EARLY GROWTH AND GENETIC VARIATION OF MAHOGANY (*SWIETENIA MACROPHYLLA*) IN PROGENY TESTS PLANTED IN NORTHERN MINDANAO, PHILIPPINES

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ABARQUEZ A, BUSH D, ATA J, TOLENTINO EL JR & GILBERO D. 2015. Early growth and genetic variation of mahogany (*Swietenia macrophylla*) in progeny tests planted in northern Mindanao, Philippines. Mahogany (*Swietenia macrophylla*) progeny trials were established at Butuan and Cagayan de Oro in Mindanao (Philippines) to examine genetic variation in growth and form traits of progenies from 73 families of six plantation seed sources. At age 50 months, mean diameters were 12.1 and 4.5 cm, while mean heights were 9.4 and 3.8 m for progenies at Butuan and Cagayan de Oro respectively. Lianga and Bislig seed sources consistently ranked among the best in growth. Additive genetic coefficients of variation for diameter were 6.5 and 10.6% and for height, 6.5 and 13.8% at Butuan and Cagayan de Oro respectively. Narrow-sense heritability ($\hat{h}^2$) for diameter was 0.29 at Butuan and 0.29 at Cagayan de Oro. For height, $\hat{h}^2$ was 0.37 at Butuan and 0.43 at Cagayan de Oro. Cross-site heritability of growth traits was significantly lower for both diameter ($\hat{h}^2 = 0.11$) and height ($\hat{h}^2 = 0.26$) due to genotype-by-environment interactions. Type-B genetic correlations for height and diameter were 0.24 and 0.34 respectively. Wood basic density at Butuan was moderately heritable ($\hat{h}^2 = 0.30$). Infusion and testing of new germplasm from natural range mahogany in the Americas are recommended to broaden the base population for tree farms and agroforestry plantations in the country.

Keywords: Heritability, conservation, plantations, tree-farming, agroforestry, *Hypsipyla*

INTRODUCTION

Mahogany (*Swietenia macrophylla*) is one of the world's most valuable and widely traded neotropical timber species. Its wood is used for high-value furniture, cabinet work, panelling, doors and jambs, face veneer, musical instruments and as decorative wood for luxury marine vessels (Lemmens 2005). Mahogany has very wide natural distribution in the tropics extending from Mexico at 23° N to the Central American Atlantic coastal strip into South America, continuing in a broad south-easterly arc from Venezuela through the Central and South American Amazon regions as far as 18° S. The species is found along tributaries and seasonal streams of the Amazon River where mean annual temperature is over 24 °C and mean annual precipitation ranges from 1000 to 2000 mm. It grows from sea level up to 1400 m in the Andean foothills of Ecuador, Peru and Bolivia (Lamb 1966). It is tolerant of a wide range of soil conditions but grows best in alluvial, volcanic, heavy clays and lateritic soils derived from a wide range of parent materials (Krisnawati et al. 2011).

The species is threatened in its natural range due to commercial exploitation which started during the 16th century. The natural range of mahogany is estimated to have reduced dramatically from 278 to around 94 Mha, with surviving stocks often comprising very low-density populations in remote regions (Grogan et al. 2010). Selective logging of natural forests is still the main production management approach in Latin America as mahogany plantations have not been successful within the native range (Shono &

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Snook 2006). Concerns about over-exploitation and dysgenic effects of selective logging practices on natural populations prompted the listing of mahogany and small-leaf mahogany (*S. mahogani*) for conservation under Appendix II of CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) in 1992 (Patiño 1997). The Tropical Agricultural Research and Higher Education Center in Costa Rica and the Institute of Terrestrial Ecology in the UK with support from the European Union and other institutions organised a collection of mahogany germplasm in seven Mesoamerican countries in 1994 which has been used in studies of genetic variation, establishment of gene banks and progeny trials mainly in Costa Rica and Mexico. In 1997, FAO (Food and Agriculture Organization of the United Nations) initiated an international network to facilitate genetic conservation and restoration of mahogany and other species of the Meliaceae family (FAO 1997).

Mahogany from Belize was introduced to India in 1872, then spread through South Asia, South-East Asia, the Pacific and to tropical Africa (Soerianegara & Lemmens 1993, Lemmens 2005). Seeds from India were introduced to Indonesia in the 1870s (Krisnawati et al. 2011).

Mahogany was introduced to the Philippines from unknown origins in 1907 as park trees in Manila (Ponce 1933). In 1913, the Forestry School at the University of the Philippines in Los Baños received 1012 seeds of mahogany from an unknown number of parent trees from the Royal Botanic Gardens at Sibpur, Calcutta, India. Three subsequent introductions of unknown quantities and number of parent trees from the same source in India followed through till 1916. Seedlings produced during these introductions were mostly planted at Los Baños, with only a few seedlings trial-planted in Baguio, Benguet province. There was no other documented report on mahogany importation into the country until the 1960s when tree planters in north-eastern Mindanao imported an unspecified quantity of seeds directly from an unknown source in Central America. It is believed that the planted stand at Los Baños became the main source of seeds for mahogany planting activities across the Philippines. However, firm genetic resource management strategy has never been implemented in the country. Local tree planters continue to rely on collecting seeds from the most-accessible mother trees in their locale. The importance of this tree to domestic and international furniture, construction and veneer industries drives the continuing inclusion of mahogany among the most-planted species in the Philippines (Lasco et al. 2001).

In the Philippines, mahogany in private farm plantations is harvested as early as 20-year rotation age due to demand for timber (Rodriguez 1996). However, rotations in farm plantations can be as long as 30–40 years in Java, Indonesia (Krisnawati et al. 2011) and up to 60 years in selectively-logged forests in Latin America (Wadsworth & Gonzales 2008). Selective logging within the native range in Belize is conducted on 40-year cycles, producing 60 cm diameter logs (Shono & Snook 2006). In 2007, seeds from key plantation seed sources in the Philippines were collected and used to establish progeny trials at two contrasting planting sites in northern Mindanao (Figure 1). The trials were designed to characterise genetic variation at the provenance and family levels for growth, form and wood density traits and to secure improved mahogany seed sources for developing new plantations in Mindanao. This paper reports the early growth performance and genetic parameter estimates for growth, form and wood quality traits of mahogany at the age of 50 months in northern Mindanao, Philippines.

MATERIALS AND METHODS

Seeds

Open-pollinated seeds were collected in 2007 from 73 mother trees in six plantation seed sources and a routine stock of seedlings from a local commercial nursery (Table 1). The mother trees were selected as the best phenotype (based on diameter, height, stem form, branching and health relative to other trees within the plantation) in each ha (ca. 1000 trees ha^{-1}) with a distance of at least 100 m from each other. The routine stock seedlings were from mix mother trees of undetermined origins.

The Makiling (southern Luzon) material was derived from the 1913–1916 introductions from India which have been regenerating naturally along the edge of the Makiling Forest Reserve (Baguinon et al. 2005). The Minglanilla (Cebu)

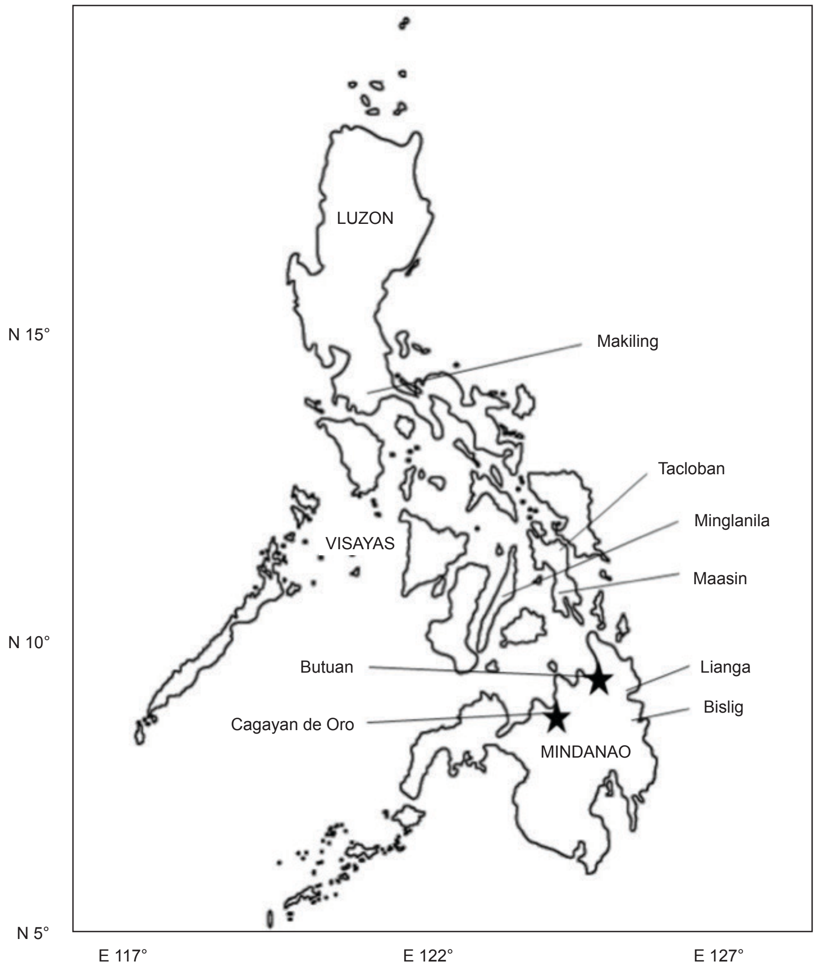

Figure 1 Locations of the six seed source plantations and two trial sites (stars) of mahogany (*Swietenia macrophylla*) in northern Mindanao, Philippines

material was part of the plantation established in the 1920s using seeds from Makiling to protect the surrounding watershed of metropolitan Cebu as well as to produce timber for the domestic furniture industry. The Maasin and Tacloban (Leyte Island) materials were part of the plantation established in 1950s and we speculate that these are descendants of the older plantations in Makiling and Minglanilla. Lianga and Bislig (eastern Mindanao) materials are reported to be part of the 1960s introduction from undocumented natural range of mahogany (Siladan 2010).

Seedling production

The seeds were sown directly in a medium composed of equal parts of top soil, sand and humus in 80 mm diameter × 200 mm deep plastic bags. About 120 to 150 seeds from each family were sown of which about 70% germinated and 90 to 100 seedlings of each family were available at the time of trial establishment. Equal numbers of seedlings were prepared for planting at the two trial sites.

Trials sites

The trials were established at two sites, Butuan and Cagayan de Oro, representing contrasting growing conditions within the target plantation region in northern Mindanao, Philippines. The trial site at Butuan was located at 8° 56' N and 125° 35' E. The site is 13–15 m above sea level within the Agusan River delta. The area receives an average annual rainfall of 2057 mm and

Table 1 Description of seed source plantations and number of families represented in the mahogany (*Swietenia macrophylla*) trials in northern Mindanao, Philippines

Seed source	Island	Latitude (N)	Longitude (E)	Elevation (m above sea level)	Mean annual rainfall (mm)	Annual temperature range (°C)	No of families
Bislig	Eastern Mindanao	8° 14'	126° 16'	120	4460	24–33	7
Lianga	Eastern Mindanao	8° 41'	126° 7'	120	4460	24–33	4
Maasin	Leyte	10° 10'	124° 52'	120	2500	24–32	5
Makiling	Southern Luzon	14° 9'	121° 14'	125	2500	24–33	5
Minglanilla	Cebu	10° 14'	123° 46'	100	2000	24–33	47
Tacloban	Leyte	11° 14'	124° 58'	120	2200	24–32	5
Routine stock	Mindanao	–	–	–	–	–	1
Total							74

temperature range of 22.8 to 30.5 °C (PAGASA 2010). Average monthly rainfall values are 231 mm from October till February (with peak rainfall in January of about 318 mm) and 129 mm from March till September. The site is flat and had been used for irrigated cropping and occasionally gets flooded following extreme rain events. The soil is deep, heavy clay loam. Soil samples (0–10 cm soil depth) have mean pH of 6.8, organic matter content of 1.2%, available phosphorus 14 ppm and extractable potassium 144 ppm. The area was covered by tall grasses (*Pennisetum purpureum* and *Saccharum spontaneum*) and isolated small trees (*Broussonetia papyrifera*) prior to establishment of the trial.

The Cagayan de Oro trial site was located at 8° 23' N and 124° 42' E and 413–415 m above sea level. The area receives an average annual rainfall of 1703 mm and temperature range of 28.1 to 31.4 °C (PAGASA 2010). The wettest months occur from June till October with monthly average rainfall of 212 mm while the rest of the year receives 92 mm average monthly rainfall. The land has about 18% slope and a southerly aspect. The land had previously been used for pasture with *Imperata cylindrica* grass and isolated remnant native trees and shrubs (*Syzigium* sp., *Psidium* sp. and *Anthocephalus chinensis*). Top soil is thin and highly eroded in some patches with pH 5.8, organic matter content 4.5%, available phosphorus 1.3 ppm and extractable potassium 48 ppm.

Trial establishment and management

The trial areas were cleared to near ground-level with brush-cutters and machetes. Planting rows were tilled using plough, then strip-sprayed (1-m wide) with 3 L ha^{-1} of glyphosate to control grass and weeds six weeks ahead of field-planting. The seedlings were planted out in September 2007. Dried, cut grass was used to mulch the base of seedlings. Manual weeding was conducted 3 and 6 months after planting, then once a year thereafter. Neither trial site was fertilised or provided with supplementary water. The trials had not been thinned or pruned at the time of assessment.

Trials design and layout

Both trial sites were planted with 32 rows spaced 3 m apart, each having 50 planting positions spaced 2 m apart. The rows were laid out near perpendicular to the general slope of the land. A single row of trees was also planted as buffer around the periphery of the trials. The spacing was selected as representative of commercial planting density, although in the Philippines, no standard spacing was used and could be anywhere between that selected here (1667 trees ha^{-1}) to as few as 500 trees ha^{-1}. CycDesign Version 2 was used to generate a latinised row–column incomplete block design for 74 family treatments in four replicates of 5-tree row plots on each site. There were six filler plots within the trial boundary established with trees of mixed source, used to maintain block stocking, which were not included in the assessment.

Trial assessments

The seedlings at both sites were assessed at age 50 months. Survival was based on the percentage of living trees in each plot. Diameter at breast-height (dbh) was measured at 1.3 m above the ground to the nearest mm. Total height of the tree was measured from the base of the tree to the top of the crown using height pole and to the nearest 0.1 m. Height to crown break, assessed in a preliminary way at this early age as the first major branch, was measured using height pole to the nearest 0.1 m. Height to crown break was assessed mainly to verify the usefulness of this parameter in selection and to allow determination of age–age correlations at later measurements when the trait was likely to more closely reflect commercial bole length. Branch thickness in proportion to diameter of tree stem was given scores relative to the range present in each trial, from 1 (thickest branching) to 6 (thinnest branching). Stem forms of trees were given relative scores from 1 (poorest stem form) to 6 (best), relevant to defects such as fluting, bends, sweeps and other stem irregularities which would reduce the recoverable volume of timber. Wood basic density was determined by water displacement method (TAPPI 1989). Wood cores were collected from the first three replicates of the trial at Butuan only as the stems at the Cagayan de Oro trial site were too small for assessment. Bark-to-bark wood core samples (5-mm diameter) were collected 1.3 m from the ground from living trees over 2 m in height using hand corer. The core samples were soaked in water to achieve fibre saturation before determining their volumes. Core samples were dried at 80 °C for at least 48 hours before measuring their mass using platform balance (accurate to 0.001 g).

Single-site analyses

Significance of fixed effects and variance components for all traits were estimated using mixed-models based on REML procedure in Genstat Version 13. Single-site analyses were carried out using the following linear model:

$$Y_{ijklmn} = \mu + R_i + P_j + P.F_{jk} + plot_l + R.row_{im} + R.col_{in} + e_{ijklmn}$$

where Y_{ijklmn} = phenotypic observation for each tree, μ = overall mean, R_i = fixed effect of the i^{th} replicate, P_j = fixed effect of the j^{th} seed source, $P.F_{jk}$ = random effect of the k^{th} family within j^{th} seed source, $plot_l$ = random effect of l^{th} plot, $R.row_{im}$ = random effect of the m^{th} row within i^{th} replicate, $R.col_{in}$ = random effect of the n^{th} column within i^{th} replicate and e_{ijklmn} = random error term associated with the $ijklmn^{th}$ tree.

Mahogany, in its native range, is predominantly out-crossed, with an estimated out-crossing rate of over 0.9 (Loveless & Gullison 2003, Lemes et al. 2007). A coefficient of relationship (r) of 0.25 has previously been used to estimate the upper limits of trait heritability among trees in natural forests (Wightman et al. 2008). Since mahogany trees in the trials at Butuan and Cagayan de Oro were open-pollinated progenies of candidate plus trees in plantations of unknown origins, a coefficient of relationship of 0.33 was chosen as appropriate to use in estimating heritability of traits to allow for the possibility of inbreeding at the source plantations.

Across-site analyses

Analyses to quantify genotype × environment interactions, i.e. seed source-by-site and family-by-site interactions, were conducted using the following linear model:

$$Y_{ijklmno} = \mu + S_i + S.R_{ij} + P_k + P.F_{kl} + S.P.F_{ikl} + S.plot_m + S.R.row_n + S.R.col_o + e_{ijklmno}$$

where $Y_{ijklmno}$ = the phenotypic observation for each tree, μ = overall mean, S_i = fixed effect of the i^{th} site, $S.R_{ij}$ = fixed effect of the j^{th} replicate nested within i^{th} site, P_k = fixed effect of the k^{th} seed source, $P.F_{kl}$ = random effect of the l^{th} family nested within k^{th} seed source, $S.P.F_{ikl}$ = random interaction effect of the l^{th} family nested within k^{th} seed source at the i^{th} site, $S.plot_m$ = random effect of m^{th} plot nested within site i, $S.R.row_n$

= random effect of n^{th} row nested within the j^{th} replicate nested within i^{th} site, $S.R.col_o$ = random effect o^{th} column nested within the j^{th} replicate nested within i^{th} site and $e_{ijklmno}$ = residual error with mean of zero.

Estimated variance components were used to estimate narrow-sense heritability ($\hat{h}^2$) of traits based on the formula:

$$\hat{h}^2 = r\hat{\sigma}^2_{f(p)} / \hat{\sigma}_{f(p)} + \hat{\sigma}_{plot} + \hat{\sigma}^2_e$$

where r = coefficient of relationship assumed to be 0.33, $\hat{\sigma}^2_{f(p)}$ = variance component of family-within-seed source (i.e. the additive variance), $\hat{\sigma}_{plot}$ = variance component of plots and $\hat{\sigma}^2_e$ = residual variance component.

The coefficient of additive variation (CV_A) was calculated as (Houle 1992):

$$CV_A = \sqrt{\hat{\sigma}^2_{f(p)}} / \overline{X}$$

where $\overline{X}$ = phenotypic trait mean.

Type-B genetic correlation provides a measure of the genotype × environment interaction as affected by rank changes across two different sites (Burdon 1977). Type-B genetic correlation (r_{Bf}) at the family-within-seed source level of the same trait across the two trial sites was calculated as:

$$r_{Bf} = \hat{\sigma}^2_{f(p)} / [\hat{\sigma}^2_{f(p)} + \hat{\sigma}^2_{f(p)s}]$$

where $\hat{\sigma}^2_{f(p)s}$ = variance component of the interaction between family-within-seed source and sites.

RESULTS

Survival and growth

Mean survival at the Butuan and Cagayan de Oro trials was 76% (standard error (SE) = 1.2%) and 69% (SE = 1.5%) respectively (results not shown). The causes of mortality were not formally assessed. However, at Butuan, mortality might be explained by flooding after a nearby irrigation levee leaked during heavy rainfall two years after planting. The cause of mortality at Cagayan de Oro was not clear although poor soil condition and aggressive competition from *Imperata* grass were possible causes.

Table 2 shows the predicted means and coefficients of variation for each trait at both sites. Mean dbh at Butuan (12.1 cm) was much greater than that at Cagayan de Oro (4.5 cm). The differences in dbh at the seed-source level were significant ($p < 0.001$) at Butuan but not at Cagayan de Oro. Trees with the largest mean dbh at Butuan were from Lianga (13.9 cm) and Bislig (12.8 cm), while dbh of trees from the rest of the seed sources (Maasin, Makiling, Minglanilla, Tacloban and routine stock) were all below the trial mean of 12.1 cm. Dbh values of Lianga and Bislig at Cagayan de Oro were also above the mean for the site of 4.5 cm. Routine stock had the smallest dbh at Butuan while Minglanilla had the smallest dbh at Cagayan de Oro. Across-sites analysis confirmed the significant differences in dbh with Lianga and Bislig being the largest.

There were also significant differences in the mean height of mahogany trees at the seed source level at Butuan ($p < 0.05$) but not at Cagayan de Oro (Table 2). Trees grew to a mean height of 9.4 m at Butuan, much taller than those at Cagayan de Oro (3.8 m). In Butuan, Lianga (10.6 m) and Bislig (10.0 m) had higher mean heights than the overall mean, while the other seed sources were close to the mean height. No significant differences were detected for height to first major crown break trait among seed sources at either trial. Height to first major crown break reached a low mean of 3.9 m at Butuan and 2.8 m at Cagayan de Oro. Branch thickness showed no significant differences among seed sources at separate trial sites but showed slight significant differences ($p < 0.05$) across sites. No significant differences in stem form among the seed sources were evident at either Butuan or Cagayan de Oro trials and nor were they evident across sites. There were no significant differences in wood density among the seed sources tested at the trial at Butuan. Mean wood density at Butuan was 441 kg m^{-3}.

Genetic parameters

Results from mixed model analysis using the 74 families from six plantation seed sources are presented in Table 3. The CV_A for dbh at

Table 2 Summary of predicted means with F probability of difference between seed sources, average standard errors of difference and coefficients of phenotypic variation (CV_P%) for traits of mahogany (*Swietenia macrophylla*) in northern Mindanao, Philippines

Trial/seed source	Dbh (cm)	HT (m)	CROWN_B (m)	BRANCH_S (1–6)	STEM_S (1–6)	DEN (kg m^{-3})
Butuan						
Bislig	12.8	10.0	4.1	2.9	3.6	437
Lianga	13.9	10.6	3.8	3.0	3.6	429
Maasin	11.8	9.4	4.0	3.1	3.9	443
Makiling	11.8	9.3	3.7	3.0	3.5	451
Minglanilla	11.9	9.6	3.9	3.0	3.6	443
Tacloban	12.0	9.5	4.0	2.8	3.9	439
Routine stock	10.5	7.9	3.5	2.6	4.3	429
Average SED	0.8	0.6	0.3	0.1	0.3	13.7
Seed source F prob	**	*	ns	ns	ns	ns
Mean (SE)	12.1 (0.3)	9.4 (0.2)	3.9 (0.1)	2.9 (0.04)	3.8 (0.1)	441 (4.2)
%CV_P	23.1	23.8	33.3	20.2	32.0	9.5
Cagayan De Oro						
Bislig	4.6	3.9	3.1	2.6	4.2	–
Lianga	5.0	3.7	2.8	2.8	4.1	–
Maasin	4.5	3.8	2.9	2.7	4.0	–
Makiling	4.5	3.6	2.8	2.8	4.4	–
Minglanilla	4.2	3.7	2.7	2.5	4.2	–
Tacloban	4.5	3.7	2.9	2.5	4.1	–
Routine stock	4.3	4.0	2.9	2.5	4.7	–
Average SED	0.4	0.4	0.3	0.2	0.3	
Seed source F prob	ns	ns	ns	ns	ns	
Mean (SE)	4.5 (0.1)	3.8 (0.1)	2.8 (0.1)	2.6 (0.1)	4.2 (0.1)	–
%CV_P	40.3	42.7	40.3	29.3	26.5	–
Across sites						
Bislig	8.7	7.0	3.6	2.7	3.9	–
Lianga	9.4	7.0	3.3	2.8	3.8	–
Maasin	8.0	6.5	3.5	2.9	4.0	–
Makiling	8.2	6.5	3.4	2.9	4.0	–
Minglanilla	8.0	6.6	3.3	2.7	3.9	–
Tacloban	8.3	6.6	3.5	2.6	4.0	–
Routine stock	7.6	6.2	3.2	2.5	4.4	–
Average SED	0.5	0.4	0.2	0.1	0.2	–
Seed source F prob	**	ns	ns	*	ns	–
Mean (SE)	8.3 (0.15)	6.6 (0.15)	3.4 (0.07)	2.7 (0.04)	4.0 (0.1)	–
%CV_P	27.6	26.9	35.9	24.0	28.8	–

Dbh = diameter at breast height, HT = total height of the trees, CROWN_B = height to the crown break, BRANCH_S = branch thickness, STEM_S = stem form, DEN = wood basic density, SED = average standard errors of difference, prob = probability, SE = standard error, %CV_P = coefficient of phenotypic variation; * and ** = significant at $p < 0.05$ and 0.01 respectively, ns = not significant

Table 3 Genetic parameters, potential gain and type B genetic correlation (r_{Bf}) of growth and traits of mahogany (*Swietenia macrophylla*) in trials at northern Mindanao, Philippines

Trial/seed Source	Dbh (cm)	HT (m)	CROWN_B (m)	BRANCH_S (1–6)	STEM_S (1–6)	DEN (kg m^{-3})
Butuan						
$\hat{h}^2$ (SE)	0.29 (0.09)	0.37 (0.10)	0.09 (0.06)	0.01 (0.04)	0.15 (0.07)	0.30 (0.10)
$\%CV_A$	6.5	6.5	6.1	1.3	7.0	3.0
Potential gain %	2.6	3.4	0.8	0.0	1.5	1.2
Cagayan De Oro						
$\hat{h}^2$ (SE)	0.29 (0.10)	0.43 (0.12)	0.34 (0.11)	0.07 (0.08)	0.19 (0.09)	–
$\%CV_A$	10.6	13.8	12.0	4.1	6.0	–
Potential gain %	4.3	8.3	5.7	0.4	1.6	–
Across sites						
$\hat{h}^2$ (SE)	0.11 (0.07)	0.26 (0.10)	0.00 (0.06)	0.03 (0.04)	0.03 (0.06)	–
$\%CV_A$	4.8	6.7	0.0	2.4	2.6	–
Potential gain %	0.7	2.4	0.0	0.1	0.1	–
r_{Bf} (SE)	0.24 (0.17)	0.34 (0.13)	0.00 (0.15)	0.21 (0.27)	0.07 (0.13)	–

Dbh = diameter at breast height, HT = total height of the trees, CROWN_B = height to the crown break, BRANCH_S = branch thickness, STEM_S = stem form, DEN = wood basic density, $\hat{h}^2$ = narrow-sense heritability, $\%CV_A$ = coefficient of additive variation, SE = standard error, r_{Bf} = type B genetic correlation

Butuan and Cagayan de Oro were 6.5 and 10.6% respectively. Across sites, CV_A was lower with a value of 4.8%. The estimated heritability values of dbh at Butuan and Cagayan de Oro were moderate at 0.29 for both sites. Across sites, estimated heritability was also at low 0.11. The estimated site-by-family interaction variance component was 162% of the family component indicating a large amount of genotype × environment interaction for dbh.

For height, the estimated site-by-family interaction variance component was 77% of the family component. CV_A for height of mahogany at Butuan was 6.5%, Cagayan de Oro was 13.8% and across sites was 6.7%. The estimated heritability of height were also moderate at Butuan, Cagayan de Oro and across sites with values of 0.37, 0.43 and 0.26 respectively. Height to crown break was less heritable at Butuan ($\hat{h}^2$ = 0.09) compared with Cagayan de Oro ($\hat{h}^2$ = 0.34).

The estimated site-by-family interaction variance component for height to first major branch was 81% of the family component. Estimates of single-site and across-site heritability for this trait were close to zero. While single site estimates of stem form heritability were significant, there was significant genotype × environment resulting in an estimate close to zero across sites.

Moderate heritability of wood density was predicted at Butuan, i.e. 0.30 kg m^{-3} while CV_A was 3.0%. Generally, family-by-site interactions were significant, resulting in type-B genetic correlations ranging from 0.00 to 0.34 for the various traits (Table 3).

DISCUSSION

Growth and quality traits

Butuan and Cagayan de Oro represent different ends of the spectrum of site quality where prospective tree planters may grow mahogany in northern Mindanao. At age 50 months, trees at Butuan had more than double diameter and height compared with trees at Cagayan de Oro. If it is assumed that most of the land available for mahogany planting in the country is likely to be more akin to the less productive Cagayan de Oro site, selecting genotypes suited to such lower quality sites will be of high importance, as will careful management of site operations such as establishment cultivation and weed control to optimise growth rates.

The 50-month-old mahogany at Butuan (mean dbh and height of 12.1 cm and 9.5 m respectively) was slightly larger than 5-year-old mahogany in small farms in South Kalimantan, Indonesia (dbh = 2.8–13.2 cm and height = 2.9–8.7 m) (Krisnawati et al. 2011). Mean diameter (4.5 cm) and height (3.8 m) of 4-year-old mahogany at Cagayan de Oro were much smaller than at Butuan. However, growth was comparable with 4- to 5-year-old trials in the Yucatan Peninsula, Mexico (mean annual rainfall from 1000 to 1600 mm) where the trees had dbh of 4.1 cm and height of 4.5 m in Zona Maya and dbh 2.6 cm and height 2.6 m in Zoh Laguna (Wightman et al. 2008).

On maturity, height to crown break affects the quality and economic value of clear merchantable length of the stem of high value timber species such as mahogany. Inherent ability of trees, combined with good silvicultural management, to produce clear stems would be advantageous in achieving higher market value of timber. Merchantable heights (height to first major branch) of 40-year-old mahogany plantations in Puerto Rico ranged from 4 to 16 m (Wadsworth & Gonzales 2008) and up to 20 m in 59-year-old plantations (Wadsworth et al 2003). Crown break after 50 months, measured as height to first branch, was low at both trials (see Table 2), with the best individual trees only achieving up to 10 m, suggesting potential for improvement achievable through selection and breeding combined with good silvicultural care.

Although shoot-borer (*Hypsipyla robusta*) infestation in Mindanao was observed in the early 1970s (Lapis 1996) there has not been a comprehensive assessment of infestation conducted in smallholder plantations in the country. Only 2% of trees (data not presented) in both trials showed deformity (multiple shoots or 'basket whorls') that might be explained by shoot-borer damage. The mean wood basic density at age 50 months (440 kg m^{-3}) at Butuan was lower than the mahogany in Brazil, Mexico and Peru, i.e. 472 kg m^{-3}, 472 kg m^{-3} and 549 kg m^{-3} respectively (Langbour et al. 2011).

Seed source and family differentiation

The individual site and across-site analyses showed that Lianga and Bislig seed sources were among the best performers for growth traits at both trials. These seed sources might have been introduced to eastern Mindanao in the 1960s from an unspecified origin, possibly Central America, by local tree planters (Siladan 2010). There were small differences in growth traits among the Makiling, Minglanilla, Maasin and Tacloban seed sources as might be expected, given the reported history of introduction and dispersal of a restricted genetic base of material from India in 1913–1916 (Ponce 1933, Chinte 1984).

Routine stock material had lower values for growth traits compared with the rest of the seed sources at Butuan (Table 2). However, at Cagayan de Oro, the routine stock material had good mean height value, being above the mean of other seedlots. The stem-form score of the routine stock material was also above the means of the rest of seed sources especially at Butuan. Stem-form assessments at Cagayan de Oro were based on much smaller trees than those at Butuan, thus, this would need to be investigated further at a later age. Also, as comparison treatment, the routine stock should be better represented in future trials, for example, by taking unselected bulk seeds from 10 or more unselected mother trees from each sampled seed source plantation. Doing so will allow firmer conclusions on its performance.

Genetic parameters

Single-site heritability estimates for diameter and height growth at the Butuan and Cagayan de Oro trials were lower than the estimated heritability of the same traits at two Yucatan Peninsula, Mexico trials which gave heritability estimates of 0.44 for height and 0.44–0.47 for dbh (Wightman et al. 2008). Likewise, coefficient of additive variation estimates from Yucatan ranged from 17 to 19% for height and 12 to 18% for dbh which were much higher than at Butuan and Cagayan de Oro. Heritability estimates for dbh and height in Costa Rican trials were as high as 0.46 and 0.35 respectively (Navarro & Hernandez 2004). Heritability calculations in Mindanao trials were based on a conservative coefficient of relationship of ⅓, whereas other authors including Wightman et al. (2008) had used ¼. Although this will reduce estimates of additive variance, single-site heritability estimates will still be lower than those of Wightman et al.

(2008) and Navarro and Hernandez (2004). Low estimates of genetic parameters among the materials in the trials at Butuan and Cagayan de Oro may be reflective of the narrow genetic base resulting from restricted range of materials introduced to the Philippines.

Although the majority of land targeted for mahogany planting in the Philippines is similar to that of Cagayan de Oro, it would be prudent for future planting programmes to allow for expansion to more productive sites similar to Butuan. Cross-site analysis has revealed significant site-by-family interaction for growth traits, with interaction variance components markedly larger than the additive (i.e. family nested within provenance for height and dbh. Shelbourne (1972) suggests interaction variance larger than 50% of the additive component is likely to be of practical significance. In this case, accounting for interaction variance has led to significantly reduced heritability estimates (see Table 3). The type-B genetic correlations of 0.24 for dbh and 0.34 for height also provided a measure of the genotype × environment interaction as affected by family rank changes across the two trial sites. The cross-site heritability estimates together with CV_A of 5–7% for height and dbh growth are sufficient to warrant selection for growth traits. Moderate genetic gains from selection can be achieved using available genetic materials in the current seed source plantations for developing mahogany plantations in northern Mindanao. Clear differences in growth of genetic materials from Bislig and Lianga compared with materials descended from the original 1913–1916 introductions suggested the need to test other materials and infuse new diversity from the natural range of mahogany in Central and South America.

Mean height to crown break of mahogany at Butuan of 3.9 m at this early assessment was less than the lowest merchantable height reported for 40- and 59-year-old mahogany plantations in Puerto Rico, which were 4 and 6 m respectively (Wadsworth et al. 2003, Wadsworth & Gonzalez 2008). The seed sources tested at Butuan and Cagayan de Oro showed very low heritability for this trait. Stem form in mahogany progeny tests in Costa Rica also did not show significant genetic differences at 32 months but differences later emerged when the trees were 44 months (Navarro & Hernandez 2004). The scope for improvement of volume and quality of recoverable mahogany timber in the Philippines will be the subject of more widespread and longer-term trials in the country. The application of good silvicultural care, including pruning and singling (i.e. reducing leaders to a single stem), will be important determinants of plantation yield improvement.

CONCLUSIONS

Growth rates of mahogany in the two trials in Mindanao were comparable with growth rates in trials and plantations elsewhere, for example, in Indonesia and Mexico. Growing mahogany for viable commercial investment on sites having similar quality to those represented by the two trial sites in Mindanao will require a strategy that combines good silviculture and genetic improvement. Results from the two trials also indicated a need for better understanding of the suitability of this species to varying conditions brought about by site quality, planting objectives and silvicultural management techniques and practices. The study indicated that key growth traits were under genetic control and there was scope for genetic improvement.

Limited differences in variation among the tested seed sources supported earlier reports that current mahogany population in the Philippines had mainly descended from a narrow genetic base derived from a few early introductions. The superior growth of progenies from Lianga and Bislig seed sources, which were supposed to originate from a more recent introduction directly from the species natural range, suggested that these populations would be primary targets for further selections. Although modest potential gains could be achieved by eliminating the worst trees in the trials at Butuan and Cagayan de Oro, new genetic materials from plantations in other parts of the Philippines should also be included in future field tests as candidates for deployment into breeding populations. With selective logging and collection of seeds from unpedigreed plantations being widely practised in the country, care must be observed to avoid dysgenic selection that could further deplete the already narrowing genetic base of mahogany (Cornelius et al. 2005). It would be preferable to create dedicated gene conservation areas managed specifically for that purpose. Infusion of new materials directly from the species natural range in Central and South America can broaden the genetic base and sustain improvement.

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