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ARTICLE

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Variation in early growth in a second-generation whitewood (*Endospermum medullosum*) progeny trial in Vanuatu

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ABSTRACT

Endospermum medullosum (whitewood) is a commercially important plantation and agroforestry timber species in Vanuatu, used locally and for export. Commercial development depends on both increased productivity and genetic resource conservation. A second-generation progeny trial on Espiritu Santo Island was measured at ages 2 and 3 years. Growth traits were of low-to-moderate heritability, varying from 0.13 for height at 2 years, to 0.30 for diameter at breast height (DBH) at 3 years. Genetic correlations between growth and form traits were generally encouraging, with form at 3 years moderately-positively correlated (0.49 to 0.56) with the growth measures at ages 2 and 3 years, and no adverse correlations evident. Families of Espiritu Santo origins were consistently amongst the highest ranked for both growth and form traits, while families of Malekula and Pentecost Island performed poorly. These results are supportive of the recurrent selection and breeding strategy being implemented to deliver economic gains in growth traits. With natural populations severely depleted or extinct, the breeding population constitutes a repository for genetic variation already lost from wild sources. The long-term sustainability of the breeding program will therefore depend on provisions made for both improvement (narrowing of variation) and conservation (broadening of variation) of genetic resources.

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Introduction

Whitewood (*Endospermum medullosum* L.S. Smith, family Euphorbiaceae) is a tall, fast-growing, pioneer forest tree species of wide natural occurrence in Vanuatu, occurring on about a dozen islands between Erromango (c. 19°S latitude) in the south of the archipelago to the Banks Group (c. 14°S) in the north. The species also occurs naturally in Solomon Islands, Papua New Guinea and Indonesia (West Papua), where it is referred to by other common names (Thomson & Uwamariya 2003; Thompson 2006).

Whitewood is among a group of commercially valuable, tropical timber species that also includes mahogany (*Swietenia* spp.), African mahogany (*Khaya* spp.) and teak (*Tectona grandis*), that have been over-harvested in the wild, and for which genetic conservation and domestication strategies are now being implemented as a matter of urgency (Koskela et al. 2014). In Vanuatu, whitewood has been exploited, to the point of extinction in numerous sub-populations (Vutilolo et al. 2008; Doran et al. 2012), for its valuable timber, which is utilised locally and exported (Viranamangga et al. 2012). Transitioning from wild resources to more sustainable plantations and woodlots is crucial for ensuring an ongoing supply of forest products that also supports livelihoods in Vanuatu. The National Forest Policy of Vanuatu recognises this, and includes a target of 20 000 hectares of plantations and woodlots by the year 2020, with whitewood identified in this policy as a key candidate plantation species (Mele 2011; Vanuatu Department of Forests 2013). With the aims of increasing

the economic value of the industry and thus increasing planting rates and conserving genetic resources, the Vanuatu Department of Forests (VDoF) commenced a tree improvement program for whitewood in 1998. This program was initially undertaken with support from the AusAID South Pacific Regional Initiative on Forest Genetic Resources (SPRIG) project (1996–2006), followed by ACIAR project FST/2008/010 2010–2015 (Page et al. 2016).

Whitewood improvement in Vanuatu started with collection of seed from 110 (female) trees from six islands. Their progeny were established in December 1998 – January 1999 in 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. Doran et al. (2012) reported the results of a combined assessment of the IFP trials at 11.4 years (c. half rotation age). This study demonstrated considerable island-level and family-level variation in diameter at breast height (DBH) and form: trees with the fastest growth and best form were from Espiritu Santo provenances, whilst the poorest performers were from Maewo island and from Forari on Efate Island. Growth and form trait narrow-sense heritability estimates ($\hat{h}^2 = 0.10\text{--}0.16.\sigma_p^2$) were low to moderate, with moderate phenotypic variation ($CV_p = 17\text{--}36\%$), indicating that a recurrent selection and breeding program should result in genetic gain. Another interesting observation was that DBH at 11.4 years was very closely genetically correlated ($r_A = 1.00 \pm 0.17$ s.e.) with the estimate at 4 years (Vutilolo et al. 2008), indicating the potential for early selection for diameter/volume growth in seedling seed orchards (SSOs).

Settle et al. (2012) have also reported that wood density is moderately heritable in selected families in the main IFP trial.

A selection index, based on DBH and form traits at 11.4 years, was used to thin the trials to convert them to a seedling seed orchard and assist in the selection of plus trees. Plots containing more than one tree were reduced to the best individual according to the index. The poorest performing families (18 families, or 16% of the 110 families present in the two trials) were mostly removed from the trials, with only exceptional phenotypes retained. Amongst the 60 best performing families, superior individual trees (candidate 'plus trees') were marked for seed collection.

In this study we report on the growth performance of seedlots from IFP at 2 and 3 years of age, as plus trees established in a second-generation progeny trial on Espiritu Santo with the support of ACIAR project FST/2008/010. Patterns and levels of variation in height and diameter (DBH) growth amongst seedlots were determined, along with heritability, to assess earlier predictions of genetic gain in diameter/volume from recurrent selection and breeding programs applied to this species.

Materials and methods

Trial site, genetic material and experimental design

This study is based on a second-generation whitewood progeny trial planted in November 2011 at Bombua (latitude 15° 30.946' S, longitude 167° 14.987' E, elevation 40 m asl) near Luganville, the capital of Espiritu Santo Island, Vanuatu. The soil was heavy black clay loam with scattered coralline rocks of neutral pH, regarded as excellent for the growth of whitewood (Fig. 1). Existing vegetation on the site was mixed-species secondary forest that was only partially removed before planting. Tree poisoning following planting reduced the overstorey further, but this was curtailed because of damage to whitewood trees from falling limbs and whole trees. Therefore, some overstorey trees remained and competed with trial trees.

The progeny trial comprises 47 seedlots (treatments), with a total of 44 families with three families represented by two seedlots (Table 1). Each seedlot apart from two (4 and 27) came from selected trees (candidate 'plus trees') in a first-generation provenance-progeny trial situated at the Industrial Forestry Plantation (IFP) site near Shark Bay on the east coast of Espiritu Santo. A resolvable, latinised, row-column (Alpha) design for 45 treatments in six replicates (in 3 x 2 arrangement) each comprising nine columns by five rows was generated using CycDesign Ver. 2 (Whitaker et al. 2002). The design was modified so that treatments representing the same family did not occur nearby each other in each of the six replicates to reduce the risk of selfing. Columns were 6 m apart and trees were planted in 4-tree line plots with 2 m between trees. The experiment was surrounded by a single-row buffer planting on three sides and a two-row buffer along the northern boundary.

A weighted index constructed following an analysis of growth and form traits in the IFP trial at 11.4 years was the basis for selecting the plus trees in high-ranking families. Selection of plus trees 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 marking of four to seven top-ranked trees within each family, from a maximum of eight to 14 trees



Figure 1. Measuring diameter at breast height (DBH) in the Bombua whitewood trial at 3 years

per family remaining after thinning (see Doran et al. 2012 for details).

The two seedlots from unselected trees in the trial were included because their family ranking was excellent and the selected trees in those families were either all males or the females had not flowered that season.

Measurement

The trial was measured two years after planting in December 2013 and again at age 3 in December 2014. Traits measured include diameter at breast height, tree height (at age 2) and form. Form was scored on a five-point scale (Table 2).

Statistical analyses

Pedigree

Second-generation mothers were in some cases related via a common grandmother. In this analysis, these mothers were modelled as half-siblings, and hence their progeny are expected to be more closely related than are trees from families with unrelated mothers. Additionally, the first-generation mothers were sourced from ten subpopulations. Each subpopulation was assumed to have had separate, homogeneous pollen pools. These relationships were included in the modelled pedigree as genetic groups (Westell et al. 1988).

Linear model

Analysis of height implemented in ASREML version 3 (VSN International, Hemel Hempstead, UK) was based on an individual-tree, linear mixed model of the following general form:

Table 1. Seedlots (treatments) in the Bombua second-generation progeny trial and their growth traits at 2 and 3 years, as estimated by BLUPs (Best Linear Unbiased Predictors). All seedlots apart from two (4 & 27) were collected from plus trees of given family and individual tree rank in the first-generation provenance/progeny trial at IFP at age 12 years.

Seedlot	Family	Provenance*	Family rank (n = 100)	Individual tree rank within family	Height (cm) 2 years	DBH (cm) 2 years	DBH (cm) 3 years
1	SBC13	IFP Santo	4	1	570	8.9	12.9
2	MS1	SE Santo	10	1	577	8.7	13.0
3	MS2	E Santo	5	2	548	8.4	12.4
4	MS3	E Santo	2	no rank	550	8.3	11.9
5	MS10	E Santo	3	4	584	9.1	13.2
6	MS32	E Santo	14	4	560	8.7	12.3
7	MS40	CE Santo	27	3	564	8.7	12.0
8	MS49	SE S Santo	47	1	551	8.4	12.2
9	MS51	SE S Santo	24	1	539	8.1	11.3
10	MS44	CE Santo	12	3	576	9.2	13.1
11	GD5	E. Santo	60	2	568	8.7	13.1
12	GD6	E. Santo	40	1	568	8.8	13.1
13	MS47	CE Santo	20	1	579	9.3	13.3
14	MS43	CE Santo	21	2	544	8.5	12.1
15	MS43	CE Santo	21	3	567	8.9	12.8
16	MS52	SE S Santo	25	1	543	8.4	13.0
17	MS53	SE S Santo	18	1	556	8.5	12.0
18	MS54	SE Santo	36	1	560	8.5	13.0
19	MS55	SE S Santo	17	2	560	8.4	11.7
20	GD3	E. Santo	9	1	572	9.2	13.4
21	GD4	E. Santo	7	4	556	8.7	12.5
22	MS45	CE Santo	51	4	592	9.0	12.7
23	MS45	CE Santo	51	4	581	8.8	12.3
24	GD7	E. Santo	6	3	572	8.7	12.9
25	GD11	E. Santo	8	2	541	8.5	12.3
26	GD11	E. Santo	8	1	556	8.6	12.6
27	GD9	E. Santo	1	no rank	577	9.1	13.6
28	GD13	E. Santo	26	2	585	9.0	13.3
29	MT6	C Pentecost	50	2	584	8.8	12.6
30	MT17	C Pentecost	37	2	560	8.2	12.0
31	MT18	C Pentecost	23	1	554	8.2	11.6
32	MT 24	Maewo	48	1	621	9.0	12.9
33	MT35	W Ambae	58	2	565	8.4	12.6
34	MT36	W Ambae	41	2	552	8.4	12.7
35	MT37	W Ambae	16	1	563	8.3	12.4
36	MT38	W Ambae	28	1	539	7.9	12.1
37	MT39	W Ambae	38	1	576	8.6	12.9
38	MT40	W Ambae	49	2	557	8.5	12.6
39	JT3	Teouma Efate	52	3	565	8.4	12.5
40	JT4	Teouma Efate	55	3	551	8.2	12.2
41	JT5	Teouma Efate	43	4	560	8.3	11.8
42	JT7	Teouma Efate	31	3	561	8.3	11.9
43	MS61	SE S Santo	33	1	554	8.5	12.5
44	JT20	Malekula	32	4	565	8.6	12.3
45	JT21	Malekula	59	2	539	8.4	11.5
46	JT13	Malekula	45	1	542	8.6	11.9
47	MS32	E Santo	14	2	575	8.8	12.6
Trial Means					621	8.6	12.5
Average standard error of difference					30.5	0.6	0.8

*IFP, a plantation source of Santo origins; SE, southeast; E, east; C, central; CE, central-east; S, south; W, west

Table 2. Form scoring system, after Doran et al. (2012)

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, major faults such as multiple leaders, ramicorns, large hollows/swellings)

$$y = \mathbf{X}b + \mathbf{Z}u + e \quad (1)$$

where y is the vector of observations on the height trait, 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. Vector b contained sub-vectors for the fixed effects of *replicate* and genetic groups, and u contained sub-vectors for the random effects of *plot*, incomplete

blocks (denoted ICB), (*rows* and *columns*) and *individual trees*. The rows and columns effectively formed a square grid. This also allowed an alternative, autoregressive spatial residual model (denoted AR1 x AR1) to be fitted. These models can sometimes prove superior for capturing within-site heterogeneity (Costa E Silva et al. 2001; Gilmour et al. 2009). An additional non-spatial, random residual term (sometimes referred to as ‘nugget’ variance) was also fitted to the AR1 x AR1 models following the rationale of Dutkowski et al. (2002).

Survival was assessed using a form of Equation (1) modified from that described above, where y contained a vector of plot-mean survival observations and u contained a term for *family*. This model did not include spatial design or error terms.

Genetic parameter estimation

Narrow-sense heritability was estimated as:

$$\hat{h}^2 = \frac{\sigma_t^2}{\sigma_t^2 + \sigma_p^2 + \sigma_e^2} \quad (2)$$

where σ_t^2 is the individual-tree variance, σ_p^2 is the plot variance and σ_e^2 is the error variance (taken as the nugget variance in the spatial models). Heritability of survival was estimated using σ_f^2 , the family variance estimate in place of σ_t^2 and not including σ_p^2 .

Correlations between pairs of traits, and the same trait in different years (termed Type-A correlations), were calculated by fitting bivariate models to simultaneously estimate variance for both traits and covariance components, as given by Burdon (1977):

$$r_A = \frac{\hat{\sigma}_{t_x t_y}}{\sqrt{(\hat{\sigma}_{t_x}^2 \hat{\sigma}_{t_y}^2)}} \quad (3)$$

where $\sigma_{t_x t_y}$ is the additive genetic covariance component between traits, and $\sigma_{t_x}^2$ and $\sigma_{t_y}^2$ are the additive variance components for traits x and y respectively. These models were fitted with heterogeneous spatial residual variance terms.

Tree volume and mean annual increment

Tree volume was estimated using a Huber equation with coefficients previously determined for whitewood (Doran et al. 2012):

$$V_H = 0.0007\text{dbh}^2 - 0.0007\text{dbh} - 0.0328 \quad (4)$$

Mean annual volume increment was estimated as

$$\text{MAI}_t = \frac{\sum_{i=1}^n v_H}{t \cdot A} \quad (5)$$

Where MAI_t is Huber volume mean annual increment at age $t = 2$ or $t = 3$ years, $\sum_{i=1}^n v_H$ is the sum of individual-tree Huber volume estimates for all n stems, t is the age of the trial in years and A is the net area of the trial in hectares, that is the area occupied by each tree for which V_H was calculated plus the area occupied by dead trees within the plots but exclusive of the buffers.

Results

Survival

Overall survival was 81% at 2 years and 74% at 3 years. Survival among families ranged between 71 and 84% at 2 years and 68 and 76% at 3 years. Heritability of survival at ages 2 and 3 was estimated to be low (0.18 and 0.09, respectively), though the estimates were of low precision (Table 3), having large standard errors relative to the estimates.

Table 3. Narrow-sense heritability estimates ($\hat{h}^2$) with standard errors for traits at 2 and 3 years

Age (years)	Survival	DBH	Height	Form
2	0.18 (0.14)	0.21 (0.14)	0.13 (0.09)	0.03 (0.07)
3	0.09 (0.14)	0.30 (0.12)	–	0.11 (0.12)

Growth

Treatment means (Best Linear Unbiased Predictors) for height at age 2 years and DBH at 2 and 3 years are given in Table 1. Height growth was moderately heritable (0.13). The estimated DBH heritability increased from 0.21 to 0.30 between ages 2 and 3 years. Height measured at age 2 years was of low heritability (Table 3). Considering the ancestry of the second-generation families, the top 11 ranked families for DBH at year 3 were from Espiritu Santo, with selections from the other islands generally not performing as well, though with some outstanding individual tree performances. Families originating from Malekula and central Pentecost performed poorly in terms of DBH ranking, with all these families among the six lowest ranked. Volume MAI estimated using Equation (5) was $3.3 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ at age 2 and $13.8 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ at age 3.

Form

Form was of low heritability and was estimated with poor precision at ages 2 and 3. An important result was the consistently poor form of the three families with origins in Malekula: these were the lowest ranked of all families. Tree form within families of Central Pentecost origins were amongst the poorest. The best-ranking families were from a mix of sources including southern, south-eastern and central Santo and west Ambae.

Correlations among traits

Type-A correlations, that is, additive genetic correlations, between pairs of traits and traits measured at ages 2 and 3 years, were estimated (Table 4). The correlations between pairs of growth traits were all high, ranging between 0.87 and 0.96. Standard errors were generally low. The correlation between form at age 2 and DBH at age 3 was also very high (0.90), although the standard error was moderately high (0.23). Form at age 3 years was moderately positively correlated with DBH at ages 2 and 3, with correlations ranging from 0.49 to 0.56 with moderate standard errors of approximately 0.2. Parameter estimation was not achievable for all pairs of traits: two of three correlations involving the 2-year measure of form failed to converge.

Discussion

The results from this early measurement of a second-generation breeding population of whitewood are broadly encouraging for the genetic improvement of this species in Vanuatu. Growth traits have low to moderate heritability, and some important trends allowing the discrimination of families on the basis of form traits are emerging. The precision of herit-

Table 4. Correlations between pairs of traits (Type-A correlations) (upper triangle) and standard errors of the correlations (lower triangle)

Trait	DBH 2 year	DBH 3 year	Height 2 year	Form 2 year	Form 3 year
DBH 2 year		0.91	0.96	NC	0.49
DBH 3 year	0.05		0.87	0.90	0.56
Height 2 year	0.03	0.07		NC	0.50
Form 2 year	NC	0.23	NC		0.83
Form 3 year	0.21	0.21	0.2	0.19	

NC, model would not converge.

ability estimation for many traits appears to be acceptable, despite the less-than-desirable clearing of the planting site at trial establishment, with the retention of scattered trees across the site. Correlations among traits are also generally encouraging, with no adverse correlations (i.e. additive genetic correlations that would result in negative impacts on one trait resulting from selection of another) being evident. Despite these early indications, it would be highly desirable to establish additional trials across a range of sites using best-practice silviculture, allowing better genetic parameter estimation and assessment of site-by-genotype interactions. If, hypothetically, the stand comprised trees of the best family only (family 27, of East Santo origins) then the MAI might increase to $23 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$. This might not necessarily be valid, however, as increased competition for the available site resources may limit overall growth (Marcar et al. 2011). Conversely, if trees of the least productive family (family 9 from SE South Santo) were established site-wide, productivity would decline to $7 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ (assuming 75% stocking).

The two trial plantings (IFP and Bombua) of the species, plus one additional genetic resource stands located at Efate Island (Onesua planted in January 2012) (Page et al. 2016), are the only remaining repositories of diversity from several populations that are now extinct: it would be highly desirable to increase the number of such plantings to provide better security. The program involving the second-generation Bombua planting reported here is an important basis for the conservation of Vanuatu whitewood, complementing the earlier plantings reported on by Doran et al. (2012). However, the overall program is being conducted on a small scale and the security of the genetic resources of this species depends on the ongoing care and maintenance of just a few planted trial sites. Doran et al. (2012) reported that many of the places where wild FGR (forest genetic resources) had been collected for the initial plantings in the 1990s no longer support whitewood populations, meaning that the only remaining repository of the genes represented by these subpopulations is now within the breeding program.

While the breeding program may act as a reasonable repository of FGR in the medium term, selection and breeding will inevitably lead to a reduction in diversity in future generations. For this reason it will be important to consider the conservation of a wider array of genetic resources. It would be highly desirable to establish parallel plantings of whitewood, including a broad range of genotypes from the original IFP planting that are not subject to further selection. This population can serve as a gene bank. These plantings could be carried out as dedicated *ex situ* plantings, and/or could be planted adjacent to remnant stands forming a *circa situm* conservation planting. This planting strategy can play an important role in conservation in fragmented landscapes (Dawson et al. 2013).

Given the narrow genetic base of the breeding population it will also be important to infuse unrelated families into the testing and breeding program, probably at the commencement of the next generation. Due to the highly fragmented nature of the existing whitewood resource on Vanuatu, this has proved to be a significant challenge, although some progress was made under ACIAR FST/2008/010 with the sourcing and gene-bank planting of seedlots from the Banks group, Malo Island and a new provenance from Malekula. One option that could be explored is the

infusion of *E. medullosum* from outside Vanuatu. This has been attempted in the past under the SPRIG project, but was curtailed because of the risks involved, including uncertain cyclone resistance and fears of genetic pollution of local sources, particularly if the imported sources proved poorly adapted to conditions in Vanuatu. If this strategy is tried again, the exotic material should be kept physically isolated from the dedicated conservation plantings already mooted, and planted to limit pollen-flow into nearby forest fragments.

The conservation and domestication of high-value Pacific forest species is an ongoing challenge, some aspects of which have been highlighted by the program described herein. Ongoing exploitation of wild genetic resources that are already critically depleted and fragmented is a widespread issue in the Pacific that affects both whitewood and other valuable forest species. Identifying suitable secure sites on which to host *ex situ* conservation and breeding plantings is an important consideration, especially given the security challenges of communal land tenure, and the limited capacity and resources of private growers throughout much of the Pacific. These issues were prominent in the current study, and influenced site preparation, resulting in variation due to incomplete clearing. The reproductive phenology and seed longevity in whitewood are biological factors that influence its breeding and rate of improvement. Flowering and seed set is highly influenced by climatic factors leading to sporadic seeding (with several consecutive seasons potentially aborted) (Dore & Page 2015), and its seeds are recalcitrant with limited storage potential beyond a few weeks (Dore 2014). Despite these issues, the results of this study demonstrate that whitewood is amenable to genetic improvement, and its further domestication and deployment can lead to more productive and commercially viable whitewood plantings in Vanuatu.

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