by combining section (billet) volume with sectional average density to calculate a whole-tree weight, which was divided by whole-tree volume.

## RESULTS

## Volume equation and stand mean annual increment

Volume over-bark (VOB) as determined by Huber's standard sectional method for the 20 felled trees gave a mean of 0.6 m<sup>3</sup> per stem. Applying a second-order polynomial equation (dbh [cm] versus Huber's Volume [m<sup>3</sup>]) to the data provided an R<sup>2</sup> of 0.99 from a regression relationship:

$$V_{\text{Huber}} = 0.0007\text{DBHOB}^2 - 0.0007\text{DBHOB} - 0.0328 \quad [4]$$

Stem volume was modelled for all standing trees in the trial (including the minor trial) using Eq.4. Trial standing volume was estimated on this basis at 954 m<sup>3</sup>. At age 11.4 years and assuming a stand area of 6.67 ha (major plus minor trial area excluding buffers) the estimated mean annual volume increment (MAI) was 12.5 m<sup>3</sup>/ha/year.

## Trial-by-family interaction

Preliminary analysis indicated no significant trial-by-genotype interaction between the spatially contiguous major and minor trials. For the families common to both trials, the

trial term was non-significant for all traits ( $p \geq 0.31$ ) as was the trial-by-family term ( $p \geq 0.09$ ). Replicate-within-trial was significant for all traits ( $p \leq 0.03$ ) except branching and family was significant for the growth traits ( $p < 0.001$ ) but not branching nor form ( $p \geq 0.06$ ). Trial residual variance was homogeneous for all traits  $\frac{\sigma_e^2(\text{major})}{\sigma_e^2(\text{minor})}$  and ranged between 77 and 99%.

Data from the minor and major trials were therefore pooled for the main analysis.

## Island and provenance variation in DBHOB and form

The applied general linear model assumed provenances nested within islands. The majority of growth and branch trait variance was partitioned at the island level, with relatively small and imprecisely estimated provenance-level variance components, while there was little variation at the island- and provenance-level for form (Table 4). Considerable variance was partitioned into the incomplete blocks (row and column) for DBHOB at 4- and 11.4- years, and the column term aided in partitioning variance in the branching and form models. Inspection of replicate means for each trait revealed that

TABLE 4 Summary of mixed model analysis of diameter at breast height over bark (DBHOB), height, branch and form traits at 11.4-year and 4 year measures with narrow-sense heritability  $\hat{h}^2$ , coefficient of phenotypic variation ( $CV_p$ ) and predicted means for each island

Trait	DBHOB 11.4 y		DBHOB 4 y		Height 4 y		Branching 11.4 y		Form 11.4 y		
Fixed term	d.f.	$\chi$ stat	$\chi$ prob.	$\chi$ stat	$\chi$ prob.	$\chi$ stat	$\chi$ prob.	$\chi$ stat	$\chi$ prob.	$\chi$ stat	$\chi$ prob.
Replicate	13	128.6	<0.001	26.9	<0.001	50.06	<0.001	40.11	<0.001	53.6	<0.001
Island	5	110.7	<0.001	18.6	0.002	14.9	0.011	10.61	0.06	5.1	0.40
Random term - variance component (standard error)											
Row-within-replicate		1.52	(0.53)	0.12	(0.08)	0.03	(0.02)	-ve (dropped)		0.00	(0.00)
Column (across replicates)		2.32	(0.68)	1.64	(0.42)	0.32	(0.08)	0.03	(0.01)	0.01	(0.00)
Plot $\sigma_p^2$		3.94	(0.83)	1.84	(0.20)	0.50	(0.04)	0.03	(0.01)	0.06	(0.02)
Provenance-within-island		0.23	(0.39)	0.15	(0.15)	0.06	(0.05)	0.01	(0.01)	0.01	(0.01)
Family-within-prov. $\sigma_a^2$		1.12	(0.42)	0.12	(0.09)	0.07	(0.03)	0.01	(0.00)	0.01	(0.01)
Residual $\sigma_e^2$		15.44	(0.81)	6.70	(0.18)	0.95	(0.03)	0.24	(0.01)	0.35	(0.02)
Heritability $\hat{h}^2$		0.16	(0.07)	0.04	(0.03)	0.14	(0.04)	0.13	(0.06)	0.10	(0.05)
$CV_p$		19%		22%		17%		36%		25%	
Estimated means (Island)											
Ambae		31.36		15.44		8.82		1.56		2.67	
Efate		28.14		15.40		8.16		1.67		2.53	
Maewo		28.21		14.65		8.31		1.61		2.56	
Malekula		30.28		15.11		8.67		1.54		2.64	
Pentecost		29.35		15.03		8.44		1.57		2.57	
Espiritu Santo		33.42		16.28		8.96		1.42		2.71	
Average s.e.		0.90		0.57		0.35		0.13		0.13	

replicates 1–8 (the major trial) were slightly better than 9–14 (the minor trial) for each trait at 11.4 years, reflecting the differences in thinning between the two with selective in the major and self-thinning in the minor trial. The differences, however, were surprisingly subtle. For example, 32.4 cm (major) versus 31.0 cm (minor) with s.e. 1.7 cm for mean DBHOB and 1.62 (major) versus 1.56 (minor) with s.e. 0.10 for mean branch score.

### Genetic parameter estimates

Variance component and narrow-sense heritability ( $h^2$ ) estimates for all traits at 4- and 11.4- years are given in Table 4. There was significant family-level (additive) variance for all traits, resulting in low narrow-sense heritability estimates ranging between 0.10 and 0.16. An exception was DBHOB at 4-years, which had a family variance parameter close to zero. The coefficients of phenotypic variation were moderate (range 17–36%) for all traits.

Genetic correlations between growth trait measures ranged from low (e.g.,  $0.10 \pm 0.29$  between DBHOB and form at 11.4 years) to high (e.g.,  $1.00 \pm 0.17$  between DBHOB at 11.4 years and DBHOB at 4 years) (Table 5).

### Variation in wood density in buffer trees of a bulked single-provenance seedlot

Wood basic density decreased up the stem and there did not appear to be any association between tree size traits and unextracted wood basic density at any of the sampling heights nor with whole tree density (Tables 6 and 7). Sampling at breast height appears to give the best overall estimate of whole tree density, with  $r^2$  of 0.99 and bias (overestimate of density) of circa +6%. Sampling at 30% of tree height gave a lower mean bias (-2%) but a weaker linear relationship ( $r^2=0.86$ ). Wood basic density at breast height was determined for 19 of the 20 felled buffer trees. The mean unextracted basic density ( $\pm$ standard deviation) of these samples was 330 ( $\pm 21$ ) kg/m<sup>3</sup> with a range of 284–364 kg/m<sup>3</sup>.

## DISCUSSION

### Island, provenance and family rankings

Variation amongst islands was significant for the growth traits, indicating that island-level selection will result in some

genetic improvement. Families from Espiritu Santo gave the best diameter growth at 11.4 years while those from Maewo and Forari on Efate were the poorest. It should be noted, however, that the trial site is on Espiritu Santo and the magnitude and practical implications of GxE interaction in this species are still unknown. Form scores for the Espiritu Santo families were mostly better than the other islands while the reverse was true for branching score. The very high genetic correlation for diameter growth between the 4-year and 11.4-year measures bodes well for early selection for growth traits, which is directly associated with volume production in future seedling seed orchards.

Families of Espiritu Santo origin dominated rankings for DBHOB, form and branching traits. Of the 18 top families, ranked by a simple index formed by summing across growth and form trait ranks, only one, from West Ambae, was from outside Espiritu Santo. However, selection of trees-within-family as candidate plus trees for seed collection also needed to cater for seeding periodicity amongst the females and the dioecious character of the species, as many of the selected trees were non seed-bearing males. This required the listing of four to seven top ranked trees within each family, from a maximum of 8 to 14 trees per family available after earlier thinning.

Despite pooling of data from the major and minor trials, eight provenances in this IFP trial were represented by fewer than ten families. Where possible, recognising the scarcity of remaining wild trees in some of these subpopulations (Table 2), progeny testing involving larger family samples would be desirable to confirm provenance performance.

### Volume growth

The estimated mean annual volume increment (MAI) for the trial trees of 12.5 m<sup>3</sup>/ha/year for this reportedly fast growing (Grant *et al.* 2012) tropical species was surprisingly low. One inherent problem with estimating MAI from first generation provenance-progeny trials is the large proportion of poorly-performing provenances and families. It is tempting to extrapolate the performance of the best performing provenances from South Santo to the entire site in which case the estimate of growth rate would be 18.3 m<sup>3</sup>/ha/year. This assumption would only hold if site factors were not limiting in the absence of the large areas of less-intense competition occupied by the poorer provenances. In this case it is reasonable to assume that the trial has produced less wood than a commercial plantation might have, since the trial was not

TABLE 5 Genetic correlations between pairs of traits and standard errors of correlation

Genetic correlations (standard error)	Form 11.4 y	Branching 4 y	Height 4 y	DBHOB 4 y
DBHOB 11.4y	0.10 (0.29)	-0.10 (0.28)	0.55 (0.2)	1.00 (0.17)
Form 11.4 y		0.40 (0.30)	*	-0.08 (0.35)
Branching 11.4 y			*	-0.01 (0.24)
Height 4 y				0.98 (0.11)

\* could not be determined

TABLE 6 Basic density and standard deviation at six sampling heights along the stem of 20 buffer trees of the one bulked provenance seedlot surrounding replicates 1–5 in the IFP whitewood trials at 11.4 years-of-age

Sample height	Basic Density (kg/m <sup>3</sup> )	Stdev (kg/m <sup>3</sup> )	R <sup>2</sup> (sample vs. whole tree density)	Mean bias (%)	n
Base	338	33	0.36	+13	8
Breast height	330	21	0.99	+6	19
10%	327	21	0.93	+6	9
30%	299	30	0.86	–2	10
50%	290	17	0.58	–6	8
70%	277	16	0.85	–11	8
Mean of all samples	313	31			62

TABLE 7 Tree size, whole tree basic density and variation in basic density with tree height in eight buffer trees of the one bulked provenance seedlot surrounding replicates 1–5 in the IFP whitewood trials at 11.4 years-of-age (\* signifies a missing value)

DBHOB (cm)	Height (m)	Tree volume (m <sup>3</sup> )	Whole tree density (kg/m <sup>3</sup> )	Wood basic density by sample height (kg/m <sup>3</sup> )					
				Base	Breast height	10% Height	30% Height	50% Height	70% Height
49	20.3	1.59	297	332	316	313	*	290	261
40.1	18.3	1.12	298	326	315	315	302	276	264
36	18	0.77	307	*	325	327	309	278	269
30.8	16.8	0.61	324	377	346	351	317	292	287
30.6	17.7	0.64	321	355	338	332	309	321	297
26.5	16.4	0.45	305	348	*	328	297	284	265
26.3	17.5	0.43	334	*	346	364	329	305	303
22.6	16	0.32	290	359	308	299	*	270	267
		Means	<b>310</b>	<b>350</b>	<b>328</b>	<b>329</b>	<b>311</b>	<b>290</b>	<b>277</b>

fertilised and was thinned and managed for seed production rather than timber production. It is possible that thinning was carried out late and not at the optimal time, as evidenced by the very minor difference between the selectively- and self-thinned parts of the trial: the self-thinned portion may have been slow to recover increment post-thinning.

As for many other tree species, the MAI of whitewood is not static but increases over time, particularly between years 7 and 15 (Grant *et al.* 2012) and, therefore, this provides further support for the prediction that the MAI of this IFP trial may approach 19 m<sup>3</sup>/ha/year at year 17.

### Genetic parameters

Single-site heritability estimates were moderate to low for growth (0.16) and form (0.10) traits at 11.4 years, similar to estimates for these traits reported in other species, for example, *Eucalyptus* (Eldridge *et al.* 1993, Borralho *et al.* 1992) and *Pinus* (Atwood *et al.* 2002, Gapare *et al.* 2010), but lower than that found for *Tectona grandis* (Narayanan *et al.* 2009, Monteuiis *et al.* 2011). This coupled with moderate

coefficients of phenotypic variation indicate that prospects for genetic improvement by recurrent selection and breeding are promising. Precision of estimation was moderately high in all but the 4-year DBHOB. As the data are drawn from a single site only, upward bias in these estimates is expected as the environmental (genotype-by-site, Gx<sub>E</sub>) component of variation cannot be quantified. Plans to establish second generation progeny trials across a range of sites from the selected individuals in this study will provide a future opportunity to quantify Gx<sub>E</sub> interactions.

Diameter at breast height over bark at the 4- and 11.4-year measures were very closely correlated (genetic correlation of 1.00 ± 0.17). Similar age-age genetic correlations were found for growth traits in *Acacia auriculiformis* (Hai *et al.* 2008), *Eucalyptus globulus* (Borralho *et al.* 1992, Stackpole *et al.* 2010) and *Pinus taeda* (Williams and Megraw 1994). In whitewood this correlation is encouraging as early selection for diameter/volume growth and early thinning in seedling seed orchards can be incorporated into the breeding strategy. Growth and form traits were not strongly correlated (–0.10 ± 0.28 for branching and 0.10 ± 0.29 for form) though

they had high standard errors of correlation. Given this low correlation it is possible these traits can be improved independently of one another. Similarly, branching and form traits were only moderately correlated ( $0.40 \pm 0.30$ ).

### Variation in wood basic density

Basic density influences many properties of wood, including its sawing and working features. It provides a good indication of the strength, stiffness and toughness of the timber as well as a guide to the severity of shrinkage (Eldridge *et al.* 1993). Wood basic density has usually been found to be under moderate to strong genetic control (e.g., in *Eucalyptus* species (Downes and Raymond 1997)), though usually with a low coefficient of variation, and is often regarded as the single most important wood property criterion for timber selection (Panshin and de Zeeuw 1980).

Given whitewood's reputation for producing low-density timber of low strength it is important to quantify genetic variation in wood density in this species and the potential for increasing it through selection and breeding. Non-destructive (coring) sampling of the major IFP provenance/family trial is therefore recommended to determine genetic parameters for wood basic density in *E. medullosum*. The preliminary investigation reported here of variation in wood density in one provenance from a bulked seedlot was undertaken to inform the sampling strategy applied in any larger study.

Basic density decreased with increasing stem height. The best linear relationship between whole tree density and density at the various sampling heights was with the samples taken at breast height ( $r^2=0.99$ ) but with an upward bias indicated of about 6% at this age. Breast height non-destructive coring in any latter studies, apart from its convenience, can also be justified as it represents the density of the butt log which is the most valuable part of any tree and perhaps more so in young whitewood. The upper wood of whitewood less than 20 years old is of poor quality (low density, wandering pith) and difficult to market even when preservative treated (N. Croucher, Vanuatu sawmiller, pers. comm. 2010).

An air-dry density range for mature whitewood trees of 365–450 kg/m<sup>3</sup> at 12% moisture content has been reported earlier (Keating and Bolza 1982, Thomson 2006). This is equivalent to a range in basic density of 292–360 kg/m<sup>3</sup> using Greenhill and Dadswell's (1940) formula to convert air dry densities to basic densities. In this study, most samples ( $n=19$  samples/trees) were taken at breast height where basic density ranged from 284–364 kg/m<sup>3</sup>, with a mean ( $\pm$ standard deviation) of 330 ( $\pm 21$ ) kg/m<sup>3</sup>. This is an almost identical range to that given in the literature for mature trees. There was no evidence in this data of a relationship between growth rate and wood basic density in whitewood trees of 11.4 years-of-age.

### CONCLUSIONS

This study has demonstrated considerable island- and family-level variation in traits of economic significance in *E. medullosum*. Both island- and family-level selection in a recurrent

selection and breeding program should result in genetic gain. The study has also underlined the importance of genetic conservation of a wide range of genetic material of this species, which like so many other timber species in the Pacific (see Elevitch 2006 for numerous examples), has suffered subpopulation degradation and extinction due to over harvesting. In this study, material from highly threatened subpopulations (e.g., Sara, which is now entirely depleted, see Table 2) have performed well. Though conducted on a modest scale, this breeding program is an important means for conserving the genes of this subpopulation. Maintenance of genetic diversity in wild populations through a conservation strategy is recommended to ensure the availability of germplasm for long-term improvement.

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