Growth variations and heritabilities of teak CSO-derived families and provenances planted in two humid tropical sites

Article *in* Tree Genetics & Genomes · October 2013

DOI: 10.1007/s11295-013-0642-8

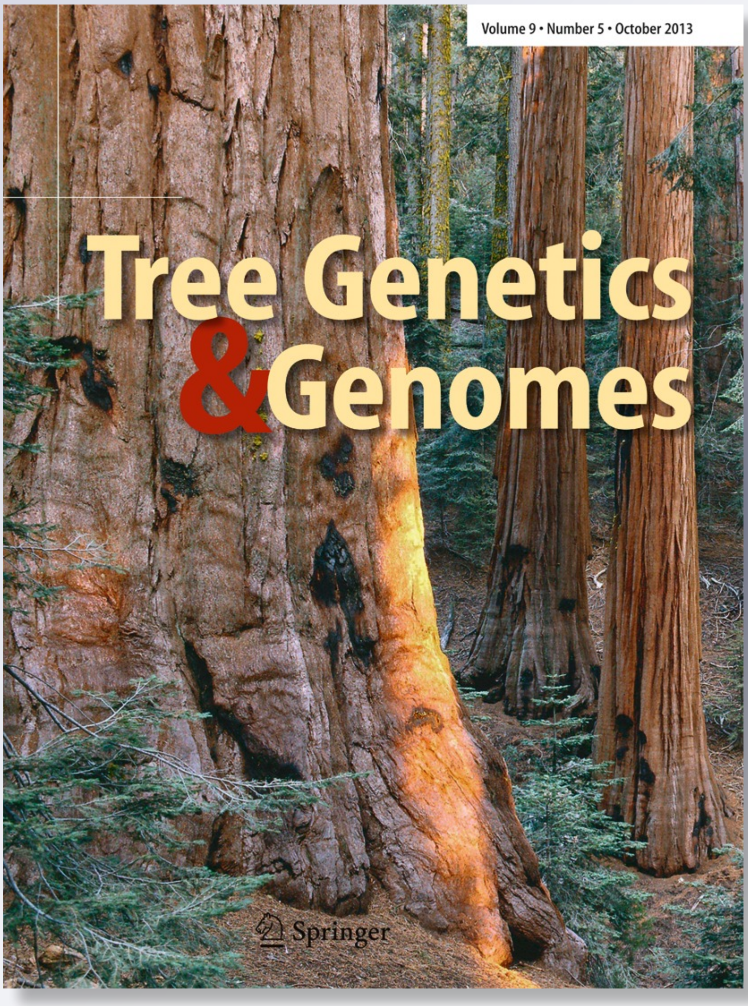
Growth variations and heritabilities of teak CSO-derived families and provenances planted in two humid tropical sites

Doreen K. S. Goh, Roberto Bacilieri, Gilles Chaix & Olivier Monteuuis

Tree Genetics & Genomes

ISSN 1614-2942
Volume 9
Number 5

Tree Genetics & Genomes (2013)
9:1329-1341
DOI 10.1007/s11295-013-0642-8



Springer

Tree Genetics & Genomes (2013) 9:1329–1341
DOI 10.1007/s11295-013-0642-8

ORIGINAL PAPER

Growth variations and heritabilities of teak CSO-derived families and provenances planted in two humid tropical sites

Doreen K. S. Goh · Roberto Bacilieri · Gilles Chaix · Olivier Monteuuis

Received: 16 November 2012 / Revised: 22 May 2013 / Accepted: 23 May 2013 / Published online: 14 June 2013

Abstract Sixteen families derived from a clonal seed orchard (CSO) and 10 "provenances" (Prov) of teak (*Tectona grandis*) were tested in two different sites to be compared with respect to their growth performances. Both sites were located in Sabah, East Malaysia, under 2,500 mm of annual rainfall and no distinct dry season. The land in Taliwas was flat but prone to waterlogging. In Luasong, the soil was more hilly, acidic, and less fertile, though deeper. Nearly 9 years after planting, the two classes of genetic entries showed significant differences for height ($P=0.0002$) and diameter at breast height (DBH) and volume ($P<0.0001$) for the two sites combined. The superiority of the CSO families compared with the Prov class was more obvious in Luasong with averages of 18.0 vs 15.2 m (+18.6 %) for height, 18.1 vs 15.1 cm (+20.2 %) for DBH, and 0.179 vs 0.107 m^3 for individual tree volume (+67.9 %), as against 17.4 vs 15.7 m (+11.2 %), 19.1 vs 16.8 cm (+13.5 %), and 0.176 vs 0.126 m^3 (+40.3 %), respectively, in Taliwas. The CSO families were also more prone to site interaction for height ($P=0.004$) and, to a lesser extent, for volume ($P=0.017$) than the "Prov" ($P=0.030$ and $P=0.057$, respectively). Narrow-sense heritabilities estimated for the 16 CSO families across the two sites were lower for DBH (0.17) and volume (0.23) than for height (0.38). Type B genetic correlations suggested also higher site × families interactions for height ($r_B=0.28$).

Keywords CSO · Genetic source · Genotype × environment interaction · Growth performance · Heritability · Provenance · Site · *Tectona grandis*

Communicated by R. Burdon

D. K. S. Goh
YSG Biotech Sdn Bhd, Yayasan Sabah Group,
Voluntary Association Complex, Mile 2 1/2, off Tuaran Road,
P.O. Box 11623, 88817 Kota Kinabalu, Sabah, Malaysia

R. Bacilieri
INRA-CIRAD-SUPAGRO, UMR AGAP 1334,
Genetic Improvement and Adaptation of Mediterranean
and Tropical Plants, 2 pl. Viala, 34060 Montpellier, France

G. Chaix
CIRAD-BIOS Department—UMR AGAP, ESALQ USP,
Piracicaba, SP, Brazil

O. Monteuuis (✉)
CIRAD-BIOS Department—UMR AGAP, TA A-108/03,
Avenue Agropolis, 34398 Montpellier Cedex 5, France
e-mail: monteuuis@cirad.fr

Introduction

Teak (*Tectona grandis* Linn. f.) is a large-growing and long-lived forest tree species belonging to the *Verbenaceae* family and occurring naturally in India, Laos, Myanmar (ex Burma), and Thailand (White 1991; Tewari 1992). It generally grows naturally under climatic conditions with a distinct dry season and mean annual rainfall of 1,200 to 1,500 mm, but can thrive in diverse tropical environments (Keiding et al. 1986; Madoffe and Maghembe 1988; Kjaer et al. 1995; Pedersen et al. 2007). Teak has gained a worldwide reputation for centuries due to the highly acclaimed properties of its wood, in particular durability, excellent dimensional stability during drying and in service, and esthetic features (Kadambi 1972; Pandey and Brown 2000; Keogh 2001). Teak wood is used as sawn timber or veneer for a wide range of end uses, from furniture making to refined ship construction (Tewari 1992; Bath 2000). This popularity has accounted for extensive establishment of plantations within and beyond its native range (Kjaer et al. 1995; Ball et al. 2000; Pandey and Brown 2000), starting first with Indonesia where it was introduced some 400–600 years ago and is now considered as subspontaneous (Kaosa-ard 2000; Siswamartana 2000). Since the early 1970s, the increasing worldwide demand for teak wood and the alarming shrinkage of available natural resources have resulted in a remarkable expansion of teak plantations, with the objective of producing large volumes of superior-quality teak timber in the shortest possible time (Ball et al. 2000;

Keogh 2000, 2001). Wet tropical conditions appear to be more conducive to reaching this goal (Chaix et al. 2011; Monteuuis et al. 2011), despite the dry season throughout the natural range. However, the extent of site influence on growth performances of teak trees from different genetic backgrounds had never been soundly and accurately analyzed to date.

We report here such a study for height, diameter at breast height ("DBH"), and estimated volume, for 16 clonal seed orchard (CSO) families and 10 "provenances" (Prov), of teak common to two trials in Sabah, East Malaysia, already assessed independently (Chaix et al. 2011; Monteuuis et al. 2011). While both sites have 2,500 mm of mean rainfall evenly distributed over the year, their soils differ markedly. Heritability estimates, still markedly scant and limited to single sites despite the importance of teak for wood production (Callister and Collins 2008), were also obtained for these three growth traits across the two sites. Due to the large areas and highly contrasted topography of these two trials, a restricted maximum likelihood (REML) mixed linear model with best linear unbiased estimators (BLUEs) for fixed effects and predictions (BLUPs) for random effects was adopted for higher accuracy of the comparative analyses. This model was also upgraded with a spatial autocorrelation covariate when justified. The advantages of using such statistical approaches have already been extensively documented (Hamann et al. 2002; Joyce et al. 2002; Zas et al. 2007; Funda et al. 2007).

Materials and methods

Plant material

The initial experimental plant material derived from a total of 57 various sources of teak seeds originated from natural and planted stands and was allocated for planting in the two sites of Luasong (Monteuuis et al. 2011) and Taliwas (Chaix et al. 2011). It encompassed open-pollinated families from the CSO of La Sangoué, Ivory Coast, established as grafts from phenotypically superior trees selected in a provenance/seed source trial (Dupuy and Verhaegen 1993). This study was focused on 16 CSO families and 10 Prov common to Luasong and Taliwas, which corresponded to a total of 26 genetic entries. Particulars of these entries are given in Table 1. The 10 Prov actually consisted of nine natural provenances and one ex situ seed source, as defined by Zobel and Talbert (1984). The seedlings from the different seed lots were produced in accordance with Monteuuis et al. (2011).

Trial characteristics

The seedlings were planted in the two sites (Table 2) in March and May 1997, respectively. The planting area in Taliwas was flat and on the bottom of a valley, close to a river, at about 0.8 m above the water table and prone to short periods of flooding, which necessitated the creation of ditches within and on the periphery of the trial. The Luasong planting site was on a slope of about 15°, but including ravines and mounds. Both sites were prepared by ripping and mounding just before planting.

In each site, the different genetic entries were established according to a randomized complete block design consisting of three contiguous blocks (replicates), trying to accommodate variation of topography for Luasong. Within each block, each entry was represented by a single contiguous plot of 15 trees in three rows of five individuals, each row being separated from the other by a row of "filler" plants which were also used to fill the ravines. The teak trees used as fillers throughout the trial were of similar age and vigor to the experimental material, but from a different genetic source. All the trees were initially planted at a spacing of 4 m between trees within rows and 2 m between rows, with alternate rows containing experimental and filler trees, respectively. All filler trees were felled after 2 years, except within ravines where one row out of two was maintained, thereafter increasing the between-line distance from 2 to 4 m and halving the overall density from 1,250 to 625 trees/ha.

Analytical procedures and statistical treatment of the data

Traits studied

The genetic analyses were performed on the following data:

1. Total tree height H (in meters) measured with a clinometer;
2. Diameter at breast height or "DBH" (in centimeters) measured with a tape at 1.30 m above soil level;
3. Bole volume V (in cubic meters), derived from the following formula:

$$V = \left(\left(\pi \times (\mathrm{DBH}/2)^2 \mathrm{x} 1.3\right) + \left(\pi \times (\mathrm{DBH}/2)^2 \times (H - 1.30)\right) /3\right) / 10,000$$

After elimination of the dead and damaged trees, 2,043 individuals were represented in 155 plots (one plot with too few living trees was discarded from the analysis), with an averages 13.2 trees per plot and 40 trees per entry. Trees were

Table 1 Particulars of the 16 CSO families (CSO) and 10 provenances (Prov) of teak tested in both the Taliwas and Luasong sites (drawn from Chaix et al. 2011; Monteuuis et al. 2011)

Entries	Source	Genetic relatedness	Longitude	Latitude	Elevation (meters above sea level)	Average annual rainfall (mm)	Average annual temperature (°C)
8367 (Prov)	Prov. India Chandrapur Maharastra[a]	na[b]	na	na	na	na	na
8668 (Prov)	Prov. Thailand Mae Huat Lampang	na	99°54′E	18°39′N	350	na	na
8823 (Prov)	Prov. India Sakrebail Karnataka	Mixture of 100 OP families[c]	75°29′E	13°48′N	600	1,000	24
8824 (Prov)	Prov. India Virnoli Karnataka	Mixture of 100 OP families	74°37′E	15°11′N	600	1,500	26
8831 (Prov)	Prov. India Karadibetta Karnataka	Mixture of 100 OP families	75°02′E	14°05′N	650	912	24
8832 (Prov)	Prov. India Gialegundi Karnataka	Mixture of 100 OP families	75°17′E	14°05′N	700	1,000	24
8833 (Prov)	Prov. India Virnoli Karnataka	Mixture of 100 OP families	74°37′E	15°11′N	600	1,500	26
8839 (Prov)	Prov. India Maukal Karnataka	1 OP family	76°00′E	12°15′N	850	1,532	22
8844 (Prov)	Prov. India Maukal Karnataka	Mixture of 100 OP families	74°37′E	15°09′N	600	1,500	26
9999 (Prov)	Ss Papoua New Guinea (PNG) Ex Brown River[d]	na	147°14′E	9°20′S	400	2,100	26
9411 (CSO)	CSO Prov. India Nilambur[e]	1 OP family	76°21′E	11°21′N	49	2,900	na
9412 (CSO)	CSO Ss Tanzania Kihuhwi	1 OP family	38°39′E	5°12′S	260	1,880	na
9418 (CSO)	CSO Prov. India Nilambur	1 OP family	na	na	na	2,900	na
9426 (CSO)	CSO Ss Tanzania Mtibwa (Morogoro)	1 OP family	37°39′E	6°00′S	460	1,160	na
9430 (CSO)	CSO Prov. Thailand Mae Huat	1 OP family	99°00′E	18°06′N	350	1,300	na
9435 (CSO)	CSO Prov. India Nellicutha	1 OP family	na	na	na	na	na
9437 (CSO)	CSO Prov. India Nilambur	1 OP family	na	na	na	2,900	na
9440 (CSO)	CSO Prov. India Nellicutha	1 OP family	na	na	na	na	na
9443 (CSO)	CSO Prov. India Vernoli rge	1 OP family	74°35′E	15°10′N	573	2,032	na
9446 (CSO)	CSO Prov. India Vernoli rge	1 OP family	74°35′E	15°10′N	573	2,032	na
9450 (CSO)	CSO Prov. India Vernoli rge	1 OP family	74°35′E	15°10′N	573	2,032	na
9452 (CSO)	CSO Prov. India Masale Valley	1 OP family	76°10′E	11°55′N	820	1,270	na
9454 (CSO)	CSO Prov. Laos Paklay	1 OP family	106°00′E	15°00′N	120	1,200	na
9457 (CSO)	CSO Prov. India Purunakote	1 OP family	84°00′E	20°00′N	133	1,200–1,500	na
9459 (CSO)	CSO Prov. India Masale Valley	1 OP family	76°10′E	11°55′N	820	1,270	na
9463 (CSO)	CSO Ss Ivory Coast Bamoro	1 OP family	5°07′W	7°48′N	330	1,100	26

[a] Denotes natural provenance, in accordance with Zobel and Talbert (1984)

[b] Denotes information not available

[c] Denotes open pollinated

[d] Seed source, in accordance with Zobel and Talbert (1984)

[e] Clonal seed orchard, La Sangoué, Ivory Coast, longitude, 5°03′W; latitude, 6°16′N; elevation, 200 m; average annual rainfall, 1,470 mm; average annual temperature, 26 °C (Dupuy and Verhaegen 1993)

measured 104 and 106 months after planting for Taliwas and Luasong, respectively.

Table 2 Taliwas and Luasong planting site particulars (drawn from Chaix et al. 2011; Monteuuis et al. 2011)

Site	Taliwas	Luasong
Trial size	3.02 ha	2.95 ha
Latitude	4°58′N	4°35′N
Longitude	118°13′E	117°40′W
Elevation (meters above sea level)	35–45	130–170
Rainfall regime	~2,500 mm MAR without distinct dry season	
Mean monthly temperatures	26–28 °C	
Soil chemical analyses[a]		
Na (me%)	0.23	0.43
K (me%)	0.05	0.22
Ca (me%)	9.8	1.4
Mg (me%)	7.1	1.4
Fe (%)	9.9	3.4
Mn (%)	0.44	271
P total (ppm)	91.5	187
P available (ppm)	2.1	2.3
Al (me%)	0.02	4.32
Org C (%)	0.86	0.61
N (%)	0.11	0.10
C/N	8.8	5.3
pH H_2O (range of variation)	6.0–6.3	4.8–5.6
CEC	16.9	12.5
Soil texture[a]		
Clay (%)	33	29
Silt (%)	19	23
Fine sand (%)	32	40
Coarse sand (%)	16	8
Soil color	Grayish	Reddish yellow

[a] Average values corresponding to 8 and 12 soil samples taken at 0 and 60 cm deep and from four and six different locations representing the whole areas planted in Taliwas and Luasong, respectively

Statistical models for estimating and partitioning environmental effects

The blocks within each of the two sites were few in number and large in size with pronounced topographic variations liable to make conventional statistical analyses inefficient, especially for Luasong. In order to minimize such experimental inefficiency, a within-site spatial autocorrelation analysis (Littell et al. 2006) was tested on the 57 entries of the two trials. For the three traits, empirical variograms (Cressie 1993) were built calculating the differences between all pairs of trees and then grouping the data according to classes of distances. The within-trial locations of every tree expressed by its row and column position transformed in meters were used as spatial coordinates. Least squares estimates of the parameters of the variogram (variance and the range) were adjusted to a nonlinear model using Statistical Analysis System (SAS) statistical package NLIN procedure (SAS Institute Inc. 2008). This process allowed the determination of the best spatial model fitting our data, taking into account the spherical, exponential, and power functions, as well as the values of the parameters. The spatial exponential structure proved to be better suited than other spatial models available in SAS for interpreting our data. Since the variograms were all significant but expressed quite different trends between the two sites according to the traits assessed, the respective efficiencies of the classical randomized complete block ("RCB") and spatial models for accommodating field heterogeneity were compared using a log-likelihood ratio test (Table 3). These two models were:

$$\text{RCB model}: Y_{ijklm} = \mu + S_i + B_{j(i)} + O_k + E_{l(k)} + SO_{ik} + SE_{il(k)} + BE_{jl(ik)} + \varepsilon_{ijklm} \quad (1)$$

where Y_{ijklm} is the observation on the *m*th individual of the *l*th entry within the *k*th origin of the *j*th block within the *i*th site;

$$\text{Spatial model}: \quad Y_{ikln} = \mu + S_i + O_k + E_{l(k)} + SO_{ik} + SE_{il(k)} + \eta_{n(i)} + \varepsilon_{ikln} \qquad (2)$$

where Y_{ikln} is the observation on the *n*th individual of the *l*th entry within the *k*th origin of the *i*th site;

with:

μ overall mean

and as fixed effects:

S_i	effect of the *i*th site
$B_{j(i)}$	effect of the *j*th block within the *i*th site
O_k	effect of the *k*th origin, namely the CSO families (k=1) vs the Prov (k=2)
$E_{l(k)}$	effect of the *l*th entry nested within the *k*th origin: CSO families (k=1) or Prov (k=2)
SO_{ik}	effect of the $S_i \times O_k$ interaction
$SE_{il(k)}$	effect of the $S_i \times E_{l(k)}$ interaction

and as random effects:

$BE_{jl(ik)}$	interaction $B_{j(i)} \times E_{l(k)}$ effect
$\eta_{n(i)}$	spatial within-site effect
ε_{ijklm}	individual tree residual (1)
ε_{ikln}	spatially independent residual (2)

The analysis was performed using the SAS REML MIXED procedure (SAS Institute Inc. 2008) using all entries represented at each site. Spatial structure main effects and

Table 3 Spatial (model 2) vs RCB (model 1) REML mixed models fits for height, DBH, and volume using a chi-square test for comparing the log-likelihood ratios with degrees of freedom equal to the difference in the number of covariance parameters between the two models (SAS Institute Inc. 2008)

Trait	Statistical model	Log-likelihood ratio[a]	Spatial covariance parameter	Estimate	SE[b]	% of the total variance[c]	P[d]
Height (m)	Spatial	15,290.3 (5)*	Variance[e] (Luasong)	7.28	0.79	52.26	<0.0001
			SP(exp)[f] (Luasong)	4.77	0.77		<0.0001
			Variance (Taliwas)	1.39	2.69	9.98	0.3022
			SP(exp) (Taliwas)	73.82	165.73		0.328
			Residual	5.26	0.21	37.76	<0.0001
	RCB	15,430.7 (2)	BE$_{jl(ik)}$[g]	1.16	0.30	12.92	<0.0001
			Residual	7.82	0.18	87.08	<0.0001
DBH (cm)	Spatial	17,699.9 (5)	Variance (Luasong)	7.267	1.41	38.55	<0.0001
			SP(exp) (Luasong)	14.020	3.52		0.0442
			Variance (Taliwas)	0.003	0.09	0.02	0.9996
			SP(exp) (Taliwas)	121.376	19.51		0.8941
			Residual	11.581	0.41	61.43	0.0001
	RCB	17,651.1 (2)*	$BE_{jl(ik)}$	2.082	0.25	16.48	<0.0001
			Residual	10.543	0.38	83.52	<0.0001
Volume (m^3)	Spatial	6,410.5 (5)	Variance (Luasong)	0.00407	0.0005	43.07	<0.0001
			SP(exp) (Luasong)	0.66200	0.0489		<0.0001
			Variance (Taliwas)	0.00001	0.0057	0.11	0.7825
			SP(exp) (Taliwas)	0.99530	0.2536		0.5182
			Residual	0.00537	0.0002	56.83	<0.0001
	RCB	6,339.6 (2)*	$BE_{jl(ik)}$	0.00167	0.0001	20.14	<0.0001
			Residual	0.00662	0.0002	79.86	<0.0001

This analysis was done on all entries at each site with the purpose of assessing for the three traits studied which of the spatial and of the RCB models absorbed best the environmental within-site variance. The advantage of the spatial model was evident for height, whereas its efficiency DBH and volume was hampered by the very low spatial variance in the flat land of Taliwas. The RCB model resulted in a better compromise for further analyzing these two traits and was therefore adopted

*$P<0.0001$, the best of the two models at this level

[a] The number of covariance (i.e., environmental effect) parameters is specified between parentheses

[b] Approximate standard error

[c] Portion of the total variance explained by the random effects

[d] Level of significance for the random effects (SAS Institute Inc. 2008)

[e] Part of the total variance absorbed by the spatial effect

[f] Practical range of the spatial process. The range is defined as the value of y at which the semivariogram reaches the sill. For distances less than the range, observations are spatially correlated. For distances greater than or equal to the range, spatial correlation is effectively zero. In models where the sill is only reached asymptotically (exponential as in our case), the practical range is defined as the distance at which the semivariogram reaches 95 % of the sill (SAS Institute Inc. 2008).

[g] Interaction between block within site and entry within origin

variances of the two sites were considered as independent. The respective fits of the RCB and spatial models were compared using a log-likelihood ratio test for each of the three traits assessed (Table 3). The superiority of the spatial autocorrelation model was established for height data only which were corrected using a kriging procedure derived from model (2) (Littell et al. 2006; Zas 2006) as a function of the measured spatial autocorrelation. For DBH and volume, the spatial model was less effective due to negative autocorrelations (the closest trees showed larger differences than more distant ones); the classical RCB was therefore adopted.

Testing of effects and estimation of genetic parameters and entry means

The influence of the different experimental factors assessed and of their possible interactions was analyzed applying model (1) with S_i, $B_{j(i)}$, O_k, and SO_{ik} as fixed effects and $E_{l(k)}$, $SE_{il(k)}$, $BE_{jl(ik)}$, and ε_{ijklm} as random effects. This model was applied to raw and spatially corrected height and to raw DBH and volume data.

BLUEs for BLUPs for random effects (Henderson 1975) were derived from the SAS REML MIXED procedure (SAS Institute Inc. 2008). BLUE/BLUP is a useful procedure for estimating jointly fixed and random effects. It is particularly suited to fit complex data with unbalanced or missing observations. In our analysis, error terms of random effects were considered separately for each site for more accurate mean and variance estimates.

Heritability and type B genetic correlations

Narrow-sense heritability ($\widehat{h}_i^2$) and type B genetic correlation estimates (r_B) were calculated across the two sites only for the 16 CSO open-pollinated families, applying the following formula (Burdon 1977; Zobel and Talbert 1984; White et al. 2007):

$$\widehat{h}_i^2 = \frac{\widehat{\sigma}_A^2}{\widehat{\sigma}_P^2} = \frac{4\widehat{\sigma}_f^2}{\left(\widehat{\sigma}_f^2 + \widehat{\sigma}_{fs}^2 + \widehat{\sigma}_{fb\ (s)}^2 + \widehat{\sigma}_e^2\right)}$$

$$r_B = \frac{\widehat{\sigma}_f^2}{\left(\widehat{\sigma}_f^2 + \widehat{\sigma}_{fs}^2\right)}$$

where:

${\sigma_A}^2$	is the additive genetic variance
${\sigma_P}^2$	is the phenotypic variance
${\sigma_f}^2$	is the family variance component
${\sigma_{fs}}^2$	is the variance component of family × site interaction
${\sigma_{fb(s)}}^2$	is the variance component of family × block within site interaction
${\sigma_e}^2$	is the residual within-plot error.

The statistical significance threshold of all the statistical tests applied was set at $P_{Ho}=0.05$.

Results

Main analysis of variance outcomes

Adopting a spatial model for height resulted in a noticeable reduction of the block effects, as well as of the residual variance for Luasong (Table 4). These analyses improved the evaluation of origin (CSO families vs Prov) and within-origin entry influences, as well as their interactions with sites (Luasong vs Taliwas) and within-site block effects (Table 4).The SAS REML MIXED analysis of variance procedure applied to the data (Table 4) indicated nearly 9 years after planting significant differences between Luasong and Taliwas for DBH (P=0.0009) and also between the two classes (origins) of entries for height (P=0.0002 for the spatial model which was adopted), DBH (P<0.0001), and volume (P<0.0001). For the two sites considered either separately or in combination, the higher values were obtained for the CSO families (Table 5). Overall, the superiority of the CSO families compared to the Prov was more obvious in Luasong than in Taliwas, with average mean estimates of 18.0 vs 15.2 m (+18.6 %) for height, 18.1 vs 15.1 cm (+20.2 %) for DBH, and 0.179 vs 0.107 m^3 for volume (+67.9 %), as against 17.4 vs 15.7 m (+11.2 %), 19.1 vs 16.8 cm (+13.5 %), and 0.176 vs 0.126 m^3 (+40.3 %), respectively. Within each origin class, height, DBH, and volume estimates varied greatly (P<0.0001) according to the entries. In addition to growing faster, the CSO families showed less within-class variation than the Prov, as reflected by the lower values of the relevant standard errors (Table 5).

Site-related genetic variations for height, DBH, and volume

Height, DBH, and volume BLUP mean estimates of the 16 CSO families and of the 10 Prov are detailed for Luasong and Taliwas in Fig. 1. Height varied more among the entries in Luasong than in Taliwas (Fig. 1a). The best performances were attained in Luasong by the CSO families 9450-India Vernoli (18.9 m), 9412-Tanzania Kihuhwi (18.6 m), and 9463-Ivory Coast Bamoro (18.6 m) and in Taliwas by the CSO families 9443-India Vernoli (17.9 m), 9430-Thailand Mae Huat (17.2 m), and 9426-Tanzania Mtibwa (17.2 m). Most of the Prov were also taller in Luasong than in Taliwas, but the taller 8839-India Maukal Karnataka (17.0 m) for Luasong and 9999-PNG (16.3 m) for Taliwas remained much shorter than the best CSO families. Several origins nevertheless did not follow this trend and grew better in height in Taliwas than in Luasong, consistently with the significant site × genetic origin interactions revealed by the analysis of variance (P=0.004 for the CSO families and P=0.030 for the Prov, Table 4). This was particularly evident for the CSO families 9443-India Vernoli, 9450-India Vernoli, and 9463-Ivory Coast Bamoro; for the natural provenance 8367-India Chandrapur Maharastra, much shorter than all the other origins in Luasong; and also for the seed source 9999-PNG. This latter outperformed all the other natural provenances and even the CSO families 9450 and 9446, both from India Vernoli, 9463-Ivory Coast Bamoro, and 9457-India Purunakote tested in Taliwas. Conversely, Prov 8831-India Karadibetta Karnataka, together with the CSO families 9426-Tanzania Mtibwa, 9430-Thailand Mae Huat, and 9435-India Nellicutha, was observed to be less site dependent for height, with an estimated difference of less than 0.1 m between Luasong and Taliwas. The standard errors

Table 4 REML mixed model analysis of variance outcomes (SAS Institute Inc. 2008) for height (spatial and RCB models compared), DBH, and volume corresponding to the 16 CSO families and 10 Prov established in Luasong and Taliwas

Trait	Fixed effects	Num DF[a]	Den DF[b]	P^c	Random effects	Variance estimate	SE[d]	P^e
Height (spatial, in m)	Site (S)	1	24	0.8973	Prov	0.561	0.947	0.277
	Block	4	1,975	0.3120	CSO families (CSO)	0.752	0.578	0.097
	Origin (O)	1	24	0.0002	Site × Prov	1.925	1.024	0.030
	S × O	1	24	0.1861	Site × CSO	1.335	0.507	0.004
					Residual Prov Luasong	3.960	0.311	<0.0001
					Residual CSO Luasong	4.096	0.227	<0.0001
					Residual Prov Taliwas	5.131	0.389	<0.0001
					Residual CSO Taliwas	3.930	0.218	<0.0001
Height (RCB, in m)	Site (S)	1	24	0.5307	Prov	0.373	0.725	0.304
	Block	4	100	<0.0001	CSO families (CSO)	0.826	0.657	0.104
	Origin (O)	1	24	<0.0001	Site × Prov	0.950	0.845	0.131
	S × O	1	24	0.3305	Site × CSO	0.933	0.621	0.067
					Block × Prov[f]	1.549	0.524	0.002
					Block × CSO[f]	1.828	0.437	<0.0001
					Residual Prov Luasong	8.921	0.724	<0.0001
					Residual CSO Luasong	9.501	0.548	<0.0001
					Residual Prov Taliwas	5.078	0.394	<0.0001
					Residual CSO Taliwas	3.986	0.226	<0.0001
DBH (RCB, in cm)	Site (S)	1	24	0.0009	Prov	1.285	1.097	0.121
	Block	4	100	<0.0001	CSO families (CSO)	0.704	0.505	0.082
	Origin (O)	1	24	<0.0001	Site × Prov	0.870	0.765	0.128
	S ×O	1	24	0.2704	Site × CSO	0.578	0.451	0.100
					Block × Prov	0.917	0.455	0.022
					Block × CSO	0.797	0.390	0.021
					Residual Prov Luasong	15.176	1.216	<0.0001
					Residual CSO Luasong	19.025	1.127	<0.0001
					Residual Prov Taliwas	9.885	0.767	<0.0001
					Residual CSO Taliwas	11.457	0.641	<0.0001
Volume (RCB, in m^3)	Site (S)	1	24	0.3283	Prov	0.00035	0.00035	0.154
	Block	4	100	<0.0001	CSO families (CSO)	0.00046	0.00034	0.086
	Origin (O)	1	24	<0.0001	Site × Prov	0.00043	0.00027	0.057
	S × O	1	24	0.1540	Site × CSO	0.00063	0.00030	0.017
					Block × Prov	0.00044	0.00019	0.009
					Block × CSO	0.00052	0.00023	0.011
					Residual Prov Luasong	0.00543	0.00043	<0.0001

Table 4 (continued)

Trait	Fixed effects	Num DF[a]	Den DF[b]	P^c	Random effects	Variance estimate	SE[d]	P^e
					Residual CSO Luasong	0.01174	0.00065	<0.0001
					Residual Prov Taliwas	0.00339	0.00026	<0.0001
					Residual CSO Taliwas	0.00528	0.00029	<0.0001

[a] Numerator degrees of freedom

[b] Denominator degrees of freedom

[c] Level of significance for the fixed effects (type III sums of squares test, SAS Institute Inc. 2008)

[d] Approximate standard error

[e] *F* test probability of a null hypothesis H_0 that there is no effect: H_0: intercept=0 (SAS Institute Inc. 2008)

[f] Not analyzed in the spatial model as the relevant variance was absorbed and the model could not converge

calculated for each entry were comparable between the two sites, ranging from 0.68 to 0.69 m for the 16 CSO families and from 0.77 to 0.78 m for the Prov, except for 8839-India Maukal Karnataka with a value of 0.68 m.

Figure 1b illustrates for DBH even more strongly than for height, the overall superiority of the CSO families compared to the Prov for the two sites, in absence of significant entry × site interaction for the CSO families and for the Prov (Table 4). The higher DBH estimates were reached by families 9450-India Vernoli (17.7 cm), 9418-India Nilambur, and 9412-Tanzania Kihuhwi (17.4 cm) in Luasong and by families 9430-Thailand Mae Huat, 9454-Laos Paklay, and 9443-India Vernoli (17.8 cm) in Taliwas. Most entries had higher DBH in Taliwas than in Luasong, except a few such as CSO families 9450-India Vernoli (17.7 vs 16.7 cm) and 9418-India Nilambur (17.4 vs 16.9 cm), as well as the Indian Prov 8833-Virnoli Karnataka (15.4 vs 14.6 cm) and 8844-Maukal Karnataka (15.4 vs 14.1 cm). In contrast, Prov 8824-India Virnoli Karnataka, CSO families 9411and 9437 both from India Nilambur, and 9446-India Vernoli did not show any noticeable DBH difference (≤0.11 cm) between Luasong and Taliwas sites. DBH variation among the various CSO families was wider in Luasong than in Taliwas. It was the opposite for the Prov, with a DBH ranging from 17.2 cm (8839-India Maukal Karnataka) to 14.1 cm (8844-India Maukal Karnataka) in Taliwas, as vs 16.0 cm (8839-India Maukal Karnataka) to 13.8 cm (8367-India Chandrapur Maharastra) in Luasong. The relevant standard errors were here again higher for the Prov (0.75 to 0.76 cm in Luasong and 0.74 to 0.75 cm in Taliwas) than for the CSO families (0.63 to 0.64 cm and 0.61 to 0.62 cm, respectively), except for Prov 8839 (0.63 cm in Luasong and 0.62 cm in Taliwas).

Consequently, in average volume, also the CSO families, with standard errors (SE) of 0.0173 to 0.0176 m^3 for Luasong and 0.0167 to 0.0173 m^3 for Taliwas, appeared to be markedly superior to the Prov (SE of 0.0144 to 0.0174 m^3 for Luasong and of 0.0141 to 0.0172 m^3 for Taliwas) in both sites (Fig. 1c). In Luasong, the higher volume estimate of 0.179 m^3 was obtained for family 9450-India Vernoli followed by family 9412-Tanzania Kihuhwi (0.168 m^3) and family 9418-India Nilambur (0.166 m^3), whereas the lowest value of 0.121 m^3 was for family 9443-India Vernoli, which corresponded to a range of variation of 0.058 m^3. In comparison, the range of variation in volume in Taliwas was only 0.032 m^3, with the best values of 0.164 m3 scored by family 9430-Thailand Mae Huath, followed by family 9443-India Vernoli (0.162 m^3), then family 9454-Laos Paklay (0.159 m^3), and the worst by family 9446-India Vernoli with 0.132 m^3. The best volume estimates obtained for the Prov were 0.129 m^3 for 8839-India Maukal Karnataka, 0.115 m^3 for Prov 8833-India Virnoli Karnataka in Luasong, and 0.143 m^3 for Prov 8839 again, followed by 0.120 m^3 for 9999-PNG in Taliwas. Contrary to

Table 5 Height, DBH, and volume mean estimates (BLUPs procedure) with relevant standard error (SE) of the 16 CSO families and the 10 Prov for Luasong and Taliwas, these two origin classes being considered as fixed effects

Trait	Site	Genetic entry	Mean	SE	P^a	CSO average superiority (%)
Height (spatial, in m)	Luasong	Prov	15.19	0.54	<0.0001	
		CSO	18.02	0.36	<0.0001	18.6
	Taliwas	Prov	15.68	0.54	<0.0001	
		CSO	17.44	0.36	<0.0001	11.2
	Both sites combined	Prov	15.44	0.42	<0.0001	
		CSO	17.73	0.29	<0.0001	14.8
DBH (in cm)	Luasong	Prov	15.08	0.57	<0.0001	
		CSO	18.14	0.35	<0.0001	20.2
	Taliwas	Prov	16.78	0.55	<0.0001	
		CSO	19.05	0.33	<0.0001	13.5
	Both sites combined	Prov	15.93	0.48	<0.0001	
		CSO	18.60	0.28	<0.0001	16.7
Volume (in m^3)	Luasong	Prov	0.1068	0.0103	<0.0001	
		CSO	0.1793	0.0091	<0.0001	67.9
	Taliwas	Prov	0.1258	0.0099	<0.0001	
		CSO	0.1765	0.0086	<0.0001	40.3
	Both sites combined	Prov	0.1163	0.0084	<0.0001	
		CSO	0.1779	0.0073	<0.0001	53.0

The predicted superiority of the CSO families compared to the Prov for each growth trait and site is also indicated

[a] Probability that entry mean estimates within each origin class are identical

the CSO families, there were wider volume differences between the 10 Prov in Taliwas than in Luasong. Although the CSO families overall grew bigger in Luasong than in Taliwas, and vice versa for the Prov (Table 5), a few entries like families 9443-India Vernoli and 9454-Laos Paklay, as well as Prov 8833-India Virnoli Karnataka and 8844-India Maukal Karnataka, did not follow this trend. Some others like families 9412-Tanzania Kihuhwi and 9450-India Vernoli rge and seed source 9999-PNG showed high differences in ranking between Luasong and Taliwas. In contrast, Prov 8367-Chandrapur Maharastra, 8824-Virnoli Karnataka, 8831-Karadibetta Karnataka, 8832-Gialegundi Karnataka from India, and 8668-Mae Huat Lampang from Thailand appeared to be less prone to site-related volume variation. These observations are consistent with the site × Prov and site × CSO family interactions found (Table 4).

Heritabilities and type B genetic correlations

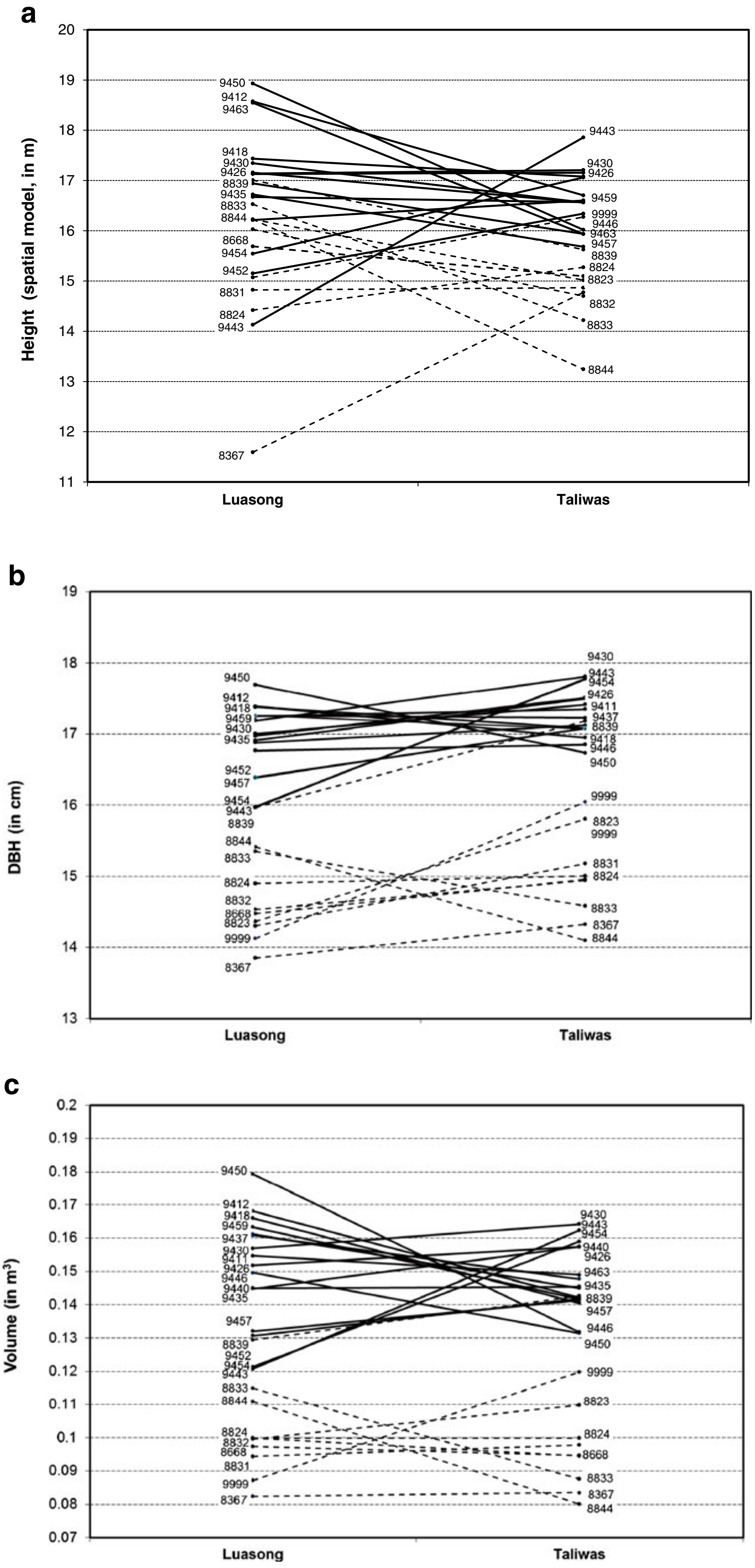
Narrow-sense heritabilities estimated for the 16 CSO families across the two sites were overall weak for the three growth traits analyzed, especially for DBH ($\widehat{h}_i^2 = 0.17$) and, to a lesser extent, for volume ($\widehat{h}_i^2 = 0.23$) (Table 6). h_i^2 values for height were higher when derived from the spatial ($\widehat{h}_i^2 = 0.17$) than from the RCB model ($\widehat{h}_i^2 = 0.30$), but the relevant standard errors also increased due mainly to higher family variance values.

The overall type B genetic correlation estimates for the same 16 CSO families and sites (Table 6) were much lower for spatially corrected height (r_B=0.28) than for raw height (r_B=0.52), DBH (r_B=0.52), and volume (r_B=0.58).

Discussion

The comparative analysis of Luasong and Taliwas site conditions on the 26 teak genetic entries considered was restricted to quantitative growth traits which are less subjective and ambiguous to evaluate than quality-related criteria such as stem straightness, bending, or fluting (Keiding et al. 1986). These latter, of great importance from a market perspective (Kadambi 1972; Tewari 1992; Bath 2000), were recently analyzed over the course of time for the same material but independently for Luasong and Taliwas (Chaix et al. 2011; Monteuuis et al. 2011). These two sites had similar climates characterized by high rainfall and no marked dry season. This could have accounted for the good survival (84 % after 106 months for Luasong and 87 % after 104 months for Taliwas) and growth rates (Chaix et al. 2011; Monteuuis et al. 2011), compared with other teak plantings (Madoffe and Maghembe 1988; Kaosa-ard 2000; Bekker et al. 2004). Luasong differed nonetheless from Taliwas in several respects. The topography in particular was markedly more variable than in Taliwas where the land was flat. The REML-BLUEs-BLUPs-mixed linear models with the

Fig. 1 Site-related variations for **a** height (spatial model), **b** DBH, and **c** volume estimates (BLUPs procedure) of the 16 CSO families (*solid lines*) and the 10 Prov (*dotted lines*) established in Luasong and Taliwas



option of a spatial autocorrelation component were more sophisticated than the classical GLM models used for comparing the behavior of same plant material in the same two sites but analyzed independently (Chaix et al. 2011; Monteuuis et al. 2011). This could explain the differences in means for height, DBH, and volume in this study from those reported in these previous works. The narrower range of variation of the estimates for the same growth traits, especially in Luasong (Monteuuis et al. 2011), is consistent with the "shrinking" effect of the mixed linear model as well as of the spatial adjustment approach applied (Zas 2006; Cappa and Cantet 2007; Funda et al. 2007). The influence of site heterogeneity in Luasong remained evident for raw height, DBH, and volume, with variance residuals (Table 4) and, to a lesser extent, standard error values higher in Luasong than in Taliwas.

In terms of chemical characteristics, the Taliwas soil with higher Ca, Mg, organic carbon, and CEC levels seemed more suitable, at least theoretically, for teak growth than Luasong which was less fertile and more acidic (Kadambi 1972; Tewari 1992; Gunaga et al. 2011). Trees in Taliwas were exposed to a high water table which could limit the rooting depth and likely account for part of the marked decline in height, DBH, and, consequently, in volume increment noticed only 25 months after planting (Chaix et al. 2011), contrary to Luasong. Teak is indeed recognized as being highly susceptible to waterlogged soils, preferring well-drained and deeper soils (Kadambi 1972; Kaosa-ard 1981; White 1991). Waterlogging thus appears to be the main factor responsible for the fact that overall, the trees planted in Taliwas, although bigger in diameter with more forks (Chaix et al. 2011; Monteuuis et al. 2011), were not taller or bigger in volume after 104 months than those in Luasong after 106 months. If such a delay of 2 months could have accounted for the difference in height between the two sites during the first years after planting when mean annual increment (MAI) averaged 4.7 m per year, this was more unlikely after 104 or 106-months due to the marked decline in MAI for height at this age (Chaix et al. 2011; Monteuuis et al. 2011). The similarities in ranking observed for height, DBH, and the derived volume in a given site were consistent with the strong phenotypic correlation values found between these traits in Taliwas (Chaix et al. 2011) and in Luasong (Monteuuis et al. 2011). More interesting were the site-induced variations in ranking or "rank–change interactions" (White et al. 2007) in growth performances noticed for some entries. The influence of genetic variation within teak on the capacity of the species to adapt to various environmental conditions mainly differing in rainfall regimes is well recognized (Keiding et al. 1986; Kjaer et al. 1995). Our results tend to suggest similar genetic effects on growth in relation to certain soil properties, especially those differentiating the two sites. This could be observed even between closely related genetic sources like the CSO families 9450 and 9443, both seed parents originating from Vernoli range, India; the Prov

Table 6 Narrow-sense heritabilities ($\widehat{h}_i^2$) ± SE calculated by the delta method (Lynch and Walsh 1998), type B genetic correlations r_B ± SE calculated by the jackknife method (Roff and Preziosi 1994), and related variance component estimates (σ_A^2, additive genetic variance; σ_P^2, phenotypic variance; σ_f^2, family variance component; σ_{fs}^2, family × site interaction variance component; $\sigma_{fb(s)}^2$, family × block within site interaction variance component; σ_e^2, residual error) for height, DBH, and volume corresponding to the 16 CSO families established on Luasong and Taliwas sites

Trait	$\widehat{\sigma}_A^2$	$\widehat{\sigma}_P^2$	$\widehat{\sigma}_f^2$	$\widehat{\sigma}_{fs}^2$	$\widehat{\sigma}_{fb(s)}^2$	$\widehat{\sigma}_e^2$	$\widehat{h}_i^2$ (±SE)	r_B (±SE)
Height (m) (spatial)	2.48	6.58	0.62 (9.6 %)	1.58 (24.4 %)	0.00 (0.0 %)	4.28 (66.0 %)	0.38 (±0.33)	0.28 (±0.04)
Height (m) (raw)	3.25	10.75	0.83 (7.8 %)	1.0 (9.4 %)	1.99 (18.7 %)	6.80 (64.0 %)	0.30 (±0.25)	0.45 (±0.05)
DBH (cm)	2.78	16.60	0.65 (3.9 %)	0.60 (3.6 %)	1.08 (6.5 %)	14.21 (85.9 %)	0.17 (±0.12)	0.52 (±0.07)
Volume (m^3)	0.0020	0.0085	0.00054 (6.5 %)	0.00040 (4.8 %)	0.00072 (8.7 %)	0.0066 (79.9 %)	0.23 (±0.17)	0.58 (±0.05)

8839 and 8844, both from Maukal Karnataka, India; and Prov 8824 and 8833 from Virnoli Karnataka, India. Such differences might be due to the fact that the seed parents, despite being geographically close, were exposed to different genetic environments and gene flows (Indira et al. 2008; Kertadikara and Prat 1995; Kjaer and Suangtho 1995).

The overall superiority for height, DBH, and volume displayed by the CSO families for the two sites compared to the Prov demonstrates the usefulness of CSO for genetic improvement of teak. This is particularly obvious for CSO family 9430 and seedlot 8668 both from the same native provenance of Mae Huat, Lampang, Thailand. This superiority of CSO families in growth and also in quality traits (Chaix et al. 2011; Monteuuis et al. 2011) may be due to various factors. Firstly, the CSO families were each derived from only one superior mother genotype (Dupuy and Verhaegen 1993), whereas more uncertainties remained for the selection and the number of seed producers from the Prov. On the other hand, and contrary to these latter, this superior grafted mother genotype was located within the CSO so as to maximize intercrossing with other unrelated genotypes for enhanced genetic gain and heterosis effects (Dupuy and Verhaegen 1993). The lower within-entry variation observed for the CSO families compared to the Prov might be due to the fact that the CSO entries consisted exclusively of single families and were thus genetically more homogeneous than the Prov entries which mostly comprised mixtures of several families. This assumption is supported by the standard errors for the single-family Prov 8839, which are similar to those of the CSO families, and lower than for the other genetically more heterogeneous mixed-family Prov entries.

For rigor and accuracy, heritability estimation across the two sites was limited to the 16 CSO families, each deriving from a single mother genotype. In line with previous studies on teak (Danarto and Hardiyanto 2001; Callister and Collins 2008; Chaix et al. 2011), the numerator coefficient of 4 for estimating the heritabilities assumed that families comprised half-sibs only. This assumption was supported by the high rate of outcrossing in teak, especially within CSO as developed above. The resulting heritability values may be overestimated if there are families containing significant proportions of full-sibs (Zobel and Talbert 1984). Heritabilities assessed across different sites reduce the risks of obtaining values upwardly biased when calculated from a single site, particularly in the case of strong genotype × site interactions (Callister and Collins 2008; White et al. 2007), as established for the current study. Estimation of across-site heritabilities needs to include the variance component of family × site interaction $\widehat{\sigma}^2_{\mathrm{fs}}$ in the denominator, while the estimated family × block within site interaction variance components (based on fewer CSO families) $\widehat{\sigma}^2_{\mathrm{f\,b\,(s)}}$ were somewhat higher for DBH and volume. All this could explain why our $\widehat{h}_i^2$ values were markedly lower and far less precise (with greater standard errors) than those obtained for the same traits independently in Taliwas (0.76 for H and 0.46 for DBH) and Luasong (0.51 for H, 0.24 for DBH, and 0.34 for V) with lower values for the more heterogeneous site of Luasong (Chaix et al. 2011; Monteuuis et al. 2011). In spite of this, our $\widehat{h}_i^2$ values were higher than those obtained for teak on a single site by Callister and Collins (2008) for height and volume (0.18 for both), but not for DBH (0.22) from a 3.5-year-old seedling trial by Danarto and Hardiyanto (2001) for DBH (0.12) from a 12-year-old progeny trial, and by Murillo and Badilla (2004) for volume (0.09) from a 4-year-old progeny test. This tends to indicate that growth in teak is, at least to some extent controlled by additive gene actions, contrary to previous assumptions (Gogate et al. 1997). However, the type B correlation analyses performed on the 16 CSO families strengthen the view that this control is liable to vary according to rank-change genotype × site interactions, more for height than for DBH and volume, in agreement with the analysis of variance findings.

Conclusion

This study confirms, under wet tropical conditions, the superiority of CSO families compared to more natural provenances for producing in a short time high yields of teak timber (Chaix et al. 2011; Monteuuis et al. 2011). It shows that height, DBH, and volume performances are, however, liable to vary markedly among different genetic sources, even closely related ones, according to soil characteristics. This offers new prospects for selecting teak material that could perform well in a broader range of soils, including acidic ones usually considered as marginal for the species (Kadambi 1972; Tewari 1992). Such investigations deserve to be extended to quality-related traits such as wood properties (Goh et al. 2007) and pursued on a wider variety of sites differing also in rainfall regimes for more extensive genotype × site interaction analyses resorting to suitable statistical approaches (Burdon 1977). In this respect, there may be a real advantage in deploying populations of selected clones (Zobel and Talbert 1984; Monteuuis and Goh 1999; White et al. 2007; Goh and Monteuuis 2012).

Acknowledgments The authors are very grateful to Professor Fikret Isik for his advice and to M. Albert Flori for his help on the use of advanced statistical procedures, as well as to Dr. Garth Nikles and anonymous reviewers for their valuable comments and suggestions on an early draft of this paper.

References

Ball JB, Pandey D, Hirai S (2000) Global overview of teak plantations. In: Site, technology and productivity of teak plantations. FORSPA publication no. 24/2000, TEAKNET publication no. 3, 11–33

Bath KM (2000) Timber quality of teak from managed tropical plantations with special reference to Indian plantations. Bois et Forêts des Tropiques 263:6–16

Bekker C, Rance W, Monteuuis O (2004) Teak in Tanzania: the Kilombero Valley Teak Co. Ltd. project. Bois et Forêts des Tropiques 279:11–21

Burdon RD (1977) Genetic correlation as a concept for studying genotype–environment interaction in forest tree breeding. Silvae Genet 26:168–175

Callister AN, Collins SL (2008) Genetic parameter estimates in a clonally replicated progeny test of teak (*Tectona grandis* Linn. f.). Tree Genetics and Genomes 4:237–245

Cappa EP, Cantet RJC (2007) Bayesian estimation of a surface to account for a spatial trend using penalized splines in an individual-tree mixed model. Canadian Journal of Forest Research 37(12):2677–2688

Chaix G, Monteuuis O, Garcia C, Alloysius D, Gidiman J, Bacilieri R, Goh DKS (2011) Genetic variation in major phenotypic traits among diverse genetic origins of teak (*Tectona grandis* L.f.) planted in Taliwas, Sabah, East Malaysia. Annals of Forest Science 68:1015–1026

Cressie N (1993) Statistics for spatial data. Wiley, New York, p 900

Danarto S, Hardiyanto EB (2001) Results of the progeny test of teak at 12 years of age at Jember, East Java. In: Potential and opportunities in marketing and trade of plantation teak: challenge for the new millennium. Proceeding of the Third Regional Seminar on Teak, Yogyakarta, Indonesia, 31 July–4 August 2000, 249–253

Dupuy B, Verhaegen D (1993) Le teck de plantation *Tectona grandis* en Côte d'Ivoire. Bois et Forêts des Tropiques 235:9–24

Funda T, Lstibůrek M, Klápště J, Permedlová I, Kobliha J (2007) Addressing spatial variability in provenance experiments exemplified in two trials with black spruce. J For Sci 53(2):47–56

Gogate MG, Gujar D, Mandal AK, Sharma R, Lal RB, Gupta BN (1997) Genetic analysis of quantitative characters in teak (*Tectona grandis*). Ann For 5(2):165–167

Goh DKS, Monteuuis O (2012) Behaviour of the "YSG BIOTECH TG1-8" teak clones under various site conditions: first observations. Bois et Forêts des Tropiques 311:5–19

Goh DKS, Chaix G, Bailleres H, Monteuuis O (2007) Mass production and quality control of teak clones for tropical plantations: The Yayasan Sabah Group and Forestry Department of Cirad Joint Project as a case study. Bois et Forêts des Tropiques 293:65–77

Gunaga RP, Kanfade AH, Vasudeva R (2011) Soil fertility status of 20 seed production areas of *Tectona grandis* Linn. f. in Karnataka. India J For Sci 57:483–490

Hamann A, Namkoong G, Koshy MP (2002) Improving precision of breeding values by removing spatially autocorrelated variation in forestry field experiments. Silvae Genet 51:210–215

Henderson CR (1975) Best linear unbiased estimation and prediction under a selection model. Biometrics 31:423–447

Indira EP, Nair PN, Prabba S, Volkaert H (2008) Genetic diversity and contempary gene flow in teak. In: Bhat KM, Balasundaran M, Bhat KV, Muralidharan EM, Thulasidas PK (eds) Proc. of the international symposium held in 2007 on processing and marketing of teak wood products of planted forests. Kerala Forest Research Institute, India and International Tropical Timber Organization, Japan, pp 205–213

Joyce DG, Ford R, Fu YB (2002) Spatial patterns of tree height variations in a black spruce farm-field progeny test and neighbors-adjusted estimations of genetic parameters. Silvae Genet 51:13–18

Kadambi K (1972) Silviculture and management of teak. Bulletin 24. Stephen F. Austin State University, Nacogdoches, p 138

Kaosa-ard A (1981) Teak its natural distribution and related factors. Nat His Bull Siam Soc 29:55–74

Kaosa-ard A (2000) Gains from provenance selection. In: Site, technology and productivity of teak plantations. FORSPA publication no. 24/2000, TEAKNET publication no. 3, 191–207

Keiding H, Wellendorf H, Lauridsen EB (1986) Evaluation of an international series of teak provenance trials. DANIDA Forest Seed Centre, Denmark, p 81

Keogh R (2000) The world of teak plantations. International Forestry Review 2(2):123–125

Keogh R (2001) New horizons for teak (*Tectona grandis* Linn. F.) plantations: the consortium support model (CSM) approach of teak 2000. In: Proc. of the Third Regional Seminar on Teak "Potentials and opportunities in marketing and trade of plantation teak: challenge for the new millennium". Yogyakarta, Indonesia, p 31–56

Kertadikara AWS, Prat D (1995) Genetic structure and mating system in teak (*Tectona grandis* L. f.) provenances. Silvae Genet 44:104–110

Kjaer ED, Suangtho V (1995) Outcrossing rate of teak (*Tectona grandis* (L.)). Silvae Genet 44:175–177

Kjaer ED, Lauridsen EB, Wellendorf H (1995) Second evaluation of an international series of teak provenance trials. DANIDA Forest Seed Centre, Denmark, p 118

Littell R, Milliken G, Stroup W, Wolfinger R, Schabenberger O (2006) SAS System for mixed models, 2nd edn. SAS Institute, Cary

Lynch M, Walsh B (1998) Genetics and analysis of quantitative traits. Sinauer Associates, Sunderland, p 980

Madoffe SS, Maghembe JA (1988) Performance of teak (*Tectona grandis* L.f.) provenances seventeen years after planting at Longuza, Tanzania. Silv Genet 37(5–6):175–178

Monteuuis O, Goh D (1999) About the use of clones in teak. Bois et Forêts des Tropiques 261:28–38

Monteuuis O, Goh DKS, Garcia C, Alloysius D, Gidiman J, Bacilieri R, Chaix G (2011) Genetic variation of growth and tree quality traits among 42 diverse genetic origins of *Tectona grandis* planted under humid tropical conditions in Sabah, East Malaysia. Tree Genetics and Genomes 7:1263–1275

Murillo O, Badilla Y (2004) Breeding teak in Costa Rica. In: Proc of the IUFRO conference on forest genetics and tree breeding in the age of genomics: progress and future. 1–5 November 2004, Charleston, South Carolina, USA, 105–110

Pandey D, Brown C (2000) Teak: a global overview. FAO/Unasylva 201(51):3–13

Pedersen AP, Hansen JK, Mtika JM, Msangi TH (2007) Growth, stem quality and age-age correlations in a teak provenance trial in Tanzania. Silvae Genet 56(3–4):142–148

Roff DA, Preziosi R (1994) The estimation of the genetic correlation: the use of the jackknife. Heredity 73:544–548

SAS Institute Inc. (2008) SAS/STAT® 9.2 User's Guide. SAS Institute, Cary

Siswamartana S (2000) Productivity of teak plantations in Indonesia. In: Site, technology and productivity of teak plantations. FORSPA publication no. 24/2000, TEAKNET publication no. 3, 137–143

Tewari DN (1992) A monograph on teak (*Tectona grandis* Linn. f.). International book distributors, Dehra Dun, p 479

White KJ (1991) Teak some aspects of research and development. FAO Regional Office for Asia and the Pacific (RAPA), Bangkok, p 53

White TL, Adams WT, Neale DB (2007) Forest genetics. CABI, Wallingford, p 682

Zas R (2006) Iterative kriging for removing spatial autocorrelation in analysis of forest genetic trials). Tree Genetics and Genomes 2(4):177–185

Zas R, Solla A, Sampedro L (2007) Variography and kriging allow screening *Pinus pinaster* resistant to *Armillaria ostoyae* in field conditions. Forestry 80(2):201–209

Zobel B, Talbert J (1984) Applied forest tree improvement. Wiley, New York, p 505