

Basic density, diameter and radial variation of Vanuatu Whitewood (*Endospermum medullosum*): potential for breeding in a low density, tropical hardwood

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SUMMARY

Vanuatu whitewood (*Endospermum medullosum* L.S. Smith) is an economically important timber species for Vanuatu. Inter- and intra-provenance genetic parameters for stem diameter at breast height, basic density and radial variation in density, were estimated for two provenances selected from a 12.4-year-old open-pollinated seed orchard on Espiritu Santo Island, Vanuatu. Kole provenance exhibited the highest mean basic density, greatest mean diameter and greatest radial variation in density across the stem.

Mean basic density at breast height was 345 ± 2 kg/m³. Growth rings were not visually discernable and colour was homogenous across all samples. For radial variation determination, each pith-bark core was sectioned into four equi-length subcores (A-D). Subcore density increased consistently and significantly from pith to bark, with mean basic density of 308 ± 3 , 327 ± 3 , 343 ± 3 and 359 ± 3 kg/m³ for cores A-D respectively.

The narrow-sense heritability estimate (\hat{h}^2) was low (0.26 ± 0.2) for diameter, with a moderate coefficient of additive genetic variation ($CV_A = 17.61\%$). Estimated \hat{h}^2 for density was moderate (0.49 ± 0.24), with a low coefficient of additive genetic variation ($CV_A = 5.39\%$). Though the precision of these estimates is modest, reflective of the small sample size, indications are that the heritable genetic variation in both growth and quality traits will result in economic gain from a recurrent selection and breeding program.

Keywords: density, diameter, radial variation, heritabilities, genetic correlation

La densité de base, le diamètre et la variation radiale de Vanuatu blancs (*medullosum Endospermum*). Trait-trait corrélations dans une faible densité, des feuillus tropicaux

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Vanuatu whitewood est une espèce de bois économiquement importants pour le Vanuatu. Les paramètres génétiques pour le diamètre de la tige (DBH), la densité de base (DEN) et de la variation radiale (RadVar) ont été estimés en deux provenances pendant 12,4 années sur l'élevage de la population *Endospermum medullosum* L.S. Smith à pollinisation libre sur île d'Espiritu Santo, au Vanuatu. La provenance Kole a été exposée au plus haut de la densité moyenne de base, au plus haut diamètre moyen et à la plus grande variation de la densité dans la tige.

Les estimations d'héritabilité (\hat{h}^2) ($0,26 \pm 0,2$) ont été faibles pour le DBH, avec une variation phénotypique modérée ($CV_A = 17,61\%$) et une estimation de l'héritabilité ($0,49 \pm 0,24$) ce qui étaient modérées pour la densité, avec une variation phénotypique faible ($CV_A = 5,39\%$). La densité moyenne de base à hauteur de poitrine était de 345 (SE ± 2) kg/m³, et a augmenté de façon constante 308 (SE ± 3), 327 (SE ± 3), 343 (SE ± 3) et 359 (SE ± 3) kg/m³ et significative de la moelle à l'écorce.

La faible taille de l'échantillon disponible peut avoir réduit la précision, toutefois il est prévu que le gain économique dû à la croissance et aux caractères de qualité peuvent être obtenue à partir d'une sélection récurrente et programme d'élevage étant donné les variations génétiques héréditaires indiqué dans cette étude.

Variabilidad de la densidad basica en el diametro y en las secciones radiales de *Endospermum medullosum* (Vanuetu whitewood). Correlaciones entre los caracteres biologicos de una especie tropical de baja densidad.

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La madera blanca (*Endospermum medullosum* L.S. Smith) es una especie maderera de importancia económica para Vanuatu. Se estimaron parámetros genéticos dentro y entre procedencias para diámetro de tallos a la altura del pecho, densidad básica y variación radial en densidad para dos procedencias seleccionadas de un huerto de semillas de polinización abierta de 12.4 años de antigüedad en la isla de Espiritu Santo,

Vanuatu. La procedencia Kole exhibió la mayor densidad básica, el mayor diámetro medio y la mayor variación radial en densidad a lo largo del tallo.

La densidad básica media a la altura del pecho fue $345 \pm 2 \text{ kg/m}^3$. No se pudieron discernir anillos de crecimiento en las muestras. Para la determinación de la variación radial, cada núcleo de médula de la corteza se seccionó en sub-núcleos de igual longitud (A-D). La densidad de sub-núcleos incrementó consistente y significativamente de médula a corteza con los núcleos (A-D) exhibiendo una densidad media básica de 308 ± 3 , 327 ± 3 , 343 ± 3 y $359 \pm 3 \text{ kg/m}^3$ respectivamente.

Las estimas de heredabilidad (\hat{h}^2 0.26 ± 0.2) fueron bajas para el diámetro, con un coeficiente moderado de variación genética aditiva ($CV_A = 17.61\%$). Las estimas de heredabilidad (\hat{h}^2 0.49 ± 0.24) fueron moderadas para la densidad, con un coeficiente bajo de variación genética aditiva ($CV_A = 5.39\%$).

El pequeño tamaño de muestra puede reducir la precisión de estas estimas. Se espera que dada la variación genética heredable indicada en este estudio, sería posible una ganancia económica tanto en caracteres de crecimiento como de calidad a través de una selección recurrente y un programa de cultivo.

INTRODUCTION

Endospermum medullosum L.S. Smith (family Euphorbiaceae), commonly known as Vanuatu whitewood, New Guinea Basswood or Sessendok, is a fast growing pioneer species, with a distribution ranging from Eastern Indonesia, New Guinea, Solomon Islands and Vanuatu (Guerrero and Welzen 2011). Whitewood is recognised as an economically important timber species in Vanuatu, comprising 60–70% of all harvested logs between 1990 and 2004 (Page 2009).

The primary demand for whitewood comes from the Japanese consumer market. Prior to the 2011 Tōhoku-Oki earthquake, the Japanese market for Vanuatu whitewood was valued as US\$3.9 million per annum for sawn timber (Page 2009). Whitewood is valued in Japan for its pale colour and smooth grain (G. Palmer, Southern Cross University, pers. comm. DEC 2011). The Vanuatu Forest Policy identifies forestry and timber production as vital for supporting sustainable livelihoods in Vanuatu and sets a national target of 20,000 ha of timber plantations by 2020 (Mele 2011). The Policy identifies whitewood as an ideal forestry species due to its rapid growth, cyclone resistance (Thomson 2006, Page 2009, McGregor and McGregor 2010, Page and Awarau 2012), resistance to brown root rot (*Phellinus noxius*) (Neil 1986, Ivory and Daruhi 1993, Ramsden *et al.* 2002) and the existence of an established export market (Page 2009, McGregor and McGregor 2010, Mele 2011). McGregor and McGregor (2010) estimate that 3,000–5,000 ha of whitewood plantation forests, harvested on a 20–25 year rotation, would produce approximately 50,000 m³ of timber annually with an estimated annual export value of \$USD35 million (approximately 6% of current GDP).

However, major concerns exist for the future security of whitewood. A decade ago, FAO noted that the majority of natural stands had been logged-out, leaving only small pockets in the relatively inaccessible, central, elevated areas of Vanuatu. They predicted that given the then-current rates of utilization, the whitewood forests of Vanuatu would be effectively exhausted within 10–14 years (FAO *et al.* 2001). That this trajectory of unsustainable logging has continued is evident in a recent survey conducted of the status of wild subpopulations from which the genetic resources examined here were drawn: many have disappeared in the recent past

(see Doran *et al.* 2012). The future of conserving and developing whitewood will be through establishment of commercial plantations.

The primary objective of whitewood plantation management is the production of large diameter logs for production of knot-free clearwood (Thomson 2006). A secondary objective is to improve wood quality via breeding for increased wood density (Doran *et al.* 2012, Thomson 2006). Whitewood air-dried density at 12% moisture content is estimated to be between 365–450 kg/m³ (Keating and Bolza 1982, Thomson 2006), and mean basic density reported as 330 (± 21) kg/m³ (Doran *et al.* 2012). These estimates have been based on limited numbers of samples from either unknown origin (Keating and Bolza 1982, Thomson 2006) or a single subpopulation (Doran *et al.* 2012). Although this emerging resource forms a crucial component of Vanuatu's sawlog industry, and despite extensive economic investment by the Australian Centre for International Agricultural Research (ACIAR) and Vanuatu Department of Forestry (VDoF), the absence of accurate information on wood density variation, the relationship between wood quality and growth and potential for genetic improvement represents a serious gap in the knowledge for this species.

Tree diameter, measured at breast height (DBH) is an economically important trait as it separates logs into different production systems with disparate cost and revenue structures (Panshin and De Zeeuw 1964, White *et al.* 2007, Blackburn *et al.* 2011). For higher density species, greater DBH equates to greater recovery of higher-value select and standard grade sawn boards as a proportion of log volume (Blackburn *et al.* 2011).

Defined as the mass of oven-dry material per unit of volume (Williamson and Wiemann 2010), basic wood density (DEN) is another important selection criterion that is correlated with numerous morphological, mechanical, physiological and ecological properties of wood (Chave *et al.* 2006). DEN is indicative of strength and stress grades, it influences sawn timber recovery, and pulp and paper production (Panshin and de Zeeuw 1964). Density is inversely correlated with porosity (Shmulsky and Jones 1990) with denser wood tending to exhibit a finer texture (Montes *et al.* 2008). Density is phenotypically correlated with heartwood darkness, (e.g., in *Acacia melanoxylon* Bradbury *et al.* 2011) and sapwood

yellowness, (e.g., in *Eucalyptus dunnii*, Vanclay *et al.* 2008). These characteristics are potentially important for whitewood as whitewood's popularity in the current Japanese market is for its pale colour and fine grain.

Narrow-sense heritability (h^2) can be defined as the proportion of phenotypic variation in a trait that is attributable to additive genetic differences and that can be transmitted to subsequent generations. It is therefore a key parameter for determining whether or not recurrent selection and breeding will result in genetic gain. Narrow-sense heritability is generally low for growth traits (e.g., DBH) and moderate to high for wood property traits (e.g., DEN) (Falconer and Mackay 1981, White *et al.* 2007) in both softwood and hardwood species. Both DEN and heritability generally increase with radial distance from the pith for both softwoods (Wu *et al.* 2008, Gapare *et al.* 2009, Raymond and Henson 2010) and hardwoods (Butterfield *et al.* 1993, Hein *et al.* 2012). However the opposite can be true for some species (Bush *et al.* 2011). Genetic correlations between DBH and DEN are often strongly negative for coniferous species (Wu *et al.* 2008, Raymond and Henson 2010, Gapare *et al.* 2012).

For hardwood species, although the sign and the genetic correlation coefficients vary between species and sites, there is generally a weak, yet positive relationship between DBH and DEN (Stackpole *et al.* 2010, Hein *et al.* 2012). Correlations range between 0.08 for sixteen year old *E. globulus* (Stackpole *et al.* 2010) and -0.05 for eighteen-year-old *Acacia melanoxylon* in Tasmania (Bradbury *et al.* 2011) Wu *et al.* (2011) reported a correlation of 0.05 between these traits for 4 year old *E. urophylla* x *E. grandis* clones in Changle, South China while Quang *et al.* (2010) report a correlation of -0.50 in nine year old *Eucalyptus urophylla* in Vietnam.

Simultaneously increasing both growth (DBH) and DEN is the objective of many tree breeding programs (Borrallho *et al.* 1993, Li *et al.* 1999, Wu *et al.* 2008, Gapare *et al.* 2009, 2011) as log value is primarily a function of size and density. Realised gain has been demonstrated in several softwood species: 162% increase in dollar value as a result of volume and sawn timber improvement (Cumbie *et al.* 2012) combined with 7%–12% increase in stand volume at age of rotation for *Pinus taeda* (Li *et al.* 1999), 11.5% increase in DBH of *P. radiata* (Carson *et al.* 1999), and 5.1% increase in two years height for *P. banksiana* (Rudolph *et al.* 1989). There are also several reports for realised gains in DBH for some hardwoods: 19% in *Eucalyptus pellita* (Leksono *et al.* 2008) and 28.2% in second generation progeny trial of *Acacia auriculiformis* in Thailand (Luangviriyasaeng and Pinyopussarerk 2002). These findings highlight the importance of quantifying genetic variation of both growth and wood property traits early in the domestication phase of a species.

The aim of this study is to quantify within-species genetic variation in the mean basic density (DEN) trait, within the Shark Bay *E. medullosum* provenance-progeny trial. Furthermore we aim to characterise patterns of radial variation (RadVar) in wood density, and estimate heritabilities and determine the presence and strength of genetic correlations between these traits and diameter at breast height (DBH). This information will contribute directly to future whitewood breeding objectives.

MATERIALS & METHODS

Sample population

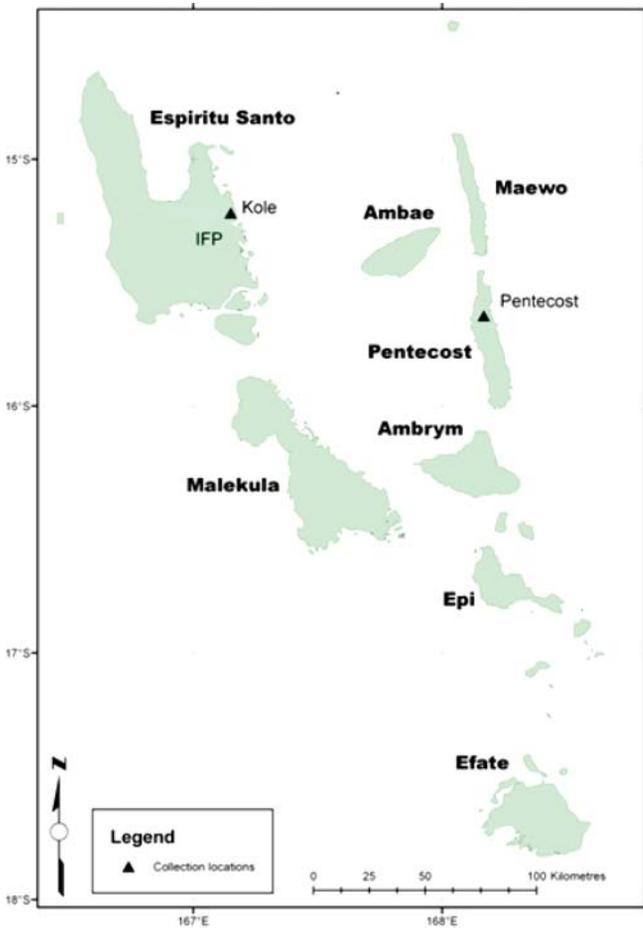
Measurements and samples were collected from an *E. medullosum* provenance-progeny trial established at the Industrial Forestry Plantation (IFP) located at the Shark Bay Research Station, Espiritu Santo Island, Vanuatu (15°13'S, 167°09'E, alt. 100 m) (Figure 1). The whitewood trial was established across a 6.25 hectare site between December 1998 and January 1999, as a randomised complete block design of eight blocks. Initial stocking was 833 trees per hectare with trees initially spaced 2 m within rows and 6 m between rows. Each block consisted of 100, six-tree lineplots, each plot comprising a single, open-pollinated family (Vutilolo *et al.* 2008). Families were drawn from 15 provenances. Blocks 1–5 of the trial were progressively thinned at ages 5, 6 (Vutilolo *et al.* 2008) and 11 years from six trees per plot to 5, 2 and 1 tree respectively. Blocks 6–8 self-thinned up until age 11 years, at which time family plots were also reduced to a single tree. This resulted in a final overall stocking density of 139 stems/ha (Vutilolo *et al.* 2008, Doran *et al.* 2012) at 11.4 years. Thinning selection was based on an index including growth and form traits.

In this wood-property study, eight trees from each of ten families from two provenances, Kole and Pentecost, were sampled at age 12.4 years giving an initial total of 160 sample trees: however, due to the mortality of one tree in each of three Pentecost families MT12, MT13 and MT19, 157 trees were sampled (Table 1). The trees were sampled after final-thinning and were effectively single-tree plots replicated in each of the eight blocks. The provenances were selected due to their contrasting (respectively high and low ranking) growth performance measured as diameter at breast height (DBH) at both 4 (Vutilolo *et al.* 2008) and 11 years (Doran *et al.* 2012).

Sampling

Trees were 12.4 years of age and approximately average of 18 m height at time of sampling. Cores of 12 mm diameter were taken using a motorised (Tanaka TED 262R) coring drill-bit (CSIRO Tree-Cor) (Downes *et al.* 1997). Breast height (1.3 m) was chosen as point of DEN core-sampling for this species based on the findings of Doran *et al.* (2012), who demonstrated that density decreased with increasing sampling height and breast height was strongly correlated ($r^2=0.99$) with whole tree density. Tree diameter (DBH) was determined at breast height over bark and a single core was taken to half tree diameter from bark to pith along a consistent (west-east) orientation for each sample tree. Upon extraction, each core was labeled with individual tree identity and immediately immersed in water to achieve and maintain fiber saturation point. All cores were stored within sealed, air-tight plastic containers and maintained in immersed, refrigerated conditions until determination of density.

FIGURE 1 Location of two *E. medullosum* provenances included in this experiment, Kole and Pentecost and the location of the IFP provenance trial in which the provenances were sampled (Doran et al. 2012).



Basic Density

In order to assess radial variation (RadVar), and as growth rings were not discernable, cores were sectioned into four equal-length subcores and labeled A (pith) to D (bark) and the volume of each subcore, (A-D), was determined using the water displacement method (TAPPI 2011).

Samples were then dried at 105°C in a fan forced oven (LABEC ODWF36) until two consecutive weight measurements were within 0.01 g. Subcore density was determined as the oven dried weight of each subcore (A-D) divided by the green volume of each subcore (TAPPI 2011). Whole-disk density was estimated as the density of each subcore weighted to represent annuli of a disk as described in Muller-Landau (2004) and Williamson and Wiemann (2010).

Statistical Analysis

Fixed and random effect parameters for DBH, DEN and RadVar were estimated using a mixed-model implemented in ASREML version 3 (VSN International, Hemel Hempstead, UK) as follows:

$$y_{ijk} = \mu + \alpha_i + \beta_j + \mathbf{F}_{k(i)} + \mathbf{e}_{ijk} \quad [1]$$

where y_{ijk} is the phenotypic value of the k th family in the j th block of the i th provenance, μ is the overall mean, α_i is the fixed effect of i th Provenance ($i=1,2$), β_j is the effect of the fixed, j th complete-block ($j=1,\dots,8$), $\mathbf{F}_{k(i)}$ is the random effect of the k th family ($k=1,\dots,20$) nested within the j th provenance and \mathbf{e} is the residual variance.

BLUPs (best linear unbiased predictors) were predicted for the random effect of family-within-provenance and BLUEs (best linear unbiased estimators) were estimated for the fixed effect of Provenance. Likelihood ratio tests (LRT) (Stram and Lee 1994) were used to test for significance of family-within-provenance effects. Log Likelihood was estimated as $LRT = 2(\text{Log } L_{p+g} - \text{Log } L_p)$ where $\text{Log } L_{p+g}$ is the Log-likelihood with the family term and $p+g$ degrees of freedom and $\text{Log } L_p$ is the Log-likelihood without the family term with p degrees of freedom. The LRT was distributed as a χ^2_q with q degrees of freedom. The Log-likelihoods were compared using the LMERConvenienceFunctions package in R (Tremblay 2011).

For each trait (DBH, DEN, and RadVar) narrow-sense heritability (σ^2_f) were estimated as follows:

$$\hat{h}^2 = \frac{3\sigma^2}{\sigma^2_f + \sigma^2_e} \quad [2]$$

The default assumption that open-pollinated families are maternal half-siblings is likely to be flawed: to allow for the likelihood of partial inbreeding (Squillace 1974, Falconer and Mackay 1981) additive genetic variance was estimated at $3\sigma^2_f$ i.e., the coefficient for relationship for the open pollinated families was assumed to be 0.33, as is common for tropical hardwood species (Hodge et al. 2002, Hodge and Dvorak 2004). Standard errors of heritability estimates were made using the Taylor series method which is implemented in ASREML (Gilmour et al. 2006).

The coefficient of additive genetic variation (CV_A) provides a standardised measure of the amount of variation relative to the trait mean. The higher the coefficient of additive genetic variation is for any trait, the higher is that trait's relative variation (Houle 1992, Cornelius 1994, Garcia-Gonzalez et al. 2012).

It was estimated as,

$$CV_A = \left(\frac{\sigma^2_f}{\bar{x}} \right) * 100 \quad [3]$$

where

CV_A coefficient of additive genetic variation

σ^2_f square root of the additive (family) genetic variance for the trait and

\bar{x} population mean for the trait

Bivariate genetic correlations (r_G) between DBH, DEN and subcore (A-D) density were obtained from the estimated additive covariance and variance components as:

$$r_G = \frac{\sigma_{a_x a_y}}{\sqrt{(\sigma_{a_x}^2 \sigma_{a_y}^2)}} \quad [4]$$

where

- $\sigma_{a_x a_y}$ additive genetic covariance between traits (x and y)
 $\sigma_{a_x}^2$ additive genetic variation component for trait x
 $\sigma_{a_y}^2$ additive genetic variation component for trait y

Standard errors were obtained by Taylor series expansion using ASREML (Gilmour *et al.* 2006).

Intra- and inter-provenance (Kole and Pentecost) differences in the mean density of subcores (A-D) were determined using a two-way ANOVA (R Development Core Team 2011).

Estimates of predictive genetic gain (PGG) in a hypothetical whitewood breeding population were calculated as outlined in White *et al.* (2007), pp 422–423. Predicted genetic gain (PGG) was calculated for a hypothetical open-pollinated, clonal seed orchard based on the best 15% of families in the study population. Families were selected on the basis of BLUP density, with the proviso that no families with DBH below the population mean were selected.

RESULTS

Provenance and overall trait means

Trait means for individual families are presented in Table 1. Provenance and overall trait means, ranges and coefficients of variation are presented in Table 2 and Figure 2 (DBH) and Table 3 and Figure 3 (DEN).

The overall mean for DBH was 32.5 cm with a 29.7 cm range in diameter between trees. Pentecost exhibited a significantly, $p < 0.001$, lower DBH than Kole (30.6 cm and 34.3 cm respectively) (Table 2). Mean basic density was 345 kg/m³ across both provenances with a 143 kg/m³ variation. DEN was significantly, ($p < 0.001$), lower in Pentecost (328 kg/m³) than Kole (361 kg/m³) (Table 3). Family means ranged between 28.2 cm and 37.7 cm for DBH (Fig. 2) and 302 kg/m³ to 390 kg/m³ for DEN (Fig. 3). No significant intra-provenance DBH variation was found in either provenance (Fig. 2). Significant ($p < 0.01$) family-within-provenance DEN variation was present in Kole but not in Pentecost. All Kole family means for DEN were greater than all Pentecost families (Fig. 3).

Radial variation

Basic wood density increased consistently and significantly ($p < 0.001$) across all subcores from pith to bark (subcores A-D), exhibiting an overall radial variation of 256 kg/m³ (199–455 kg/m³). Across all samples, mean basic wood density was measured at 308, 327, 343 and 359 kg/m³ across the four subcores from pith to bark (annuli A to D respectively) (Fig. 4). Mean subcore DEN was higher for each Kole subcore than each corresponding Pentecost subcore (Fig. 4). Kole exhibited a greater range in density for subcore A, however Pentecost exhibited a greater range for subcores B, C and D. Significant ($p < 0.001$) within provenance radial variation (Tukey's HSD test) was observed in both Kole ($F_{(3,316)} 35.871$, $p < 0.001$) and Pentecost ($F_{(3,308)} 38.899$, $p < 0.001$) provenances (Fig. 4) *viz.* the mean density of each subcore was significantly ($p < 0.001$) different from all other subcores within the same provenance.

FIGURE 2 Mean DBH (cm) for twenty, open-pollinated, half-sib families, (ten in each of two provenances: Kole, east Santo (white columns) and Pentecost (black columns)). All trees were 12.4 years of age and sourced from *E. medullosum* provenance-progeny trial in Vanuatu

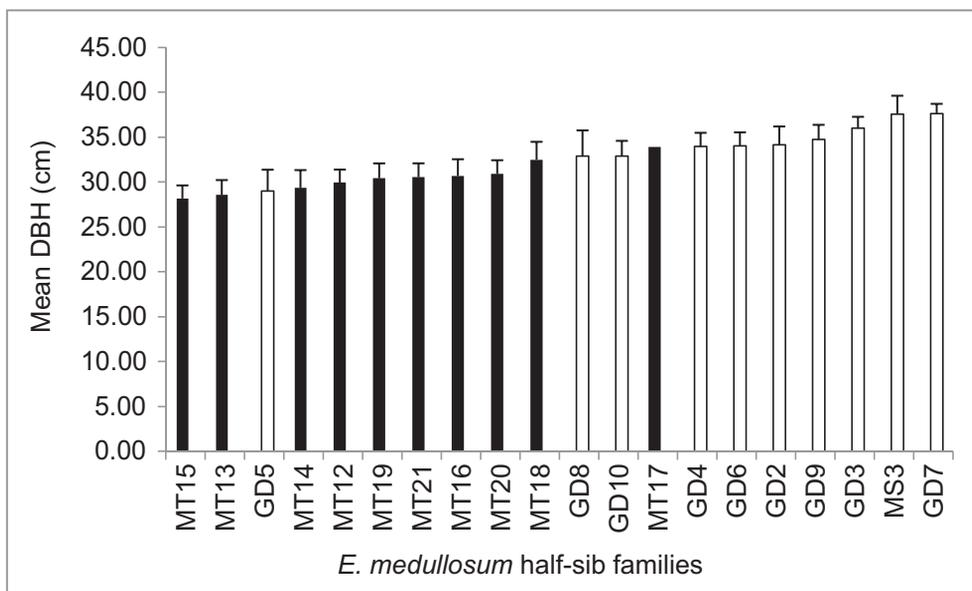


FIGURE 3 Mean basic density (kg/m^3) for twenty, open-pollinated, half-sib families, (ten in each of two provenances: Kole, east Santo (white columns) and Pentecost (black columns)). All trees were 12.4 years of age and sourced from E. medullosum provenance-progeny trial in Vanuatu

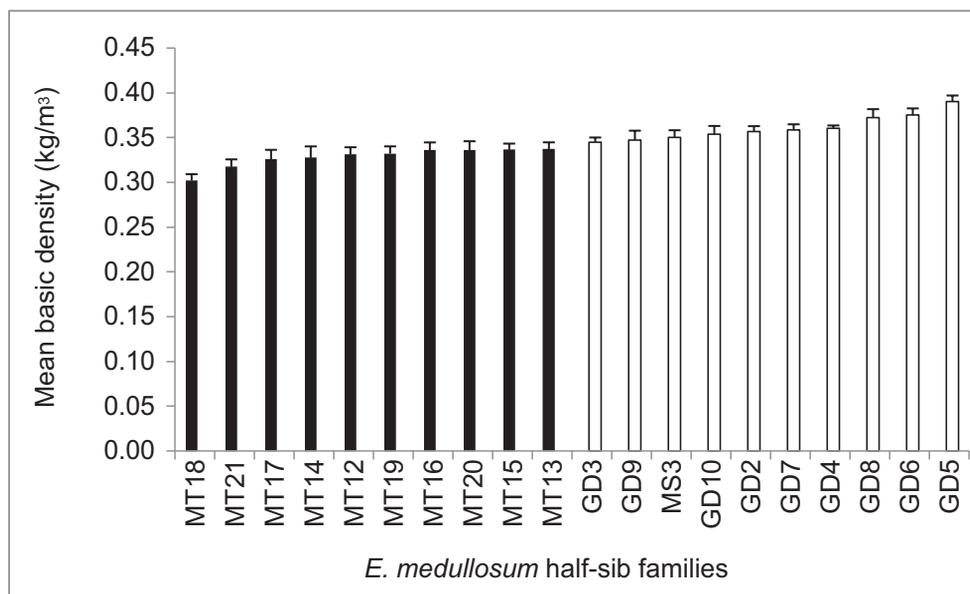


TABLE 1 Diameter at breast height (DBH), density (DEN) and subcore (A - D) family means, in two provenances of 12.4-years-old E. medullosum provenance-progeny trial in Vanuatu

Provenance	Family	DBH (cm)	DEN (kg/m^3)	A (kg/m^3)	B (kg/m^3)	C (kg/m^3)	D (kg/m^3)
KOLE	GD10	34.15	354	337	337	357	364
	GD2	35.70	357	326	340	371	358
	GD3	34.60	345	302	322	343	362
	GD4	35.14	360	317	352	357	372
	GD5	35.90	390	344	368	385	410
	GD6	32.45	375	317	355	381	388
	GD7	32.16	358	319	340	364	368
	GD8	33.53	373	336	357	363	391
	GD9	35.69	347	337	346	343	354
	MS3	33.60	350	314	339	352	358
PENTECOST	MT12	32.60	332	261	315	321	356
	MT13	29.89	337	291	323	330	356
	MT14	30.76	328	307	298	316	352
	MT15	31.76	337	286	306	330	362
	MT16	30.51	336	295	322	340	345
	MT17	28.09	326	289	293	332	340
	MT18	30.03	302	266	287	302	314
	MT19	32.04	332	308	325	331	340
	MT20	30.96	336	293	319	330	354
	MT21	29.36	317	303	304	316	326
MT12	32.60	332	261	315	321	356	
MT13	29.89	337	291	323	330	356	

Genetic parameters

Narrow-sense heritability (\hat{h}^2) and additive genetic coefficient of variation (CV_A) for DBH was 0.26 ± 0.20 and 17.61% respectively (Table 2). Narrow-sense heritability (\hat{h}^2) and additive genetic coefficient of variation (CV_A) for DEN was 0.41 ± 0.20 and 5.39% respectively (Table 3). Both DEN and

\hat{h}^2 increased with distance from pith (Table 4). CV_A estimates were low to moderate for all traits across both provenances. Kole exhibited higher CV_A than Pentecost for both DEN and DBH.

Log likelihood test results indicate that family-within-provenance is a highly significant determinant of density. The test statistic is $2 \times \text{LogL difference} = 2 * (459.995 - 455.063)$

TABLE 2 DBH, means, range, significance of provenance (*F* test), standard deviation, additive genetic variance (σ^2_A), narrow sense heritabilities \hat{h}^2 , associated standard errors and coefficients of variation (CV_A) in two provenances of 12.4-years-old *E. medullosum* provenance-progeny trial in Vanuatu

DBH (cm)	Pentecost	Kole	All Groups
N	77	80	157
Mean (SE)	30.56(0.59)	34.29(0.63)	32.46 (0.46)
Range (Min-Max)	20.50–46.50	16.80–43.20	16.80–46.50
Standard Deviation	5.202	5.619	5.715
Additive Variance (σ^2_A)	1.4	10.5	11.189
Coefficient of Variation (CV_A)	16.39%	17.02%	17.61%
\hat{h}^2 (standard error)			0.26 (0.20)
F probability			0.001

FIGURE 4 Radial variation (pith - bark) in basic density (kg/m^3) across four subcores (A - D) in two provenances, Pentecost (black) Kole (grey) sampled in a *E. medullosum* provenance-progeny trial in Vanuatu

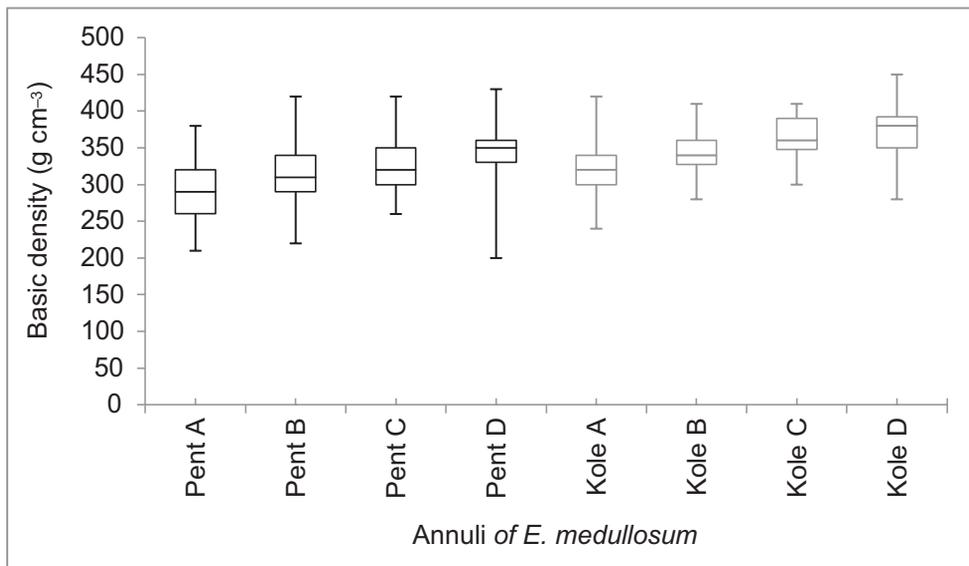


TABLE 3 DEN, means, range, significance of provenance (*F* test), standard deviation, additive genetic variance (σ^2_A), narrow sense heritabilities \hat{h}^2 , associated standard errors and coefficients of variation (CV_A) in two provenances of 12.4-years-old *E. medullosum* provenance-progeny trial in Vanuatu

DEN kg/m^3	Pentecost	Kole	All Groups
N	77	80	157
Mean (SE)	328(3)	361(3)	345(2)
Range (Min-Max)	0.26–0.39	0.31–0.41	0.26–0.41
Standard Deviation	0.025	0.003	0.068
Additive Variance (SE) σ^2_A	0.05(0.007)	0.02(0.01)	0.03(0.006)
Coefficient of Variation (CV_A)	6.10%	4.40%	5.39%
\hat{h}^2 (SE)			0.49(0.24)
F probability			<0.001

TABLE 4 Subcores A-D means, ranges (min.-max), additive variance estimates coefficient of additive genetic variation (CV_A) and heritabilities of *E. medullosum* provenance-progeny trial in Vanuatu

Subcore	A (pith)	B	C	D
N	157	157	157	157
Mean (kg/m ³) (SE)	308(3)	328(3)	343(3)	359(3)
Range (kg/m ³)	207–420	219–418	259–417	199–455
Additive Variance	53.89	168.92	231.46	514.93
CV_A	2.39%	3.97%	4.43%	6.33%
\hat{h}^2 (SE)	0.03 (0.14)	0.18 (0.18)	0.31 (0.21)	0.50 (0.24)
F probability	<0.001	<0.001	<0.001	0.002

= 9.864, which has $p < 0.001$ against the Chi-square distribution with 0.5 degrees of freedom.

Predicted genetic gain (PGG) indicated an 8% gain in DEN with a hypothetical CSO select subpopulation, comprised of families GD8, GD6 and GD5, exhibiting a combined mean DEN 28 kg/m³ higher than the population mean (μ) (365 kg/m³ and 337 kg/m³ respectively). The resultant PGG in DBH was also positive, 3% (Fig. 5 and Fig. 6).

Phenotypic and genetic correlations

Phenotypic (r_p) correlations were all positive with the exception of DBH-D which was negative (Table 5). Significant phenotypic correlations were identified for all trait (DBH * DEN * A-D) combinations, excluding DBH-DEN, and DBH-D. Trait-trait correlations (Table 6) could not be determined in most cases: those involving DBH were all indeterminate and others had high associated standard errors (Table 6). However, moderate to strong trait-trait correlations were

identified between DEN-C (0.9 ± 0.1), B-C (0.75 ± 0.3), C-D (0.91 ± 0.19).

DISCUSSION

The mean basic density, radial variation in density and trait-trait correlations of *E. medullosum* have been quantified and reported here for the first time. *Endospermum medullosum* produces a low density timber (345 kg/m³), which varies significantly between individuals (range of 143 kg/m³) and populations (328 and 361 kg/m³ for Pentecost and Kole populations respectively). Radial variation in wood density was also significant with a 16.5% increase in wood density from the inner to outer wood. Moderate heritability estimates for wood density (\hat{h}^2 0.49 ± 0.24) in this species enables this trait to be included in efforts to bring about its domestication. The results of this study found the mean basic density of whitewood to be within the upper estimates provided by

FIGURE 5 DBH BLUPs for ten open-pollinated families in each of two provenances, Kole (white columns) and Pentecost (black columns) (total of twenty families). All trees were 12.4 years of age and sourced from *E. medullosum* provenance-progeny trial in Vanuatu. X axis set at population mean (μ)

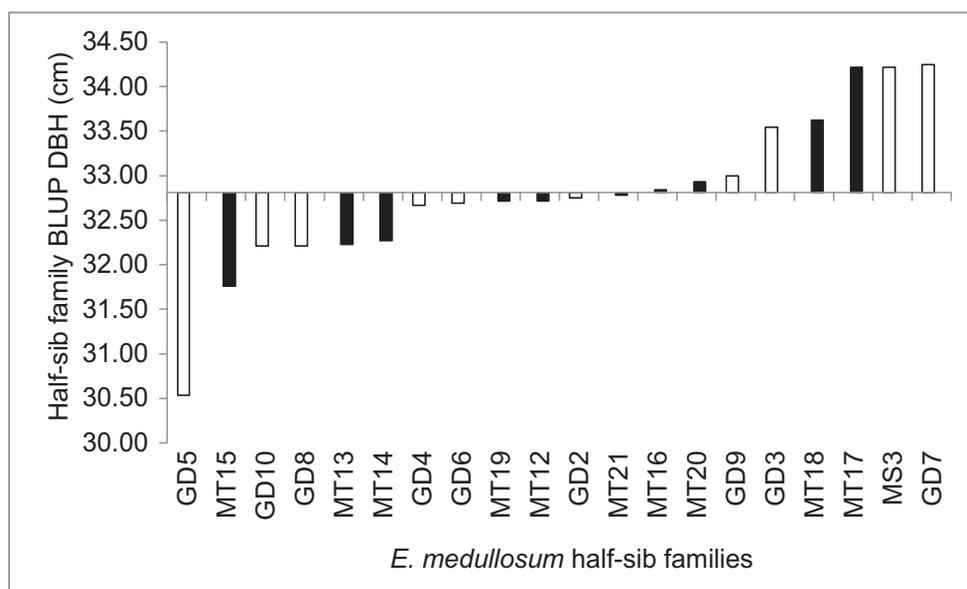


FIGURE 6 DEN BLUPs for ten open-pollinated families in each of two provenances, Kole (white columns) and Pentecost (black columns) (total of twenty families). All trees were 12.4 years of age and sourced from E. medullosum provenance-progeny trial in Vanuatu. X axis set at population mean (μ)

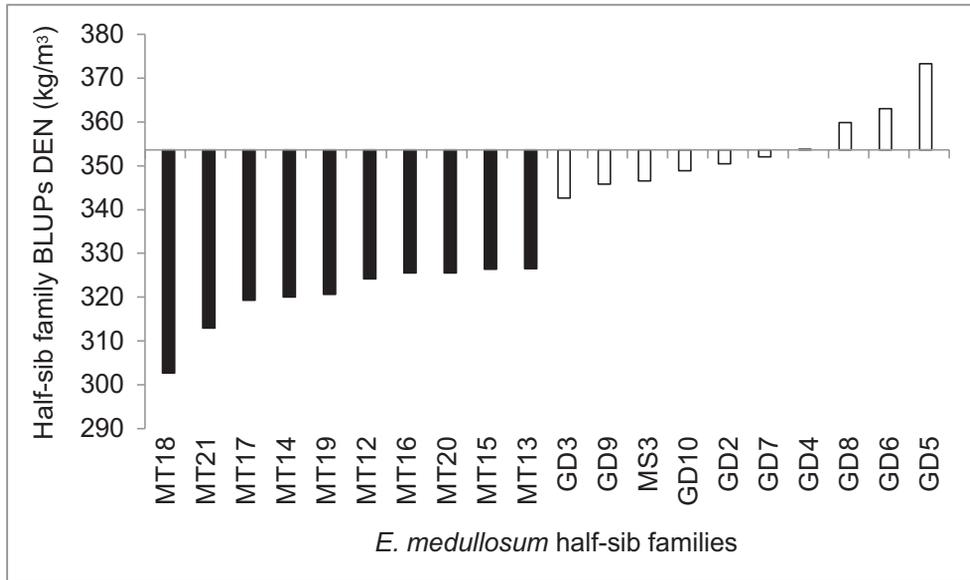


TABLE 5 Pearson's phenotypic (r_p) and genetic correlations (r_G) (SE) between pairs of traits in 12.4-year-old E. medullosum provenance-progeny trial in Vanuatu

	DBH	DEN	A	B	C
Phenotypic correlation, (r_p)					
DEN	0.15				
A	0.16*	0.56**			
B	0.27*	0.81**	0.61**		
C	0.23*	0.90**	0.56**	0.76**	
D	-0.03	0.86**	0.24*	0.47**	0.61**
Genetic correlation, (r_G)					
DEN	N.D.				
A	N.D.	0.6 (1.36)			
B	N.D.	N.D.	0.18 (1.47)		
C	N.D.	0.9 (0.10)	-0.03 (1.56)	0.75 (0.30)	
D	N.D.	N.D.	N.D.	N.D.	0.91 (0.19)

ND not determined due to non-convergence of ASREML algorithm

** $p < 0.001$, * $p < 0.05$ (phenotypic correlations significantly different from zero)

Thomson (2006) and Doran *et al.* (2012). The density result ranks whitewood with other low density southeast Asian, tropical Euphorbiaceae including *Endospermum peltatum* (300 kg/m³), *Macaranga sampsoni* (330 kg/m³) and *Macaranga myriantha* (400 kg/m³) (Chave *et al.* 2009, Zanne *et al.* 2009).

Provenance rankings

There were significant ($p < 0.001$) differences found between the two provenances sampled for both DEN and DBH,

indicating that there is scope for future breeding objectives to be based on provenance-level selection for genetic improvement of these traits. The apparent superiority of Kole in DBH is consistent with previous studies measuring the same family provenance trial (Doran *et al.* 2012, Vutilolo *et al.* 2008). Santo Island provenances, such as Kole, have been shown to exhibit superior DBH at age 4 (Vutilolo *et al.* 2008), 11.4 (Doran *et al.* 2012) and now 12.4 years in the IFP plantation on Espiritu Santo Island. The close proximity of the IFP trial to the origin of Kole provenance (Fig. 1) may indicate greater local adaptation to this region by Kole. However, as

environmental variation undoubtedly exists across Vanuatu's numerous islands, Genotype by Environment (GxE) experiments, established across varying climatic and edaphic conditions (White *et al.* 2007) will be necessary to test the assumption of superiority of Santo provenances and identify whether or not other locally specialised provenances exist (Doran *et al.* 2012).

Variation in wood density

At the time of this study the trees were approximately half rotation age (20–25 years) (Thomson 2006). Greater variation in density was found within trees (radially at breast height) than between trees, families or provenances. This large pith-to-bark increase in density is characteristic of tropical pioneer angiosperm species (Wiemann and Williamson 1988, Butterfield *et al.* 1993, Raymond and Henson 2010, Lachenbruch *et al.* 2011). Juvenile trees, such as those sampled in this experiment, are adapting to changing hydraulic and mechanical demands placed upon wood due to growth. Therefore any radial variation in wood structure is likely to be a reflection of ontogenetic changes (Lachenbruch *et al.* 2011) and would be expected to decrease as age increases. Predicted genetic gains for density also indicated that a small positive gain in diameter was also achievable. Breeding whitewood for higher density could be a desirable breeding objective as improved density may increase options for end usage (Kataoka *et al.* 2004). However high density can result in utilisation problems such as splitting during nailing, shelling along the heartwood/sapwood interface and poor nail penetration, as has been found in mature slash × Caribbean pine, a hybrid with comparable density to whitewood (Harding and Copley 2000).

Wood grain and colour are a product of density and maturity of the tree (Butterfield *et al.* 1993, Chave *et al.* 2006, Lachenbruch *et al.* 2011). Outerwood often has wider cambial cells and therefore is uneven and rough in texture. Mature heartwood has more consistent cambial spacings which produces a finer grain (Panshin and de Zeeuw 1964). As whitewood has historically been sourced from the wild (FAO *et al.* 2001, Page 2009), it is likely that historic whitewood stocks were of a greater age and DBH, and therefore consisted almost entirely of heartwood (Lachenbruch *et al.* 2011) from which whitewood earned its reputation as a fine-grained species. Breeding for higher density may improve wood colour and grain (Vanclay *et al.* 2008, Bradbury *et al.* 2010), which may be a further breeding objective trait for future assessment.

The proportion of heartwood to sapwood for trees was not measured, in this study. However, due to the relatively young age of the trees (12.4 y), it is probable that this proportion is lower than that of larger, wild-harvested trees. Without significant genetic and silvicultural intervention, whitewood growers are likely to follow the global trend of harvesting trees of a younger age (Lachenbruch *et al.* 2011) and also increasingly market thinned material to maximize the rate of return on investment in land and silviculture. This will result in an inevitable increase in the proportion of sapwood to heartwood. Genetic variation in heartwood to sapwood ratio

has been found in eucalypts (see Bush *et al.* 2011), and therefore, further research is required to determine if this is an issue for whitewood since a higher proportion of sapwood may have the potential to degrade the grain and texture qualities for which whitewood is popular. If whitewood is to persist as a quality decorative timber, these issues will need to be addressed or alternative markets found for thinnings, e.g., fuel for clean energy production utilising woody biomass in Japan (Yamamoto 2011). Future breeding objectives for whitewood should focus primarily on increasing the proportion of heartwood to sapwood and secondly breeding for larger diameter and increased density.

Genetic estimates

Genetic improvement of a given trait through recurrent breeding and selection is a function of its heritability and variability (White *et al.* 2007). Typically wood quality traits have high \hat{h}^2 but low CV_A while traits associated with overall fitness have low \hat{h}^2 and high CV_A (Garcia-Gonzalez *et al.* 2012). The results from this study adhere to this trend. CV_A estimates for DBH (17.6%) were double that for DEN (8.7%) whilst heritability estimates were lower for DBH than DEN (0.26±0.20 and 0.49±0.24 respectively). Species of comparable basic density to whitewood, e.g., *Eucalyptus nitens*, have been shown to have similar heritabilities for both DEN and DBH (Hamilton *et al.* 2009). The moderate heritabilities and coefficients of phenotypic variation for DEN and DBH in this study indicate that there is scope for genetic gain through selection for both these traits. The large between-provenance variation indicates that there is enough genetic variation should breeders choose to select for high or low DEN.

The limited number of individuals per family and families per provenance sampled in this study are likely to reduce precision of genetic correlation estimates. For heritability and correlation estimates to be considered precise and widely applicable, it is desirable that they be based on a large number of families, a large number of trees per family and for tests to be conducted across a range of sites to quantify genotype-by-environment interaction (White *et al.* 2007). This study should be considered as preliminary: more precise estimates involving a wider range of genetic material should proceed as the genetic improvement program progresses. The apparent absence of either phenotypic or genotypic correlations between DBH and DEN, is encouraging and suggests that improvement of these traits might proceed in tandem without adverse effect, though again, this finding should be checked by more precisely determining genetic correlations in future. Adverse genetic correlations between growth and wood property traits in some *Pinus* spp., particularly *P. radiata*, (Wu *et al.* 2008, Kumar *et al.* 2008, Raymond and Henson 2010, Gapare *et al.* 2011) have been a serious impediment to progress, particularly as the adverse correlation (i.e., high growth correlated to high proportions of juvenile wood with low density and strength) was not identified until well after selection for growth had taken place, necessitating expensive and time-consuming remedial restructuring of breeding populations.

Concluding remarks

The aim of this study was to quantify basic wood density, identify patterns of radial variation and phenotypic correlations and provide initial heritability estimates for these wood properties in Vanuatu whitewood. The material included in this preliminary study was chosen to represent the total phenotypic range in variability for DBH in order to identify any genetic relationship between DBH and DEN. The number of trees available to represent each of the two provenances was restricted, which has undoubtedly reduced the precision of the genetic parameter estimates, particularly genetic correlations. However, the study has indicated significant provenance- and family-within-provenance variation in traits of economic significance in *E. medullosum* at approximately half rotation age. Both levels of selection have the potential to result in significant genetic gain. The future success of the whitewood breeding program is well-served by the relatively broad range of genetic resources incorporated in the IFP germplasm. Given the demise of many of the wild stands from which the material was originally drawn, this is an important resource for future improvement of *E. medullosum* growth and wood properties. Future breeding programs would best be served by exploiting genetic variation in DBH and DEN to improve log size and quality. The authors recommend genetic variation analysis of DBH, DEN and RadVar for all families in the whitewood trial at 15 years (2014) and 20 years (2019). This would provide breeders with a snapshot of trends in genetic variation at 50% (this study), 75% and 100% of harvest age. Age-age genetic correlations between those years, this study and earlier studies (Doran *et al.* 2012, Thomson 2006, Vutilolo *et al.* 2008) will provide whitewood breeders the information needed to assess and select for improved families, provenances and traits at appropriate ages (White *et al.* 2007).

This study has again demonstrated open-pollinated families from Kole provenance, East Santo as exhibiting superior phenotypic trait means although GxE experiments will be necessary to test this pattern across a range of edaphatic conditions. This early identification of Espiritu Santo Island provenances, e.g., Kole, as exhibiting superior trait means will have direct benefits for the Vanuatu whitewood industry, as Espiritu Santo island, being the largest of Vanuatu's islands, has been identified as the centre for future whitewood production (Mele 2011). For Espiritu Santo at least, this early identification of superior genetic material could lead to earlier distribution of improved germplasm and in turn greater realised gain in less time.

Finally, as Vanuatu now has an accurate estimate of basic density for whitewood, reliable accounting of carbon stocks sequestered within Vanuatu's whitewood forests can be determined (Wiemann and Williamson 1989, Baker *et al.* 2004, Chave *et al.* 2006, Williamson and Wiemann 2010). This information could aid Vanuatu in accessing carbon payments for avoided deforestation, offering diversified revenue for landholders.

Taken as a whole, this study has successfully identified the potential for significant genetic gain in wood quality (DEN) and stem volume production (DBH) in Vanuatu Whitewood.

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